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ARTICLE

Orders of *Ascomycota*

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Abstract
Ascomycota, the most speciose phylum of fungi, is a complex entity, comprising three diverse subphyla: *Pezizomycotina*, *Saccharomycotina*, and *Taphrinomycotina*. The largest and most diverse subphylum, *Pezizomycotina*, is a rich tapestry of 16 classes and 171 orders. *Saccharomycotina*, the second largest subphylum, is a diverse collection of seven classes and 12 orders, while *Taphrinomycotina*, the smallest, is a unique assembly of six classes and six orders. Over the past decade, numerous taxonomic studies have focused on the generic, family, and class classifications of *Ascomycota*. These efforts, well-documented across various databases, are crucial for a comprehensive understanding of the classification. However, the study of taxonomy at the ordinal level, a crucial tier in the taxonomic hierarchy, has been largely overlooked. In a global collaboration with mycologists and lichenologists, this study presents the first comprehensive information on the orders within *Pezizomycotina* and *Taphrinomycotina*. The recent taxonomic classification of *Saccharomycotina* has led to the exclusion of this subphylum from the present study, as an immediate revision is not necessary. Each order is thoroughly discussed, highlighting its historical significance, current status, key identification characteristics, evolutionary relationships, ecological and economic roles, future recommendations, and updated family-level classification. Teaching diagrams for the life cycles of several orders, *viz*. *Asterinales*, *Helotiales*, *Hypocreales*, *Laboulbeniales*, *Meliolales*, *Mycosphaerellales*, *Ophiostomatales*, *Pezizales*, *Pleosporales*, *Phyllachorales*, *Rhytismatales*, *Sordariales*, *Venturiales*, *Xylariales* (*Pezizomycotina*) and *Pneumocystidales*, *Schizosaccharomycetales* and *Taphrinales* (*Taphrinomycotina*) are provided. Each diagram is

explained with a representative genus/genera of their sexual and asexual cycles of each order. Within *Pezizomycotina*, *Dothideomycetes* contains the highest number of orders, with 57, followed by *Sordariomycetes* (52 orders), *Lecanoromycetes* (21 orders), *Eurotiomycetes* and *Leotiomycetes* (12 orders each), *Laboulbeniomycetes* (3 orders), and *Arthoniomycetes* and *Xylonomycetes* (2 orders each). *Candelariomycetes*, *Coniocybomycetes*, *Geoglossomycetes*, *Lichinomycetes*, *Orbiliomycetes*, *Pezizomycetes*, *Sareomycetes*, and *Xylobotryomycetes* each contain a single order, while *Thelocarpales* and *Vezdaeales* are treated as *incertae sedis* within *Pezizomycotina*. Notably, the classes *Candelariomycetes*, *Coniocybomycetes*, *Geoglossomycetes*, *Sareomycetes*, and *Xylonomycetes*, all recently grouped under *Lichinomycetes*, are treated as separate classes based on phylogenetic analysis and current literature. Within *Lecanoromycetes*, the synonymization of *Sporastatiales* with *Rhizocarpales* and *Sarrameanales* with *Schaereriales* is not supported in the phylogenetic analysis. These orders are retained separately, and the justifications are provided under each section as well as in the discussion. Within *Leotiomycetes*, the order *Medeolariales*, which was once considered part of *Helotiales*, is treated as a distinct order based on phylogenetic evidence. The classification of *Medeolariales* may change as more data becomes available from different gene regions. *Lahmiales* (*Leotiomycetes*) is not included in the phylogenetic analysis due to a lack of molecular data. *Sareomycetes* and *Xylonomycetes* are treated as separate classes. *Spathulospora* mixed with *Lulworthiales* and the inclusion of *Spathulosporales* within *Lulworthiomycetidae* is supported and extant molecular sampling is important to resolve the phylogenetic boundaries of members of this subclass. The majority of the classes of *Pezizomycotina* and *Taphrinomycotina* formed monophyletic clades in the phylogenetic analysis conducted based on SSU, LSU, 5.8S, TEF and RPB2 sequence data. However, *Arthoniomycetes* nested with the basal lineage of *Dothideomycetes* and formed a monophyletic clade also known as the superclass, *Dothideomyceta.* In *Taphrinomycotina*, a single order is accepted within each class.

Keywords – Classification – Morphology – *Pezizomycotina* – Phylogeny – *Taphrinomycotina* – taxonomy

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Class *Arthoniomycetes* O.E. Erikss. & Winka
Arthoniales Henssen & Jahns ex D. Hawksw. & O.E. Erikss. – Contributed by Anders Tehler & Damien Ertz
Lichenostigmatales Ertz, Diederich & Lawrey – Contributed by Vinodhini Thiyagaraja

Class *Candelariomycetes* Voglmayr & Jaklitsch
Subclass *Candelariomycetidae* Timdal & M. Westb.
Candelariales Miądl. Lutzoni & Lumbsch. – Contributed by Lidia S. Yakovchenko

Class *Coniocybomycetes* M. Prieto & Wedin
Coniocybales M. Prieto & Wedin – Contributed by Maria Prieto & Ibai Olariaga

Class *Dothideomycetes* O.E. Erikss & Winka
Abrothallales Pérez-Ort. & Suija – Contributed by Vinodhini Thiyagaraja
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Arthrocatenales Piątek, Stryjak-Bogacka & Czachura – Contributed by Vinodhini Thiyagaraja & Surapong Khuna
Aulographales Crous, Spatafora, Haridas & I.V. Grig. – Contributed by Vinodhini Thiyagaraja
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Aureoconidiellales Hern.-Restr. & Crous – Contributed by Zhiyang Wang & Vinodhini Thiyagaraja

Botryosphaeriales C.L. Schoch, Crous & Shoemaker. – Contributed by Nethmini P. Samaradiwakara, Asha J. Dissanayake & Alan J. L. Phillips
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Gloniales Jayasiri & K.D. Hyde – Contributed by Mingkwan Doilom & Vinodhini Thiyagaraja
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Homortomycetales Maharachch. & Wanas. – Contributed by Saowaluck Tibpromma
Hysteriales Lindau – Contributed by Subashini Chathumini Jayasiri
Jahnulales K.L. Pang, Abdel-Wahab, El-Shar., E.B.G. Jones & Sivichai – Contributed by Mark S. Calabon
Kirschsteiniotheliales Hern.-Restr. R.F. Casta~neda, Gene & Crous – Contributed by Zin H. Htet & Yee M. Htet
Lembosinales Crous – Contributed by Junfu Li
Lineolatales Crous, Spatafora, Haridas & I.V. Grig. – Contributed by Junfu Li
Lichenotheliales K. Knudsen, Muggia & K.D. Hyde – Contributed by Vinodhini Thiyagaraja
Microthyriales G. Arnaud. – Contributed by Diana S. Marasinghe
Minutisphaerales Raja, Oberlies, Shearer & A.N. Mill. – Contributed by Elaheh Seifollahi
Monoblastiales Lücking, M.P. Nelsen & K.D. Hyde – Contributed by Vinodhini Thiyagaraja
Murramarangomycetales Crous. – Contributed by Naruemon Huanraluek
Muyocopronales Mapook, Boonmee & K.D. Hyde – Contributed by Ashani D. Madagammana
Mycosphaerellales P.F. Cannon, In: Kirk et al. – Contributed by Pedro W. Crous, Johannes Z. Groenewald, Jafar Abdollahzadeh & Uwe Braun
Myriangiales Starbäck – Contributed by Asha J. Dissanayake
Mytilinidiales E.W.A. Boehm, C.L. Schoch & Spatafora – Contributed by Tania Raymundo, Ricardo Valenzuela & Michelle Martínez Pineda
Natipusillales Raja, Shearer, A.N. Mill. & K.D. Hyde – Contributed by Mark S. Calabon & Lilcah Angelique D. Opiña
Neodactylariales H. Zheng & Z.F. Yu – Contributed by Vinodhini Thiyagaraja
Neophaeothecales Abdollahz. & Crous – Contributed by Elaheh Seifollahi
Oncopodiellales Y.R. Sun, Yong Wang bis & K.D. Hyde – Please refer Sun et al. 2025
Parmulariales D.Q. Dai & K.D. Hyde – Contributed by Dong-Qin Dai
Patellariales D. Hawksw. & O.E. Erikss. – Contributed by Vinodhini Thiyagaraja
Phaeosclerales G.G. Barreto, Souza-Motta, G.A. Silva, J.Z. Groenew., Crous & J.D.P. Bezerra – Contributed by Vinodhini Thiyagaraja
Phaeothecales Abdollahz. & Crous – Contributed by Jafar Abdollahzadeh
Phaeotrichales Ariyaw. Jian K. Liu & K.D. Hyde – Contributed by Vinodhini Thiyagaraja
Pleosporales Luttrell ex M.E. Barr – Contributed by Dhanushka N. Wanasinghe & Meike Piepenbring
Racodiales Abdollahz. & Crous – Contributed by Jafar Abdollahzadeh

Stigmatodiscales Voglmayr & Jaklitsch – Contributed by Jian-Kui Liu
Strigulales Lücking, M.P. Nelsen & K.D. Hyde – Contributed by Shu-Hua Jiang
Superstratomycetales van Nieuwenh., Miądl., Houbraken, Adan, Lutzoni & Samson – Contributed by Naruemon Huanraluek & Vinodhini Thiyagaraja
Trypetheliales Lücking, Aptroot & Sipman – Contributed by Vinodhini Thiyagaraja
Tubeufiales Boonmee & K.D. Hyde – Contributed by Yong-Zhong Lu, Jian Ma & Saranyaphat Boonmee
Valsariales Jaklitsch, K.D. Hyde & Voglmayr – Contributed by Dong-Qin Dai
Venturiales Y. Zhang ter, C.L. Schoch & K.D. Hyde – Contributed by Darbhe J. Bhat & Danushka S. Tennakoon
Zeloasperisporiales Hongsanan & K.D. Hyde – Contributed by Sinang Hongsanan & Diana S. Marasinghe

Class *Eurotiomycetes* Tehler ex O.E. Eriksson & K. Winka
Arachnomycetales Gibas, Sigler & Currah – Contributed by Vinodhini Thiyagaraja
Chaetothyriales M.E. Barr – Contributed by Yu Quan, Sybren de Hoog & Wu Dong
Coryneliales Seaver & Chardon – Contributed by Andrei Tsurykau & Vinodhini Thiyagaraja
Cryptocaliciales M. Prieto, Etayo & Olariaga – Contributed by Vinodhini Thiyagaraja
Eurotiales G.W. Martin ex Benny & Kimbr. – Contributed by Ajay Kumar Gautam, Shubhi Avasthi & Rajnish Kumar Verma
Mycocaliciales Tibell & Wedin – Contributed by Nuwan D. Kularathnage
Onygenales Cif. ex Benny & Kimbr. – Contributed by Zhi-Yuan Zhang
Phaeomoniellales K.H. Chen, A.E. Arnold, Gueidan & Lutzoni – Contributed by Ko-Hsuan Chen
Pyrenulales Fink ex D. Hawksw. & O.E. Erikss. – Contributed by André Aptroot
Sclerococcales Réblová, Unter. & W. Gams – Contributed by Ibai Olariaga
Tuberculiformales Zhi Yuan Zhang & Y.F. Han – Contributed by Vinodhini Thiyagaraja
Verrucariales Mattick ex D. Hawksw. & O.E. Erikss. – Contributed by Laura Selbmann & Claudia Coleine

Class *Geoglossomycetes* Zheng Wang, C.L. Schoch & Spatafora
Geoglossales Zheng Wang, C.L. Schoch & Spatafora – Contributed by Disha Dasgupta, Aouali Souhila, Eleni Martzoukou, Jorge Luiz Fortuna, Krishnendu Acharya & Nilanjan Chakraborty

Class *Laboulbeniomycetes* Engler
Laboulbeniales Lindau – Contributed by Michiel D. de Groot, Aimée Blondelle, Jonathan Cazabonne, Michał Gorczak & Danny Haelewaters
Herpomycetales Haelew. & Pfister – Contributed by Michiel D. de Groot, Aimée Blondelle, Jonathan Cazabonne, Michał Gorczak & Danny Haelewaters
Pyxidiophorales P.F. Cannon – Contributed by Michiel D. de Groot, Aimée Blondelle, Jonathan Cazabonne, Michał Gorczak & Danny Haelewaters

Class *Lecanoromycetes* O.E. Erikss. & Winka
Acarosporales V. Reeb, Lutzoni & Cl. Roux – Contributed by Vinodhini Thiyagaraja & R.G. Udeni Jayalal
Baeomycetales Lumbsch, Huhndorf & Lutzoni – Contributed by Vinodhini Thiyagaraja
Caliciales Bessey – Contributed by Vinodhini Thiyagaraja & Xin Yu Wang
Graphidales Bessey – Contributed by Vinodhini Thiyagaraja & R.G. Udeni Jayalal
Gyalectales Henssen ex D. Hawksw. & O.E. Erikss**.** – Contributed by Vinodhini Thiyagaraja & R.G. Udeni Jayalal
Lecanorales Nannf. – Contributed by Vinodhini Thiyagaraja & R.G. Udeni Jayalal
Lecideales Vain. – Contributed by Vinodhini Thiyagaraja & R.G. Udeni Jayalal

Leprocaulales Lendemer & B.P. Hodk. – Contributed by Vinodhini Thiyagaraja & R.G. Udeni Jayalal
Micropeltidales X.Y. Zeng, H.X. Wu & K.D. Hyde – Contributed by Hai-Xia Wu
Odontotrematales Lücking – Contributed by Vinodhini Thiyagaraja
Ostropales Nannf. – Contributed by Vinodhini Thiyagaraja
Peltigerales W. Watson – Contributed by Vinodhini Thiyagaraja & R.G. Udeni Jayalal
Pertusariales M. Choisy ex D. Hawksw. & O.E. Erikss. – Contributed by Vinodhini Thiyagaraja & R.G. Udeni Jayalal
Rhizocarpales Miądl. et al. – Contributed by Vinodhini Thiyagaraja, Worthy R. Fiona & R.G. Udeni Jayalal
Sarrameanales B.P. Hodk. & Lendemer – Contributed by Vinodhini Thiyagaraja & R.G. Udeni Jayalal
Schaereriales Lumbsch & Leavitt – Contributed by Gerhard Rambold
Sporastatiales Lumbsch & Leavitt – Contributed by Evgeny A. Davydov
Teloschistales D. Hawksw. & O.E. Erikss. – Contributed by Vinodhini Thiyagaraja, Xin Yu Wang & R.G. Udeni Jayalal
Thelenellales Lumbsch & Leavitt – Contributed by Vinodhini Thiyagaraja & R.G. Udeni Jayalal
Turquoiseomycetales Crous – Contributed by Vinodhini Thiyagaraja
Umbilicariales J.C. Wei & Q.M. Zhou, in Zhou & Wei – Contributed by Evgeny A. Davydov

Class *Leotiomycetes* O.E. Erikss. & Winka
Chaetomellales Crous & Denman – Contributed by Thiago Kossmann & Alisha C. Quandt
Helotiales Nannf. ex Korf & Lizon – Contributed by Peter Johnston
Lahmiales O. Eriksson – Contributed by Anis S. Lestari & K. W. Thilini Chethana
Lauriomycetales Hern.-Restr. R.F. Castañeda & Guarro – Contributed by Hongli Su & K. W. Thilini Chethana
Leotiales Korf & Lizoň – Contributed by Vinodhini Thiyagaraja
Marthamycetales P.R. Johnst. & Baral – Contributed by Cuijinyi Li & K. W. Thilini Chethana
Medeolariales Korf – Contributed by Hongli Su & K. W. Thilini Chethana
Micraspidales Quijada & Tanney – Contributed by Anis S. Lestari & K. W. Thilini Chethana
Phacidiales Bessey – Contributed by Vinodhini Thiyagaraja
Rhytismatales M.E. Barr ex Minter – Contributed by Cheng-Lin Hou & Meike Piepenbring
Thelebolales Haeckel – Contributed by Yanfeng Han
Umbellidiales G.G. Barreto & Gusmão – Contributed by Vinodhini Thiyagaraja

Class *Lichinomycetes* V. Reeb, Lutzoni & Cl. Roux
Lichinales Henssen & Büdel – Contributed by Matthias Schultz & Maria Prieto

Class *Orbiliomycetes* O.E. Erikss. & Baral
Orbiliales Baral, O.E.Erikss. G.Marson & E.Weber – Contributed by Wei Deng & Xingzhong Liu

Class *Pezizomycetes* O.E. Erikss. & Winka
Pezizales J. Schröt. – Contributed by Vinodhini Thiyagaraja

Class *Sareomycetes* Beimforde, A.R. Schmidt, Rikkinen & J.K. Mitch.
Sareales Beimforde, A.R. Schmidt, Rikkinen & J.K. Mitch. – Contributed by Vinodhini Thiyagaraja

Class *Sordariomycetes* O.E. Erikss. & Winka
Amphisphaeriales D. Hawksw. & O.E. Erikss. – Contributed by Rekhani H. Perera
Amplistromatales M.J. D'souza, Maharachch. & K.D. Hyde – Contributed by Vinodhini Thiyagaraja & Ratchadawan Cheewangkoon
Annulatascales M.J. D'souza, Maharachch. & K.D. Hyde – Contributed by Wei Dong

Atractosporales H. Zhang, K.D. Hyde & Maharachch. – Contributed by Ya-Ru Sun, Yong Wang & Ruvishika S. Jayawardena
Barbatosphaeriales K.D. Hyde & Hongsanan – Contributed by Vinodhini Thiyagaraja
Boliniales P.F. Cannon – Contributed by Sahar Absalan & Ruvishika S. Jayawardena
Calosphaeriales M.E. Barr – Contributed by Vinodhini Thiyagaraja & Ratchadawan Cheewangkoon
Cancellidiales K.D. Hyde & Hongsanan – Contributed by Dan-Feng Bao
Catabotryales K.D. Hyde – Contributed by Indunil C. Senanayake
Cephalothecales Hubka & Réblová – Contributed by Wenhui Tian & Sajeewa S.N. Maharachchikumbura
Ceratolentales K.D. Hyde & Hongsanan – Contributed by Vinodhini Thiyagaraja
Chaetosphaeriales Huhndorf, A.N. Mill. & F.A. Fernández – Contributed by Rekhani H. Perera
Conlariales K.D. Hyde & Hongsanan – Contributed by Vinodhini Thiyagaraja
Coniochaetales Huhndorf, A.N. Mill. & F.A. Fernández – Contributed by Vinodhini Thiyagaraja
Conioscyphales Réblová & Seifert – Contributed by Digvijayini Bundhun
Coronophorales Nannf. – Contributed by Digvijayini Bundhun
Delonicicolales R.H. Perera, Maharachch. & K.D. Hyde – Contributed by Deecksha Gomdola & Ruvishika S. Jayawardena
Diaporthales Nannf. – Contributed by Indunil C. Senanayake
Distoseptisporales Z.L. Luo, K.D. Hyde & H.Y. Su – Contributed by Zong-Long Luo & Wen-Peng Wang
Falcocladiales R.H. Perera, Maharachch. Somrith, Suetrong & K.D. Hyde – Contributed by Rekhani H. Perera
Fuscosporellales Jing Yang, Bhat & K.D. Hyde – Contributed by Feng-Ming Yu & Qi Zhao
Glomerellales Chadef. ex Réblová, W. Gams & Seifert – Contributed by Nuwan D. Kularathnage & Ruvishika S. Jayawardena
Hypocreales Lindau – Contributed by Peng Xingcan, Huang Shike, Wen Tingchi & Zeng Xiang-Yu
Jobellisiales M.J. D'souza & K.D. Hyde – Contributed by Deecksha Gomdola & Ruvishika S. Jayawardena
Koralionastetales Kohlm., Volkm.-Kohlm., J. Campb. & Inderb. – Contributed by Vinodhini Thiyagaraja
Lulworthiales Kohlm., Spatafora & Volkm.-Kohlm. – Contributed by E.B. Gareth Jones, Ka-Lai Pang, Sajeewa S.N. Maharachchikumbura & Dhanushka N. Wanasinghe
Magnaporthales Thongk. Vijaykr. & K.D. Hyde – Contributed by De-Ping Wei
Meliolales Gäum. ex D. Hawksw. & O.E. Erikss. – Contributed by Xiang-Yu Zeng
Microascales Luttr. ex Benny & Kimbr. – Contributed by Lakmali S. Dissanayake
Myrmecridiales Crous – Contributed by Venkateswara V. Sarma
Ophiostomatales Benny & Kimbr – Contributed by Alireza Armand & Ruvishika S. Jayawardena
Pararamichloridiales Crous – Contributed by Nattawut Boonyuen
Phomatosporales Senan. Maharachch. & K.D. Hyde – Contributed by Lijian Xu, Jian Wang & Yao Liu
Pinibarreniales J. Luo & N. Zhang – Contributed by Vinodhini Thiyagaraja
Pisorisporiales Réblová & J. Fourn. – Contributed by Tian WH & Sajeewa S.N. Maharachchikumbura
Planisphaeriales J.F. Zhang, Jian K. Liu & K.D. Hyde – Contributed by Vinodhini Thiyagaraja
Pleurotheciales Réblová & Seifert – Contributed by Carlo Chris S. Apurillo
Pseudodactylariales Crous – Contributed by Chuan-Gen Lin
Phyllachorales M.E. Barr – Contributed by Melissa Mardones
Rhamphoriales K.D. Hyde & Hongsanan – Contributed by Vinodhini Thiyagaraja
Savoryellales Boonyuen, Suetrong, Sivichai, Pang & E.B.G. Jones – Contributed by Sheng-Nan Zhang
Sordariales Chadef. ex D. Hawksw. & O.E. Erikss. – Contributed by Marin-Felix Yasmina & Miller AN

Spathulosporales Kohlm. – Contributed by Vinodhini Thiyagaraja
Sporidesmiales Crous – Contributed by Zong-Long Luo & Wen-Peng Wang
Thyridiales R. Sugita & Kaz. Tanaka – Contributed by Vinodhini Thiyagaraja
Tirisporellales Suetrong, E.B.G. Jones & K.L. Pang – Contributed by Vinodhini Thiyagaraja
Togniniales Senan. Maharachch. & K.D. Hyde – Contributed by Li Lu, Saowaluck Tibpromma & Samantha C. Karunarathna
Torpedosporales E.B.G. Jones, Abdel-Wahab & K.L. Pang – Contributed by Mohamed A. Abdel-Wahab
Tracyllalales Crous – Contributed by Nattawut Boonyuen
Vermiculariopsiellales Hern.-Rest. J. Mena, Gené & Crous – Contributed by Chuan-Gen Lin
Xenodactylariales D.F. Bao, K.D. Hyde & Z.L. Luo – Contributed by Vinodhini Thiyagaraja
Xenospadicoidales Hern.-Restr. J. Mena & Gene – Contributed by Martina Réblová & Kunhiraman C. Rajeshkumar
Xylariales Nannt – Contributed by Omid Karimi, Zoha Daroodi & K. W. Thilini Chethana

Class *Xylobotryomycetes* Voglmayr & Jaklitsch
Xylobotryales Voglmayr & Jaklitsch – Contributed by Naghmeh Afshari

Class *Xylonomycetes* Gazis & P. Chaverri
Symbiotaphrinales Baral & E. Weber – Contributed by Vinodhini Thiyagaraja
Xylonales Gazis & P. Chaverri – Contributed by Maryam Tavakol Noorabadi

Pezizomycotina* order *incertae sedis
Thelocarpales Lücking & Lumbsch – Contributed by Mubashar Raza & Waseem Abbasi
Vezdaeales Lumbsch & Lücking – Contributed by W.A. Erandi Yasanthika

Subphylum *Taphrinomycotina* O.E. Erikss. & Winka
Class *Archaeorhizomycetes* Rosling & T.Y. James
Archaeorhizomycetales Rosling & T. James – Contributed by Anujani Gunarathne

Class *Neolectomycetes* O.E. Erikss. & Winka
Neolectales Landvik, O.E. Erikss. Gargas & P. Gust. – Contributed by Nalin N. Wijayawardene & Madhara K. Wimalasena

Class *Novakomycetes* Dlauchy, Péter & Čadež
Novakomycetales Dlauchy, G. Péter & Čadež – Contributed by Vinodhini Thiyagaraja

Class *Pneumocystomycetes* O.E. Erikss. & Winka
Pneumocystidales O.E. Erikss. – Contributed by Achala J. Gajanayake & Ruvishika S. Jayawardena

Class *Schizosaccharomycetes* O.E. Erikss. & Winka
Schizosaccharomycetales O.E. Erikss. – Contributed by Achala J. Gajanayake & Ruvishika S. Jayawardena

Class *Taphrinomycetes* O.E. Erikss. & Winka
Taphrinales Gäum. & C.W. Dodge – Contributed by Gábor Péter, Neža Čadež & Marizeth Groenewald

INTRODUCTION

Carl Linnaeus applied taxonomic rules consistently to the division of all three kingdoms of nature in his Systema Naturae (1735, 1st. ed.). His taxonomic principles are used in the universal system of scientific taxonomic nomenclature. In Linnean's taxonomy, fungi were considered part of

the ‘Regnum Vegetabile’. Fungal classification began to take shape in the 18th century, with the significant publications of Persoon (1794a, b, 1801, 1822–1828), Nees von Esenbeck (1817), Fries (1821–1832, 1825, 1835, 1836–1838, 1849a, b), Link (1833) and Saccardo (1882a, b). Throughout the 19th century, several classifications were proposed, primarily based on morphological features. With the advent of molecular approaches, the classification has undergone numerous changes. Presently, 19 Phyla, 83 classes, 1,220 families, 10,685 genera and ca 140,000 species are accepted under Kingdom Fungi (Hyde et al. 2024b).

The phylum *Ascomycota* is the largest and most species-rich group of fungi. It encompasses a wide range of taxa that exhibit diverse morphologies, including filamentous, unicellular and more complex cup fungi (Bennett & Turgeon 2016). They have a cosmopolitan distribution and occur in various ecologies, with multiple lifestyles (Kirk et al. 2008a, Schoch et al. 2009a, Naranjo-Ortiz & Gabaldón 2019). *Ascomycota* species are frequently studied due to their beneficial and harmful impacts on humans, plants, and ecosystems (Hyde et al. 2019, Naranjo-Ortiz & Gabaldón 2019).

The phylum name “*Ascomycota*” was initially used by Bold (1957) but without a Latin diagnosis. However, the name was validated by Cavalier-Smith (1998). Eriksson (1982) notably classified all lichen fungi at the generic level within the kingdom Fungi. Walker (1985) classified three groups within the phylum, including *Schizosaccharomyces* and *Protomyces*, budding yeasts and filamentous fungi based on the sequence data from 5S rRNA sequences of ascomycetes. The subsequent phylogenetic studies led to changes in the taxonomy of this group (Berbee & Taylor 1993, Kurtzman & Robnett 1994). Notably, Cavalier-Smith (1998) treated two subphyla under *Ascomycota*, *Hemiascomycotina* (classes *Taphrinomycetes*, *Geomycetes*, *Endomycetes*) and *Euascomycotina* (classes *Discomycetes*, *Pyrenomycetes*, *Loculomycetes*). However, with the advent of molecular data, Hibbett et al. (2007) accepted three subphyla *Pezizomycotina*, *Saccharomycotina*, and *Taphrinomycotina* which remain widely accepted to this day.

The concept of ‘One fungus - One name’ also resulted in several changes in the naming of pleomorphic genera. In later studies, numerous changes were made to the ordinal to species level classification, including in *Arthoniomycetes* (Ertz et al. 2014), *Coniocybomycetes* (Prieto et al. 2013), *Dothideomycetes* (Nelsen et al. 2011a, Hyde et al. 2013, Raja et al. 2015a, Schoch & Grube 2015, Hongsanan et al. 2020a, b, Pem et al. 2024), *Eurotiomycetes* (Gueidan et al. 2014a, Chen et al. 2015a, Geiser et al. 2015, Prieto et al. 2021), *Geoglossomycetes* (Hustad et al. 2013, Melie et al. 2023), *Laboulbeniomycetes* (Goldmann & Weir 2018, Haelewaters 2018, Haelewaters et al. 2019c, 2021a, Blackwell et al. 2020), *Lecanoromycetes* (Baloch et al. 2010, Miadlikowska et al. 2014, Resl et al. 2015, Lücking et al. 2017, Kraichak et al. 2018b, Lücking 2019), *Leotiomycetes* (Zhang & Wang 2015, Ekanayaka et al. 2019a, Johnston et al. 2019b, Karakehian et al. 2019, Prieto et al. 2019, Quandt & Haelewaters 2021, Quijada et al. 2022), *Lichinomycetes* (Kauff et al. 2018, Prieto et al. 2024), *Orbiliomycetes* (Kumar et al. 2012, Zhang et al. 2023b), *Pezizomycetes* (Pfister 2015, Ekanayaka et al. 2018, Murat et al. 2018, Pfister & Healy 2021), *Sordariomycetes* (Maharachchikumbura et al. 2015, 2016, Senanayake et al. 2015, Samarakoon et al. 2016, Hongsanan et al. 2017a, Samarakoon et al. 2022, Bao et al. 2023, Chen et al. 2023b,), *Xylonomycetes* (Gazis et al. 2016, Hashimoto et al. 2021) and *Xylobotryomycetes* (Voglmayr et al. 2019b).

The concept of an ‘order’ as a distinct rank of biological classification was first introduced by the German botanist Augustus Quirinus Rivinus (1652–1723) in his classification of plants. Generally, the suffix "-ales" is used to denote that the rank is an order or suborder of the vascular plants or fungi (McNeill et al. 2012). An order is a compilation of families, which may comprise a single family or many families. The order should form a distinct and monophyletic lineage in which families should be morphologically comparable and at least share common characteristics. Since molecular methods have become available, the additional rule has been introduced that orders should have stable statistical support in cladistics analyses, based on at least two genes (Liu et al. 2016b, 2017b). Key orders in the ascomycetous series included the *Myriangiales*, *Dothideales*, and *Pseudosphaeriales* (Luttrell 1955).

In the past decade, several studies have focused on familial (Hyde et al. 2013, Jones et al. 2015, Jaklitsch et al. 2016b, Maharachchikumbura et al. 2016, Hongsanan et al. 2020a, b) and generic

concepts of *Ascomycota* (Wijayawardene et al. 2017a, Li et al. 2020, Pem et al. 2024), with some studies restricted to particular groups. No comprehensive studies have been conducted on the ordinal-level classification of *Ascomycota* since the classification of Hibbett et al. (2007). However, the ordinal classification within each class and subphylum has undergone numerous changes, driven by advancements in phylogenetic analysis, which has contributed to the expansion of recognized orders over time. According to the phylogenetic framework proposed by Hibbett et al. (2007), *Pezizomycotina* included ten classes and 55 accepted orders, and four classes and four orders were accepted *Taphrinomycotina,* whereas the single order *Saccharomycetales* and the class *Saccharomycetes* were accepted under *Saccharomycotina.* In a recent study based on molecular analyses, *Saccharomycotina* underwent high-level classification, which resulted in the inclusion of twelve orders in seven classes (Groenewald et al. 2023), which remained with a single class and order over the years until recently.

This paper provides an updated classification for all orders of *Ascomycota* (subphyla *Pezizomycotina* and *Taphrinomycotina*), including their taxonomic history, major changes in classification, key morphological characteristics that are used to distinguish the order, and phylogenetic studies. Ecology, economic applications and limitations of current research are also discussed. One or more authors contributed to the entries for each order. Due to the latest taxonomic classification available for *Saccharomycotina*, immediate further revision of the orders of *Saccharomycotina* would be redundant, and *Saccharomycotina* has been excluded from the present study.

MATERIALS AND METHODS

Structure of entry: *Pezizomycotina* and *Taphrinomycotina*

We have updated the information on the accepted orders within each subphylum based on the recent outline by Hyde et al. (2024b). The introduction provides an overview of each order and historical studies are detailed in a separate section. However, information on recently established and poorly studied orders remains limited. Thus, we have included comprehensive notes under the same subtopic. Each order is discussed based on the available literature, though aspects such as evolution and chemical diversity are lacking, limiting the documentation of certain subtopics. All the accepted orders are well-detailed and the morphological characters are represented in photoplates for both sexual and/or asexual morphs based on available information. Due to the limited availability of illustrations, especially for the asexual morphs of lichenized groups, the plates primarily represent sexual characteristics. Images for each order have been included with authorization from the leading authors of each entry or used with permission from the original author of the respective image, or appropriate citations are provided where necessary. Line drawings have been used to illustrate characters that are not available in color photographs or where image accessibility is limited. The descriptions are provided to circumscribe the morphological characteristics of the order based on the latest studies. However, for orders which lack the latest studies were written based on compiling available literature. The lifecycle diagrams are provided for several orders. We have also provided the current phylogenetic status of the orders of *Pezizomycotina* and *Taphrinomycotina* based on phylogenetic analysis. This manuscript is intended to serve as a comprehensive summary of the available data. Accordingly, we have proposed potential taxonomic revisions to the orders based on their phylogenetic relationships. A detailed discussion of the phylogenetic analyses is provided at the end of the discussion section.

Phylogenetic methods

Phylogenetic analyses were conducted based on LSU, SSU, TEF, RPB2, and 5.8S sequence data for orders of *Ascomycota,* using 706 strains with *Basidiomycota* and *Chytridiomycota* are selected as outgroups. All the data were generated from Genbank and were incorporated for phylogenetic analysis, and the discussion for the phylogenetic analyses is summarized in the end section.

RESULTS

***Pezizomycotina* O.E. Erikss. & Winka, Myconet 1(1): 9 (1997)**
***Arthoniomycetes* O.E. Erikss. & Winka, Myconet 1(1): 4 (1997)**
***Arthoniales* Henssen ex D. Hawksw. & O.E. Erikss. Syst. Ascom. 5(1): 177 (1986)**

Subphylum : *Pezizomycotina*
Class : *Arthoniomycetes*
Subclass : *Arthoniomycetidae*

Introduction

Arthoniomycetes with two orders, *Arthoniales* and *Lichenostigmatales*, is one of the largest groups of predominantly lichen-forming fungi, sister to *Dothideomycetes* (Schoch et al. 2009a) in the phylum *Ascomycota* and includes ca. 133 genera and ca. 1161 species (https://www.catalogueoflife.org/data/taxon/84), but only 119 genera are accepted here for *Arthoniales*. *Arthoniales* is a very diverse order ranging from small lichenicolous taxa to large conspicuous fruticose lichen-forming taxa (Follmann 2001, Tehler & Irestedt 2007, Tehler et al. 2009a, 2009b, 2010). Arthonialean ascomata are usually apothecial with partially ascolocular development and bitunicate asci (Henssen & Jahns 1974, Eriksson & Winka 1997, Spatafora et al. 2006).

The *Arthoniales* reaches its highest diversity in subtropical coastal habitats with a Mediterranean or desert type climate (Mediterranean area, Socotra Island, southern California, Galapagos Islands, the central Chilean coast and southern Africa) (Tehler 1983, 1990, Follmann & Werner 2003, Aptroot & Sparrius 2008). In contrast to vascular plants and animals, endemism is low in most cryptogamic groups, including lichen-forming fungi, owing to their ability for long-distance dispersal. However, *Arthoniales* is amongst the few exceptions having a high percentage of endemic taxa (Tehler 1990, Aptroot & Sparrius 2008). Endemism is common in the family *Roccellaceae*, in which many monotypic genera were described with an often much reduced distribution area, and particularly in the genera *Roccella* and *Roccellina*. For example, the genus *Roccella* contains not less than 13 endemic species, more than half of the currently recognised 24 species (Tehler et al. 2004, 2009a, 2009b, 2010).

History

Henssen & Jahns (1974) established the order *Arthoniales* (but without diagnosis) and included the families *Arthoniaceae*, *Opegraphaceae*, *Lecanactidaceae*, and *Roccellaceae*. *Arthoniales* was later validated by Hawksworth & Eriksson (1986a) who attributed them to Henssen & Jahns (1974) as *Arthoniales* Henssen & Jahns ex D. Hawksw. & O.E. Erikss. The order is based on the genus *Arthonia* which was described by Acharius (1806) and the type species is *Arthonia radiata* (Pers.) Ach. (Acharius 1808b) [= *Opegrapha radiata* Pers (Persoon 1791 #316) lectotype H-ACH 38]. Contrary to Henssen & Jahns (1974), Hawksworth & Eriksson (1986) separated the *Opegraphales* into its own order. A few years later, Hafellner (1988) included the family *Chrysotrichaceae* into *Arthoniales*. The family *Arthoniaceae* (Reichenbach 1841) was emended by Eriksson (1981) to include also the genera *Cryptothecia* Stirt. and *Stirtonia* A.L. Sm.

Today *Opegraphales* have been shown to be an ingroup of the monophyletic order *Arthoniales* and are now included as the family *Opegraphaceae* together with five other families: *Roccellaceae*, *Roccellographaceae*, *Lecanographaceae*, *Arthoniaceae* and *Chrysotrichaceae* (Ertz & Tehler 2011, Frisch et al. 2014). *Arthoniales* is well-supported and divided into two main lineages, the first one corresponding to the *Chrysotrichaceae* which forms the sister group to the other, the second lineage, which includes the rest of the order. Based on thallus and ascomata morphology and anatomy, the families *Arthoniaceae*, *Celidiaceae*, *Chiodectonaceae*, *Chrysotrichaceae*, *Cryptotheciaceae*, *Dirinaceae*, *Lecanactidaceae*, *Opegraphaceae* and *Roccellaceae* were earlier distinguished in the *Arthoniales*.

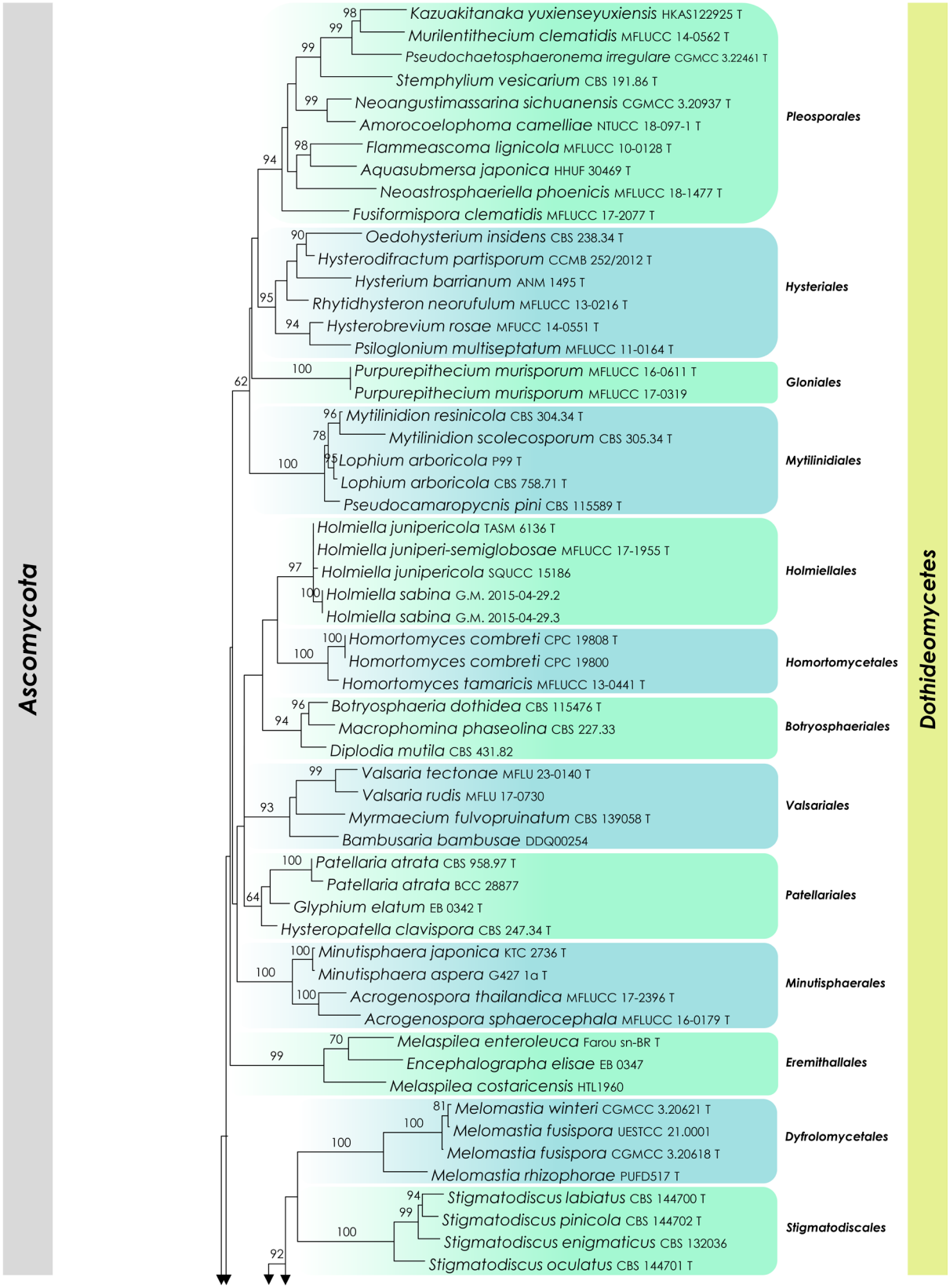


Figure 1 – Phylogram generated from maximum likelihood analysis based on combined SSU, LSU, 5.8S, TEF and RPB2 sequence data of 706 taxa, which comprised 4083 characters. The best-scoring RAxML tree with a final likelihood value of -352873.165373 is presented. The matrix had 3780 distinct alignment patterns, with 50.45% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.255578, C = 0.235929, G = 0.279159, T = 0.229334; substitution rates: AC = 1.297314, AG = 3.050069, AT = 1.285077, CG = 1.153621, CT = 6.282873, GT = 1.0; gamma distribution shape parameter α = 0.532586. Bootstrap support values for maximum likelihood

(ML) equal to or greater than 60% are labelled at each node. Ex-type strains are indicated by "T" and the orders which have doubtful phylogenetic positions are indicated in purple font. The tree is rooted to *Basidiomycota* and *Chytridiomycota.*

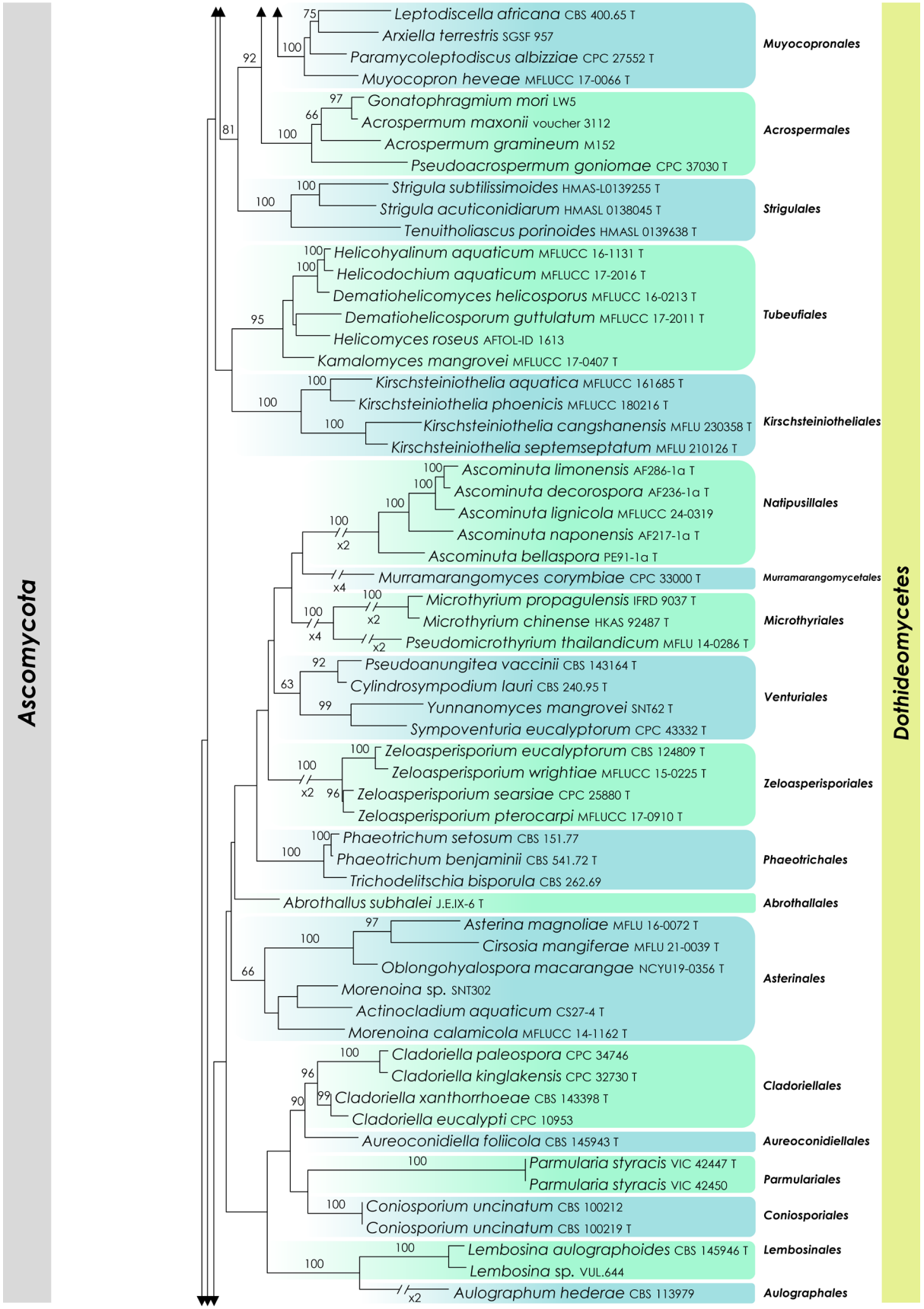


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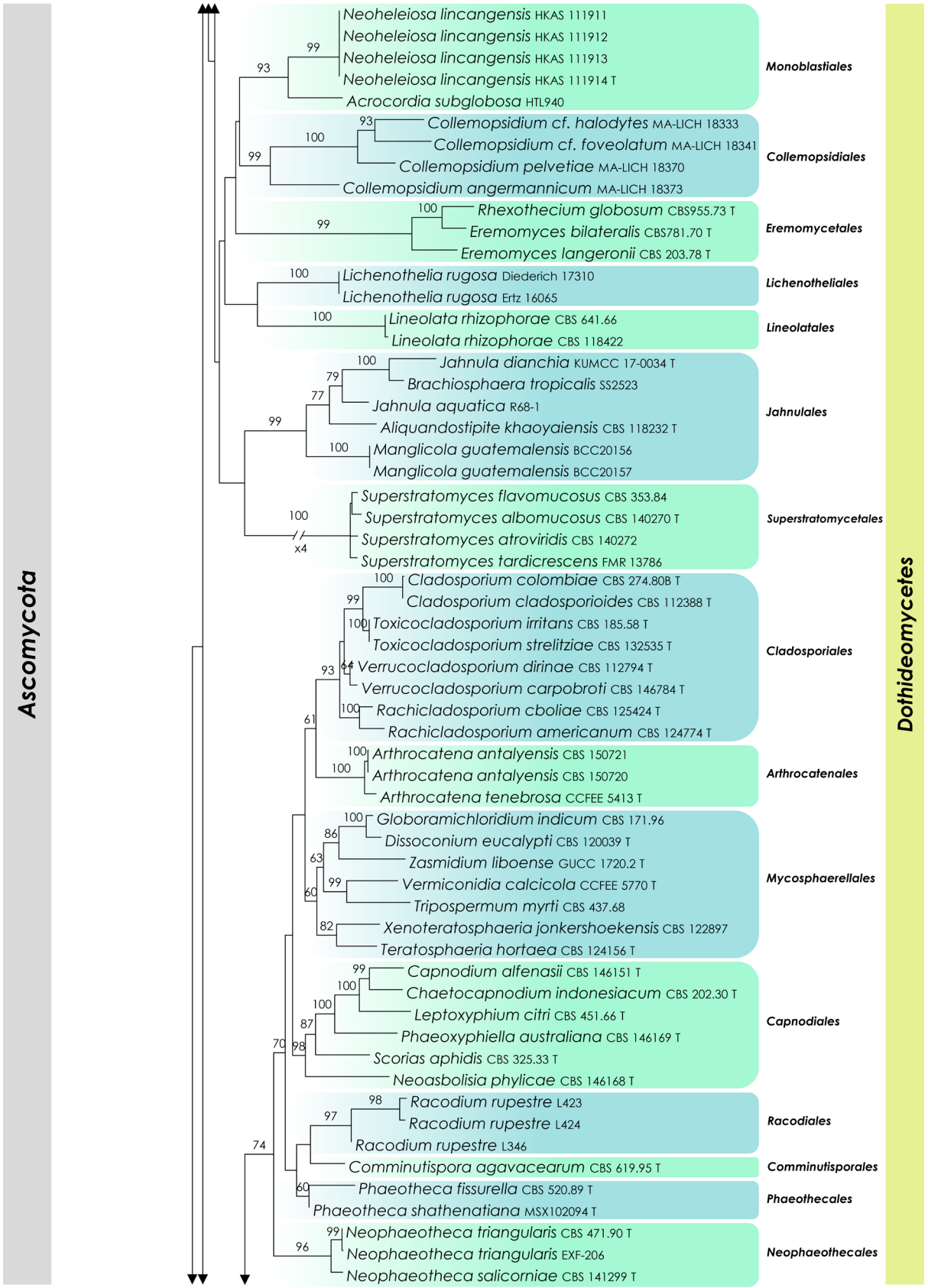


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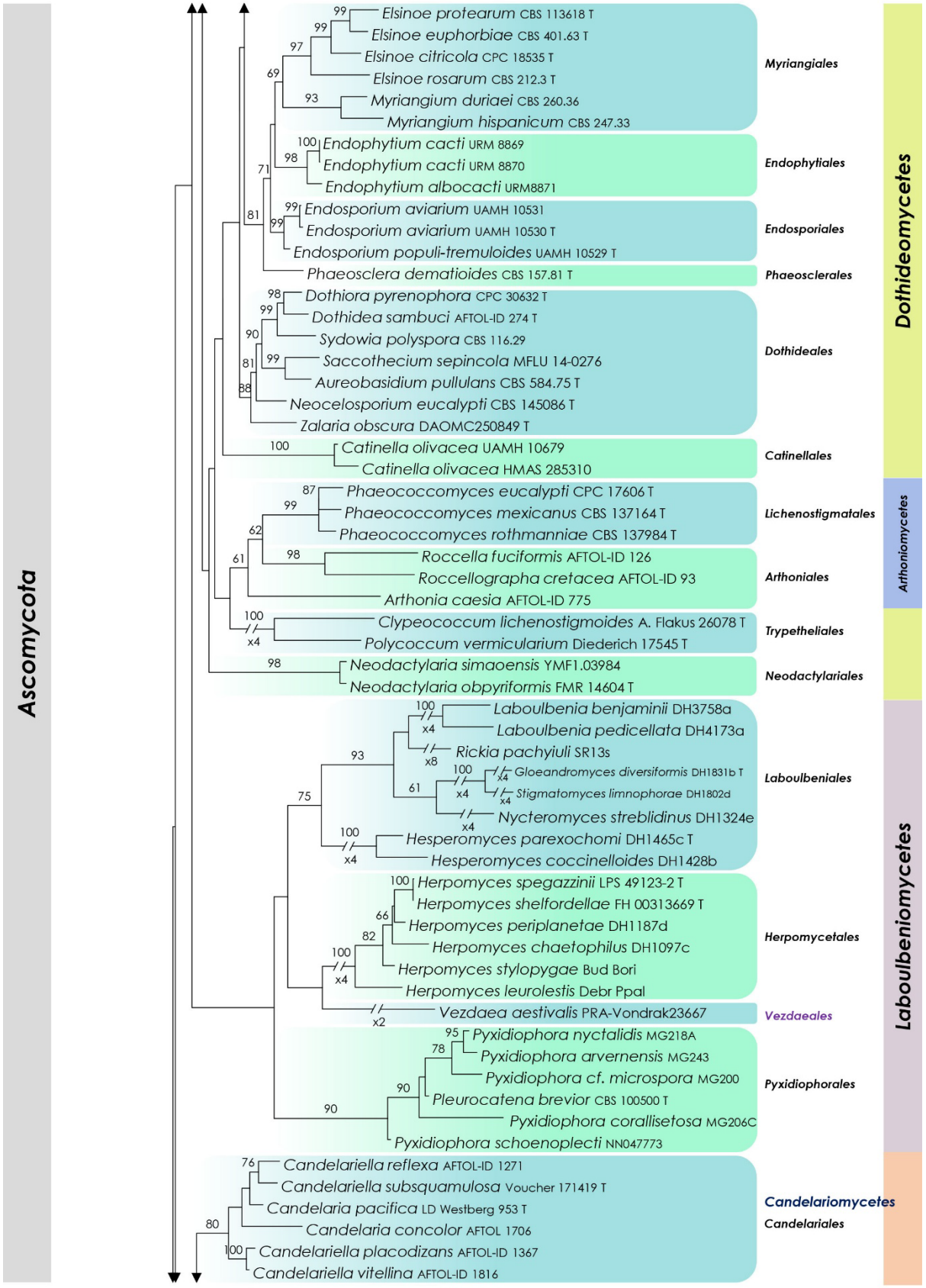


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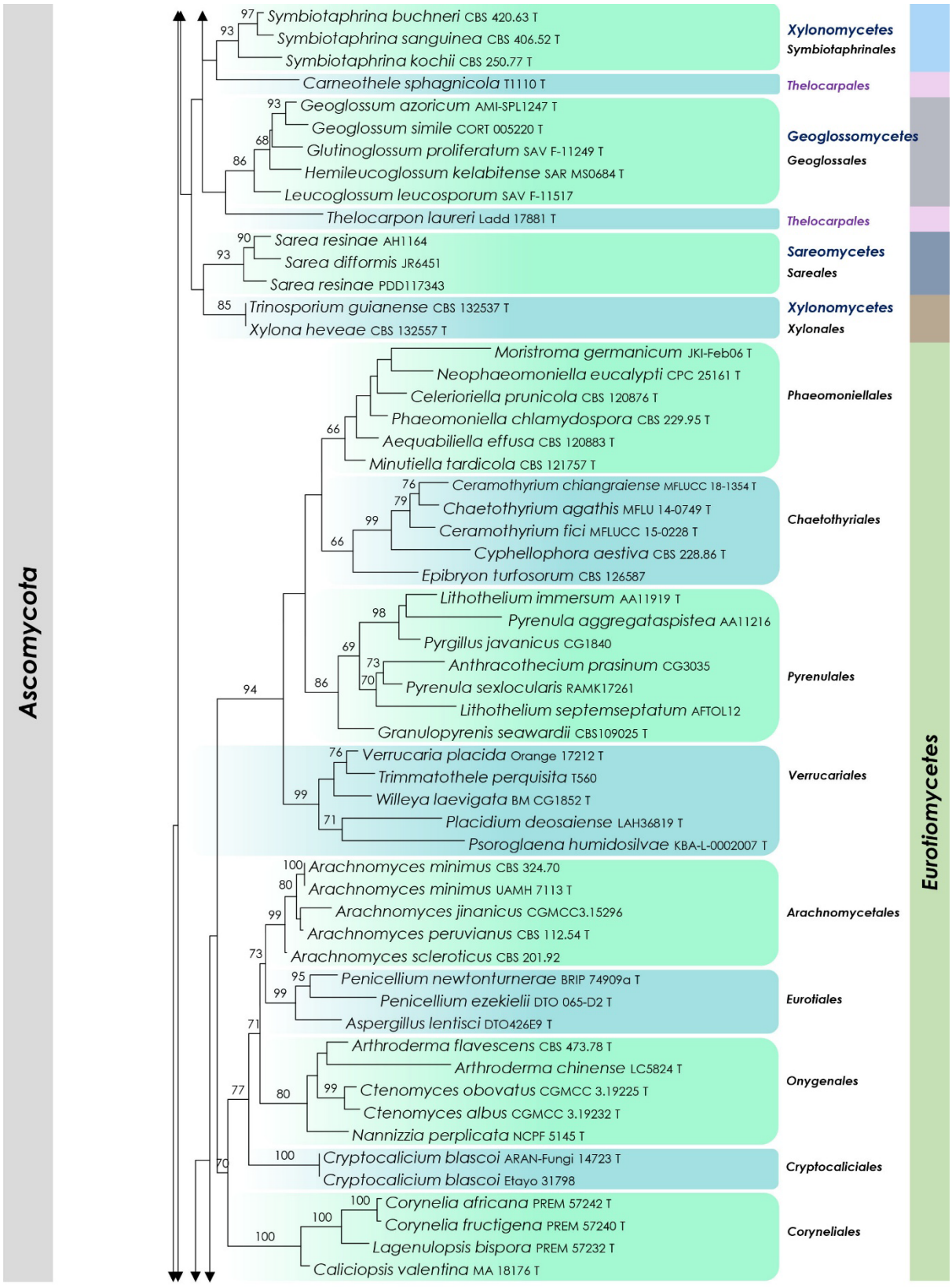


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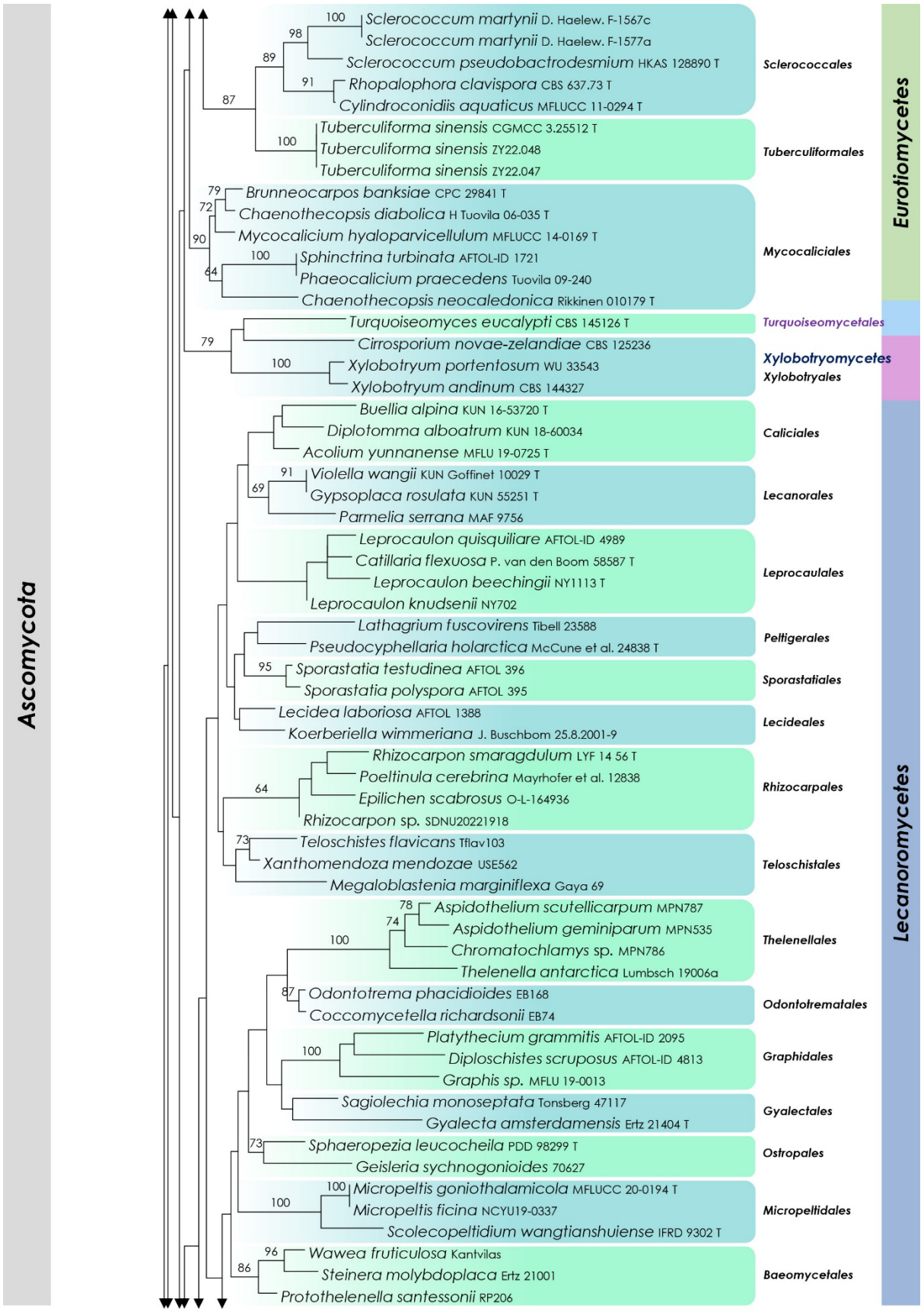


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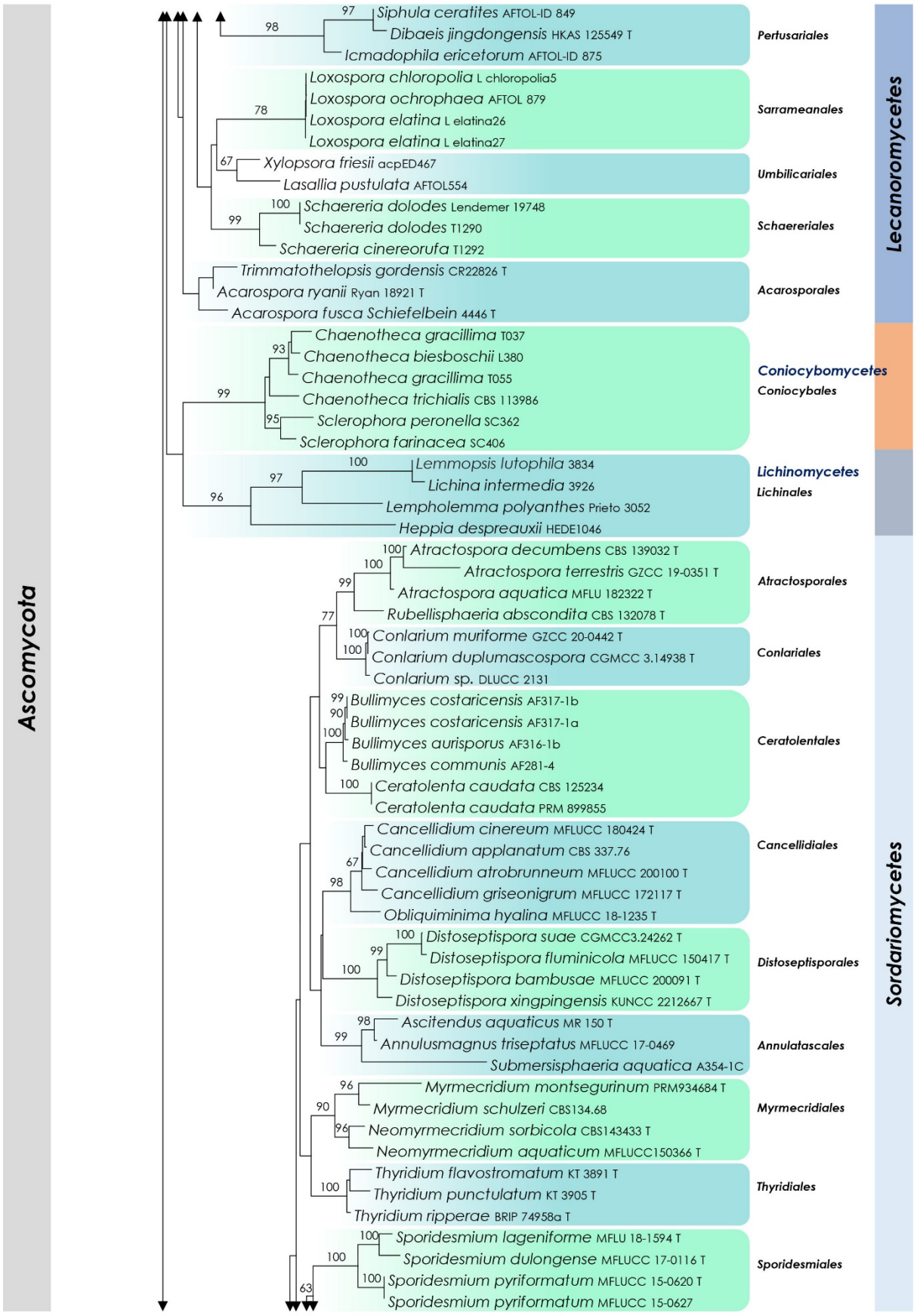


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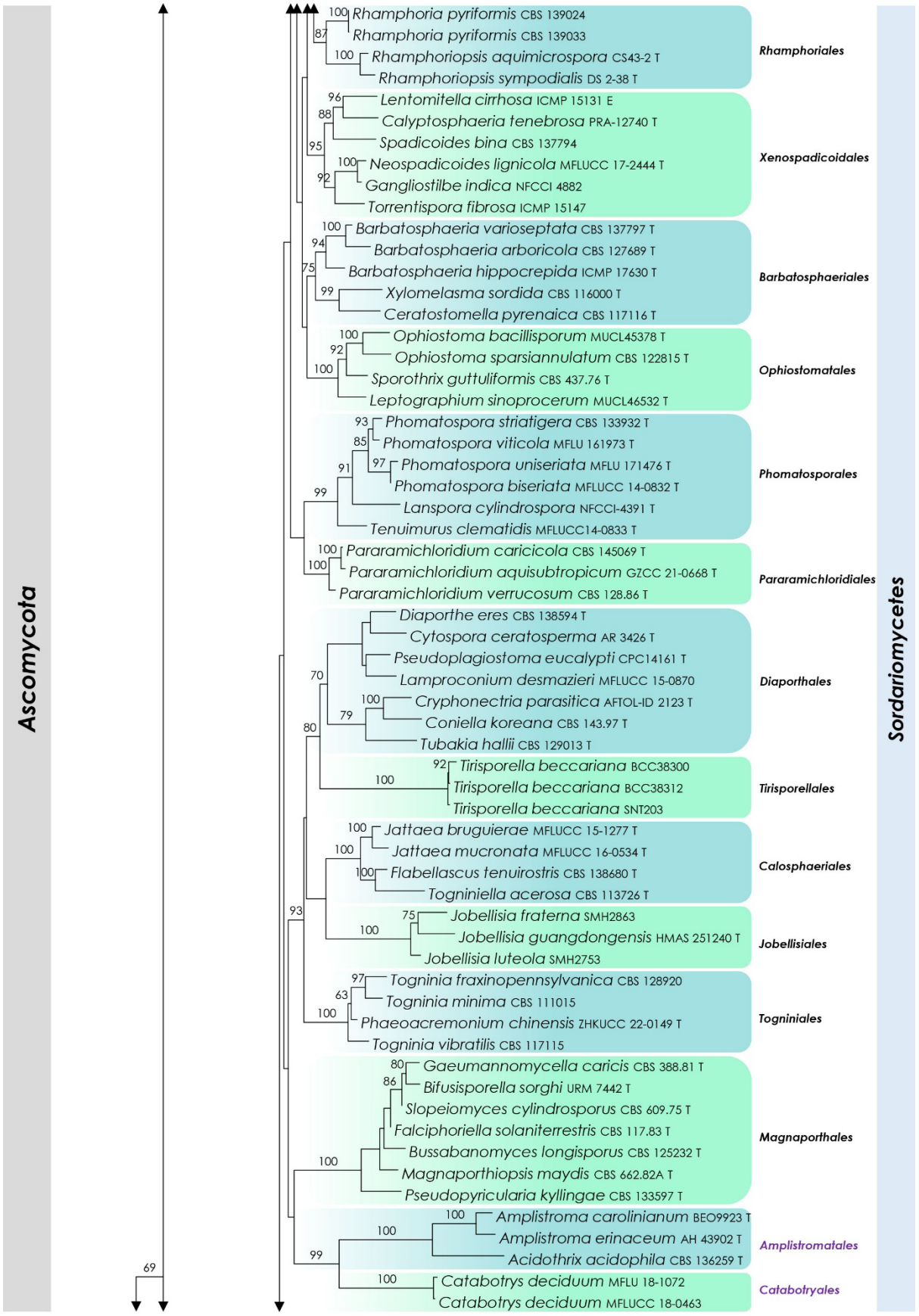


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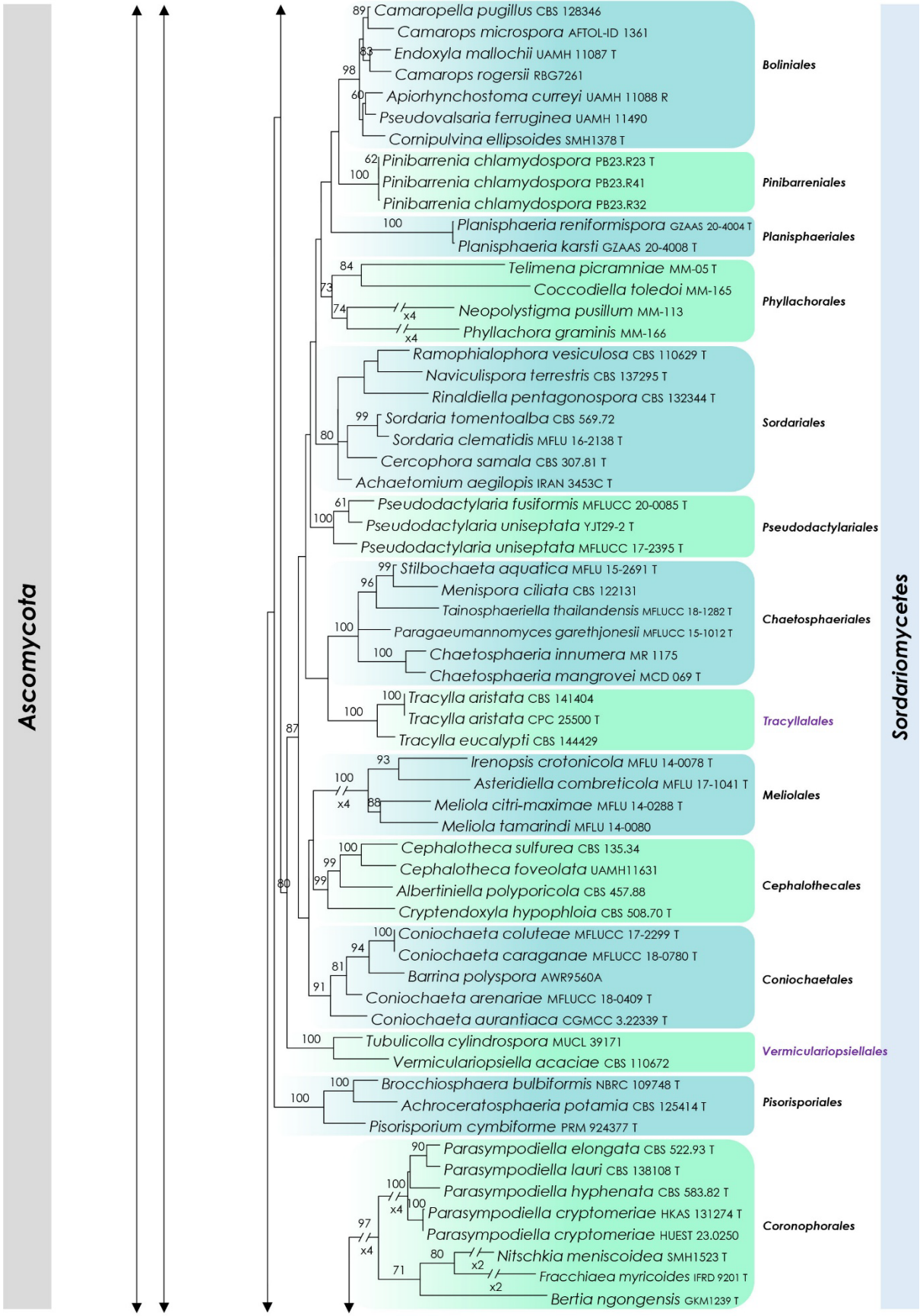


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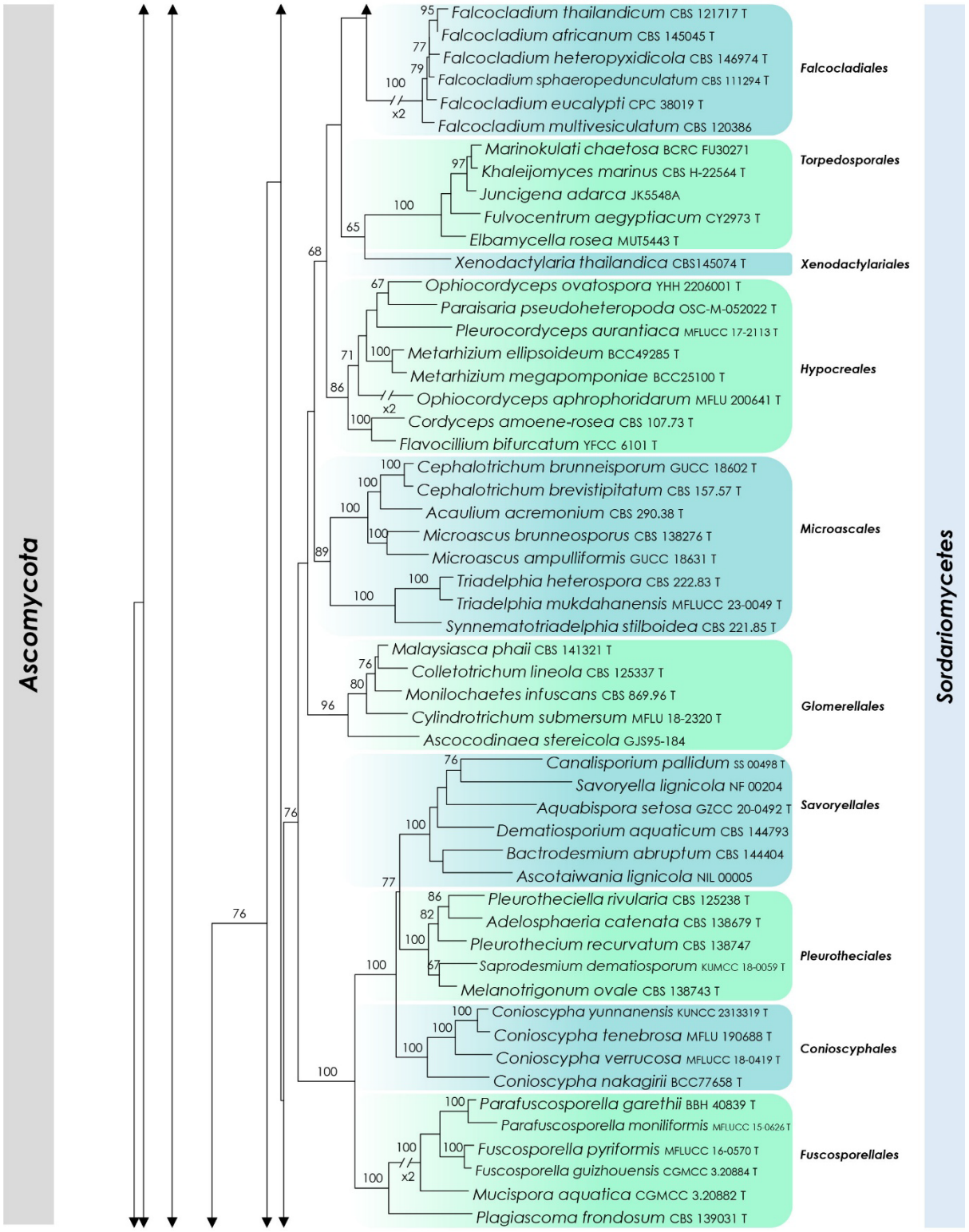


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Chiodectonaceae was established on account of the aggregation of the ascomata in the stroma (Zahlbruckner 1905 ('1907')). Watson (1929) rejected *Chiodectonaceae* as an autonomous family already in 1929 since the aggregation of the ascomata is not a character of such a high taxonomic value. The family *Celidiaceae* was considered as being part of the *Arthoniaceae* because the distinction with the *Arthoniaceae* was based on the biology of its species, i.e. non-lichenized versus lichenized (Nannfeldt 1932).

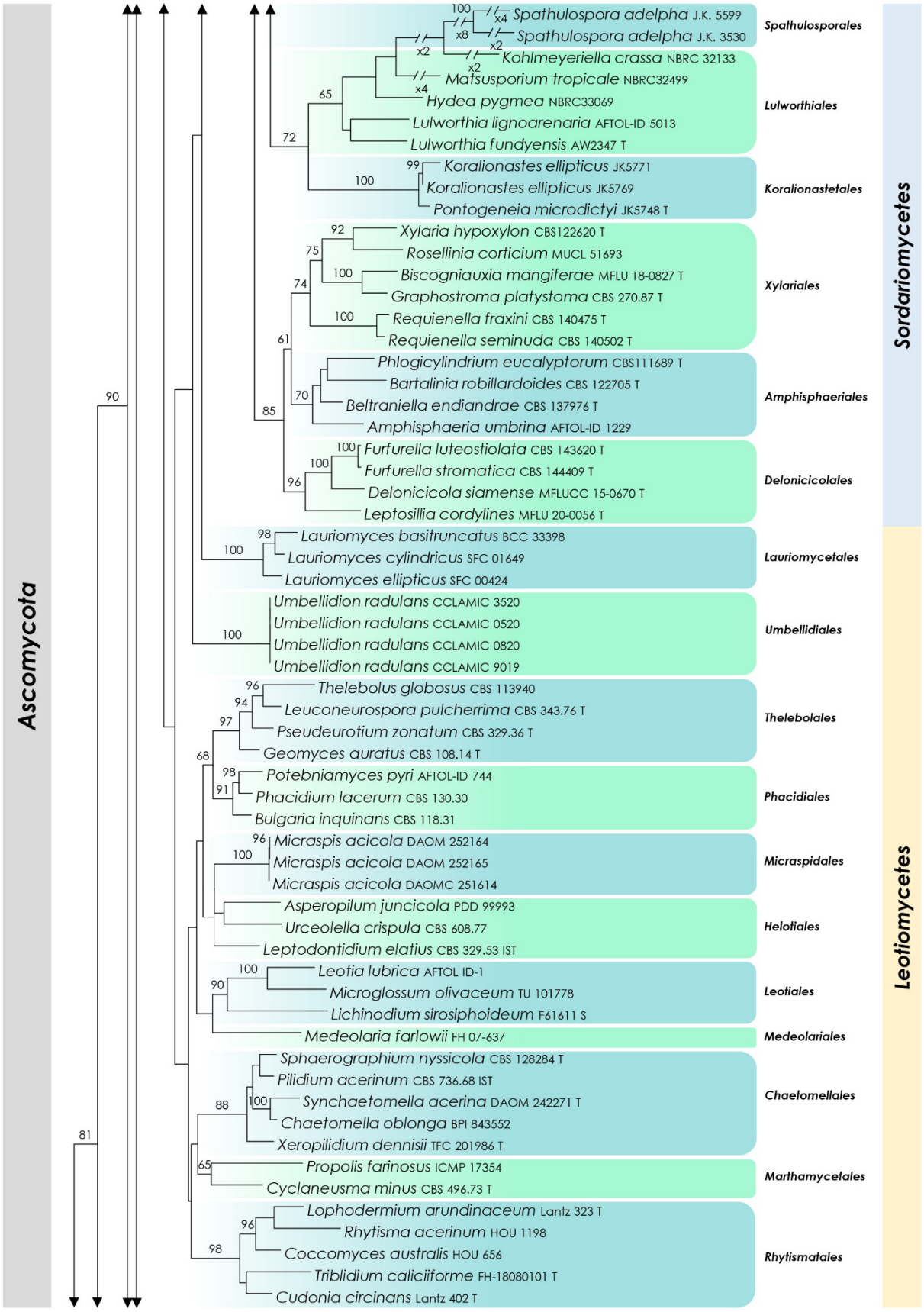


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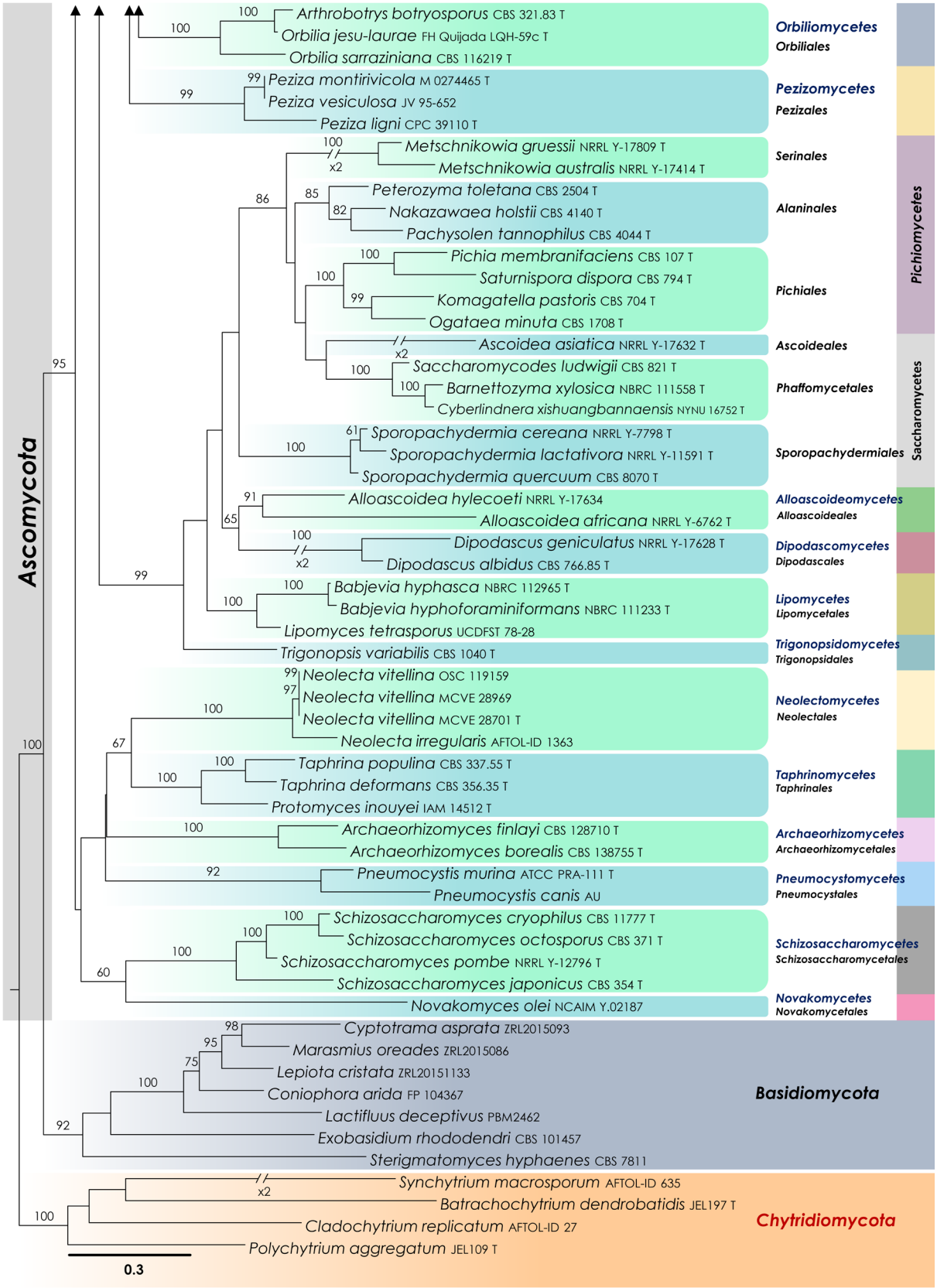


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The family *Cryptotheciaceae* was established by Smith (1926) for the genera *Cryptothecia* and *Stirtonia* having the asci loosely scattered in the thallus or in distinct ± white thallus patches of hydrophobic plectenchyma. *Arthoniaceae* differs from *Cryptotheciaceae* by asci more densely aggregated into black or variously colored ascomata with paraphysoids. Santesson (1945, 1952), one

of the first workers to arrange lichens with reference to the fungus system, suggested uniting the *Cryptotheciaceae* with the *Arthoniaceae* because several species of both families have intermediate ascomata as showed by Groenhart (1938).

The family *Roccellaceae* first included only fruticose lichens. Santesson (1949) suggested including *Dirinaceae* within *Roccellaceae*, the two families differing only by the thallus type being crustose in the former and fruticose in the latter. Later, several crustose genera have been transferred to *Roccellaceae* (Tehler 1990, 1993, Hawksworth et al. 1995, Grube 1998). According to Poelt (1973) the *Lecanactidaceae* should not be segregated from the *Opegraphaceae*, a family including species with a crustose, ecorticate thallus and lecideine ascomata. *Roccellaceae sensu* Tehler (1990, 1993) included species with a crustose or fruticose, usually corticated thallus and ascomata with a well-developed thalline margin. Hawksworth et al. (1995) and Grube (1998) expanded the *Roccellaceae* to include the *Opegraphaceae* and other genera, such as *Chiodecton*, *Schismatomma*, and *Syncesia*, considered of uncertain family affiliation by Tehler (1993). During the last decade, the *Arthoniales* was thus only divided into three families: *Arthoniaceae*, *Chrysotrichaceae* and *Roccellaceae*, but phylogenetic studies highlighted a more complex situation, with two more families recognized, *Andreiomycetaceae* and *Lecanographaceae*, and several main lineages of uncertain family affiliation (Ertz & Tehler 2011, Hodkinson & Lendemer 2013, Frisch et al. 2014).

General description

Sexual morph: Ascolocular, multi-ascal ascomata, hypothecium tissue distinct and usually dark brown or carbonaceous, paraphysoids present, branched, often anastomosing, asci bitunicate with apical pore apparatus with hemiamyloid layer in endotunica, ascospores strictly transseptate, photobiont frequently filamentous, green algae, commonly trentepohlioid, rarely chlorococcoid. Mainly lichen-forming fungi. Asexual morphs normally propagate with soredia, rarely isidia. Conidia are probably also important for asexual dispersion (e.g., Tehler 1988).

Arthoniaceae Rchb. (Reichenbach 1841: 13). *Thallus* crustose, usually thin without cortex, photobiont trentepohlioid, rarely chlorococcoid. *Ascomata* circular in outline although often irregularly-shaped, rarely lirelliform, asci usually globose to clavate with a strongly thickened apical wall, mostly on bark and often endophloeodal, i.e. growing inside the host cortex. The family affiliation of several genera (e.g., *Bryostigma*, *Diarthonis*) remains uncertain, because they form distinct main lineages with species of *Arthonia sensu lato*.

Chrysotrichaceae Zahlbr. (Zahlbruckner 1905 (‘1907’): 117). *Thallus* crustose, leprose to byssoid (cotton-like) bright yellow, ascomata immersed and eventually becoming embedded in thallus, asci clavate, mostly on bark.

Lecanographaceae Ertz, Tehler, G. Thor & Frisch (in Frisch et al. 2014: 740). *Thallus* crustose, ecorticate, rarely corticate and placodioid, photobiont trentepohlioid, rarely chlorococcoid. *Ascomata* lirelliform to rounded, thalline margin absent, hymenial disc often exposed, often pruinose, excipulum conspicuous, dark brown. *Asci* cylindrical to clavate. *Spores* hyaline, fusiform, septate, with gelatinous sheath.

Opegraphaceae Stizenb. (Stizenberger 1862). *Thallus* crustose to fruticose, rarely with cortex, ascomata lecideine, rarely with thalline margin, asci clavate, on bark or rocks.

Roccellaceae Chevall. (Chevallier 1826). *Thallus* crustose to fruticose, usually with cortex, ascomata usually with a well-developed thalline margin, asci clavate, on bark or rocks. The members of this family are mostly restricted to the dry coastlines, mostly in climates of the Mediterranean type.

Roccellographaceae Ertz & Tehler (Ertz & Tehler 2011). *Thallus* crustose to suffruticose, ascomata immersed lirelliform or dendroid, dot-like dispersed in radiating lines, hypothecium hyaline to pale brownish, ascospores hyaline or brown (Fig. 2).



Figure 2 – Diversity of *Arthoniales*. a *Arthonia radiata* (Ertz 10094). b Ascospores of *Arthonia cinnabarina* (Ertz 8783). c *Lecanographa dialeuca* (Ertz 10569). d *Roccellographa cretacea* (Tehler 9381). e *Fulvophyton rostratum* (van den Boom 25114). f Cross section through an ascoma of *Fulvophyton rostratum* (van den Boom 25114). g *Dictyographa arabica* (Ertz 11537). h Cross section through an ascoma of *Dictyographa arabica* (Ertz 11537). i *Pentagenella fragillima* (Tehler 8381). j *Paraingaderia placodioidea* (Tehler 9344). k *Paralecanographa grumulosa* (Ertz 13565). l *Dirina ceratoniae* (Tehler 9047). m *Roccella tinctoria* (Tehler 8309). n *Lecanactis borbonica* (Ertz 4780). o Cross section through an apothecium of *Lecanactis borbonica* (4780), p *Chrysothrix candelaris* (Ertz 2651). q *Syncesia myrticola* (Ertz 10555). r Ascospore of *Syncesia myrticola* (Ertz 10555). s *Dendrographa decolorans* (holotype of *Schismatomma hafellneri*). t *Plectocarpon serusiauxii* (Ertz 4609). Scale bars: a = 500 µm, b, r = 10 µm, c, p, q, s, t = 2 mm, d = 2 cm, e, g, j, k, n = 1 mm, l = 5 mm, f, h, o = 100 µm, i, m = 1 cm.

Families included in *Arthoniales*

Andreiomycetaceae B.P. Hodk. & Lendemer
Arthoniaceae Reichenb. ex Reichenb.
Chrysotrichaceae Zahlbr.
Lecanographaceae Ertz, Tehler, G. Thor & Frisch
Opegraphaceae Körb. ex Stizenb.

Roccellaceae Chevall.
Roccellographaceae Ertz & Tehler

Arthoniales genera *Incertae sedis*
Angiactis Aptroot & Sparrius
Arthophacopsis Hafellner
Bactrospora A. Massal.
Bryostigma Poelt & Döbbeler
Catarraphia A. Massal.
Felipes Frisch & G. Thor
Glyphopsis Aptroot
Gossypiothallon Aptroot
Helminthocarpon Fee
Hormosphaeria Lév.
Minksia Müll. Arg.
Nipholepis Syd.
Paradoxomyces Matzer
Perigrapha Hafellner
Phacothecium Trevis.
Sporostigma Grube
Synarthothelium Sparrius
Tarbertia Dennis
Trichophyma Rehm
Tylophorella Vain.
Wegea Aptroot & Tibell

Evolution

Most species of *Arthoniales* form lichen symbioses with trentepohlioid algae, but over 170 species are lichenicolous and a few are considered as being doubtfully or not lichenized. It is obvious that lichenisation has been subjected to multiple gains and losses during their evolutionary history (Gargas et al. 1995, Lutzoni et al. 2001, Ertz et al. 2008, Schoch et al. 2009a), but the *Arthoniales* appears to be the result of a single lichenisation and it is presumed that non-lichenised and lichenicolous species within the order represent reversions to the non-lichenised state (Nelsen et al. 2009, Thiyagaraja et al. 2020). Photobiont switching between *Trebouxia* (*Trebouxiophyceae*) and trentepohlioid (*Ulvophyceae*) photobionts has been shown to cause changes in the reproduction strategy and phenotypic dimorphism for *Lecanographa amylacea* (Ertz et al. 2018a).

Phylogenetic studies using molecular data focusing on the *Arthoniales* began with Myllys et al. (1998, 1999). Sequences of nucSSU and ITS were used to investigate the phylogenetic relationships in the order *Arthoniales* focusing on the family *Roccellaceae*. Incongruence between the molecular and morphological datasets were found and assumed to be due to a high level of homoplasy in the morphological data. The generic concept of the genera *Roccella*, *Roccellina* and *Pentagenella* was reinvestigated using nucLSU and RPB2 sequences (Tehler & Irestedt 2007). It was shown that the fruticose growth habit has evolved or been lost multiple times in the *Roccellaceae* and several times even within genera. More recently, the origin, evolution, and taxonomy of the genera *Dirina* and *Roccella* were studied in detail using several loci (Tehler et al. 2004, 2009a, 2009b, 2010, 2013).

Those studies mainly included macrolichens. The phylogenetic relationship of several crustose genera was recently investigated, showing notably the homoplastic nature of morphological characters traditionally used to circumscribe genera within *Arthoniales*, such as exciple carbonisation and ascomatal structure (Ertz et al. 2009). Some genera such as *Enterographa* and *Opegrapha* were found to be polyphyletic, species of the latter being even nested in nearly all the major clades identified within *Arthoniales*. Moreover, it became clear that the family concept was not accepted, *Roccellaceae* being paraphyletic and formed of two distinct well-supported clades. As evidenced by

molecular data (Ertz & Tehler 2011, Frisch et al. 2014), *Arthoniales* currently include the families *Arthoniaceae*, *Chrysothricaceae*, *Lecanographaceae*, *Opegraphaceae*, *Roccellaceae* and *Roccellographaceae* (Fig. 2). The family *Andreiomycetaceae* was newly described in *Arthoniales* for two sterile lichens previously placed in *Lepraria* (Hodkinson & Lendemer 2013) but it is phylogenetically close to *Chrysothricaceae* leaving doubts about its distinctness. The family *Arthoniaceae* was found to be polyphyletic with the *Bryostigma* clade, including mainly lichenicolous taxa, related to *Arthoniaceae*, while the *Felipes* clade, including exclusively lichenized taxa, showed close affinities with *Chrysotrichaceae* (Frisch et al. 2014). The polyphyly of the large genera *Arthonia* and *Arthothelium* highlighted the necessity to revise generic circumscriptions in these groups. Since then, several genera were described or reinstated in *Arthoniaceae* in order to circumscribe small, monophyletic groups, such as *Cryptophaea*, *Glomerulophoron*, *Inoderma*, *Leprantha*, *Snippocia* and *Sporodophoron* (Frisch et al. 2015, Van den Broeck & Ertz 2016, Ertz et al. 2018b). More recently, the genus *Naevia* was resurrected from *Arthonia* to accommodate several species with a saprotrophic lifestyle (Thiyagaraja et al. 2020). The crustose and mazaediate genera *Heterocyphelium* and *Tylophoron*, which were previously believed to be related to *Caliciales sensu lato* (Tibell 1996) and to pyrenocarpous lichens (Aptroot et al. 2008b), respectively, has been reclassified as members of the *Arthoniales* based on molecular data (Lumbsch et al. 2009a, Van den Broeck et al. 2017).

Justification of order and problems

Arthoniales is recognized as a monophyletic group, sister to the *Lichenostigmatales* within the class *Arthoniomycetes* (Muggia et al. 2021a). However, the phylogenetic placement of *Arthoniomycetes* as a sister group to *Dothideomycetes* sometimes remains unresolved, with conflicting results in previous studies (e.g., Ruibal et al. 2009, Muggia et al. 2012). Additionally, the sister relationship between *Arthoniales* and *Lichenostigmatales* has not consistently received robust support (e.g., Ertz et al. 2014). To clarify these phylogenetic relationships, especially in the early diversification of the group and its connection to *Dothideomycetes*, a broader taxon sampling and the inclusion of additional molecular markers are required. However, many genera within *Arthoniales* are rare, making it challenging to obtain fresh material necessary for high-quality sequencing result.

Significance

Ecological and economic roles

Arthoniales have a world-wide distribution from arctic-alpine regions to the tropics, growing on a wide variety of substrates including rocks, bark, wood and living leaves. They are primarily composed of lichen-forming taxa but some are parasites or commensals growing on other lichens. They play a significant role in various ecosystems, particularly in tropical and subtropical regions where they are most diverse. They are even one of the main components of the lichen vegetation in some subtropical coastal habitats with a Mediterranean or desert type climate (e.g., Tehler 1983, 1990, Follmann & Werner 2003, Aptroot & Sparrius 2008). These lichens play a significant role in the biodiversity and nutrient cycling of these ecosystems, colonizing bare substrates such as rocks, tree bark, and man-made surfaces. Some are pioneer creating habitats that can be colonized by other organisms. Many of the species are restricted to substrates that are sheltered from rainfall. They serve as microhabitats for various microorganisms and invertebrates. Some species also grow exclusively on leaves (e.g., Lücking 2008). Like other lichens, *Arthoniales* are bioindicators due to their sensitivity to environmental changes, particularly air quality, forest management and climate change, and can be used to assess ecosystem health. Some species produce secondary metabolites with potential medicinal properties. Recently, scientists from the National Genome Research Network NGFN-Plus have discovered that a dye derived from the lichen *Roccella tinctoria* may neutralize the harmful Alzheimer's deposits (beta-amyloid peptides), although this has only been demonstrated in cell culture experiments (https://www.gesundheitsforschung-bmbf.de/de/roter-farbstoff-gegen-alzheimer-naturstoff-aus-flechten-macht-offenbar-alzheimer-3293.php). Historically, *Arthoniales* have also been valuable sources of natural dyes. The genus *Roccella* is particularly notable, as its

name is etymologically linked to "orchil", a historical dye derived from lichens. This dye, known for its rich purple or red hues, has been used since ancient times, with its earliest mention found in the Bible. The dyeing properties of *Roccella* are primarily attributed to the presence of lecanoric acid and erythrin. During the Renaissance, particularly in Florence, orchil was highly sought after for dyeing textiles such as cotton and silk, leading to a robust trade in *Roccella* lichens. Major collection sites for these lichens included the Macaronesian Islands, the Azores, the Canary Islands, and Cape Verde. The Rucellai family, prominent in this trade, derived their name from *Roccella* and amassed considerable wealth (Tehler & Irestedt 2007).

Chemical diversity

Many secondary metabolites have been reported from lichenized *Arthoniales* (e.g., Huneck 1995, Tehler et al. 2013, Frisch et al. 2015). Their ecological functions ranging from defense mechanisms to symbiotic interactions and their uses need to be studied further.

Other relevant data and future recommendations

The broad range of lifestyles and remarkable variability in ascomatal and thallus structures make *Arthoniales* an ideal model to gain a more comprehensive understanding of the evolution of lichenization and phenotypic characters within *Ascomycota*. Future studies should focus on expanding taxon sampling, as many genera lack molecular data, and several remain of uncertain family affiliation (cf. list of genera *incertae sedis*). Special attention should be given to underrepresented regions, such as some tropical and subtropical regions, where *Arthoniales* are most diverse, and to taxa with rare lifestyles within the order, such as lichenicolous and saprotrophic species. Additionally, future research should focus on exploring the genetic diversity within taxa to improve species boundaries delineation and to identify cryptic species that may have been overlooked in phenotypic classifications. Enhanced molecular techniques could further clarify phylogenetic relationships, aiding in the generic classification of species and deepening our understanding of lichenization processes within this group. Sequencing of photobionts and other organisms living within thalli may also provide interesting insights into the evolution and ecological adaptations of the mycobionts in *Arthoniales* (e.g., Borgato et al. 2022).

***Lichenostigmatales* Ertz, Diederich & Lawrey, Fungal Diversity 66: 123 (2014)**

Subphylum : *Pezizomycotina*
Class : *Arthoniomycetes*
Subclass : *Arthoniomycetidae*

Introduction

The order presently accommodates a single family *Phaeococcomycetaceae* with four genera including *Antarctolichenia*, *Etayoa*, *Lichenostigma* and *Phaeococcomyces* (Hyde et al. 2024b). The order is phylogenetically closely related to *Arthoniales* but its members are recovered in both *Arthoniomycetes* and *Dothideomycetes* (Ert et al. 2014) and accommodate lichenicolous, borderline lichen and rock-inhabiting fungi (Muggia et al. 2021a).

History

Lichenostigmatales was introduced by Ertz et al. (2014) for a single family *Phaeococcomycetaceae*. The family was originally established for dematiaceous yeast genera including *Phaeoannellomyces* and *Phaeococcomyces* (McGinnis et al. 1985b). Ertz et al. (2014) resurrected the family to include the generic type *Lichenostigma* with *Etayoa*, *Phaeococcomyces* and some undescribed rock-inhabiting fungi that are known only from cultures. The generic type, *Lichenostigma* was established by Hafellner (1982) for the type species *L. maureri*, growing on *Usnea* spp. and *Pseudevernia furfuracea* from Austria. Hawksworth & Hafellner (1986) questioned that *L. maureri* could be the teleomorph of *Phaeosporobolus usneae* due to shared superficial characteristics in ascomata and conidiomata and the intermixed occurrence. *Phaeosporobolus usneae* was collected from various hosts including many *Usnea* species worldwide. Consequently, several

species were added to *Lichenostigma* and *Phaeosporobolus* based on morphological characters (Thor 1985, Calatayud & Barreno 2003, Ihlen 2004, Vondrák & Jaroslav 2007, Halıcı et al. 2009, Fernandez-Brime et al. 2010, Valadbeigi & Von Brackel 2011, Flakus & Kukwa 2012, Roux 2021).

Later, the generic type *Phaeosporobolus usneae* was considered as the anamorph of *Lichenostigma maureri* and consequently, *Phaeosporobolus* and the lichenicolous genus *Diederimyces* were synonymized under *Lichenostigma*. Ertz et al. (2014) established a new genus *Etayoa* for *E. trypethelii* that was previously reported as *Phaeosporobolus trypethelii* based on molecular and morphological characteristics. *Etayoa trypethelii* formed a distinct clade in *Lichenostigmatales* and was sister to unidentified rock isolates. The taxon was originally reported on the thallus of corticolous *Trypethelium ochroleucum* from Bolivia (Flakus & Kukwa 2012). The genus differs from the generic type in spherical and compact conidia, external cells of stromata with a distinct, dark greyish-brown mosaic-like ornamentation (Ertz et al. 2014). The genus has been also reported in subtropical or tropical regions from various hosts: *Bathelium carolinianum*, *Laurera megasperma*, *Trypethelium ochroleucum*, *Pertusaria ramulifera* and many *Graphidaceae* species in both sexual and asexual morphs (Ertz et al. 2014).

Phaeococcomyces was introduced with the type *Phaeococcomyces nigricans* (= *Cryptococcus nigricans*) (Hoog 1977) with two additional species *P. catenatus* and *P. exophialae*. The genus was characterized by restricted, glistening, and black colonies, lack of hyphae, thick-walled, dark olivaceous brown, globose to broadly ellipsoidal budding cells which give rise to secondary conidia from 1–3(–5) loci, and chains of globose cells (Hoog 1977, Sugiyama et al. 1987).

General description

The taxa of *Lichenostigmatales* are characterized by cells multiplying by budding in either black yeasts or species in which conidiomata and ascomata are entirely made of an organised agglomeration of spherical yeast-like cells. The order shares both similar and dissimilar morphological characteristics to the phylogenetically closely related order *Arthoniales*.

The type species, *Lichenostigma maureri* shared similar morphological characteristics to *Arthoniales* in the presence of K/I+ blue ring in the lower part of the apical dome, ascus tholus (Calatayud & Barreno 2003, Ertz et al. 2014) and young hyaline ascospores (Ertz et al. 2014). However, *Lichenostigma maureri* and the related members of *Phaeosporobolus* differ from *Arthoniales* in possessing cells forming conidiomata and ascomata (these are spherical and multiply by budding) and the presence of dense and organized agglomeration of yeast cells. *Phaeococcomyces* exclusively reproduces by budding but does not agglomerate (Ertz et al. 2014) (Fig. 3).

Families included in *Lichenostigmales*

Phaeococcomycetaceae McGinnis & Schell

Evolution

Several studies revealed that the lichenicolous lifestyle has evolved several times independently in different lineages including *Arthoniomycetes* (Ertz & Tehler 2011, Frisch et al. 2015, Thiyagaraja et al. 2020). The non lichenized order *Lichenostigmales* accommodates not only lichenicolous species but also several rock isolates (Ertz et al. 2014) assumed to represent a transitional group between the *Arthoniomycetes* and *Dothideomycetes*. Before the establishment of the order, Ruibal et al. (2009) suggested that the rock isolates could represent early diverging *Dothideomycetes* lineage by supporting the hypothesis that rock surfaces were important substrates for ancient fungal lineages. This hypothesis was also supported by the phylogenetic study conducted by Ertz et al. (2014), which showed that several "*Lichenostigma*" cladded with *Lichenothelia* in *Dothideomycetes* suggesting that transitions between rock inhabiting fungi and the lichenicolous habit possibly occurred several times in the evolution of closely related species.

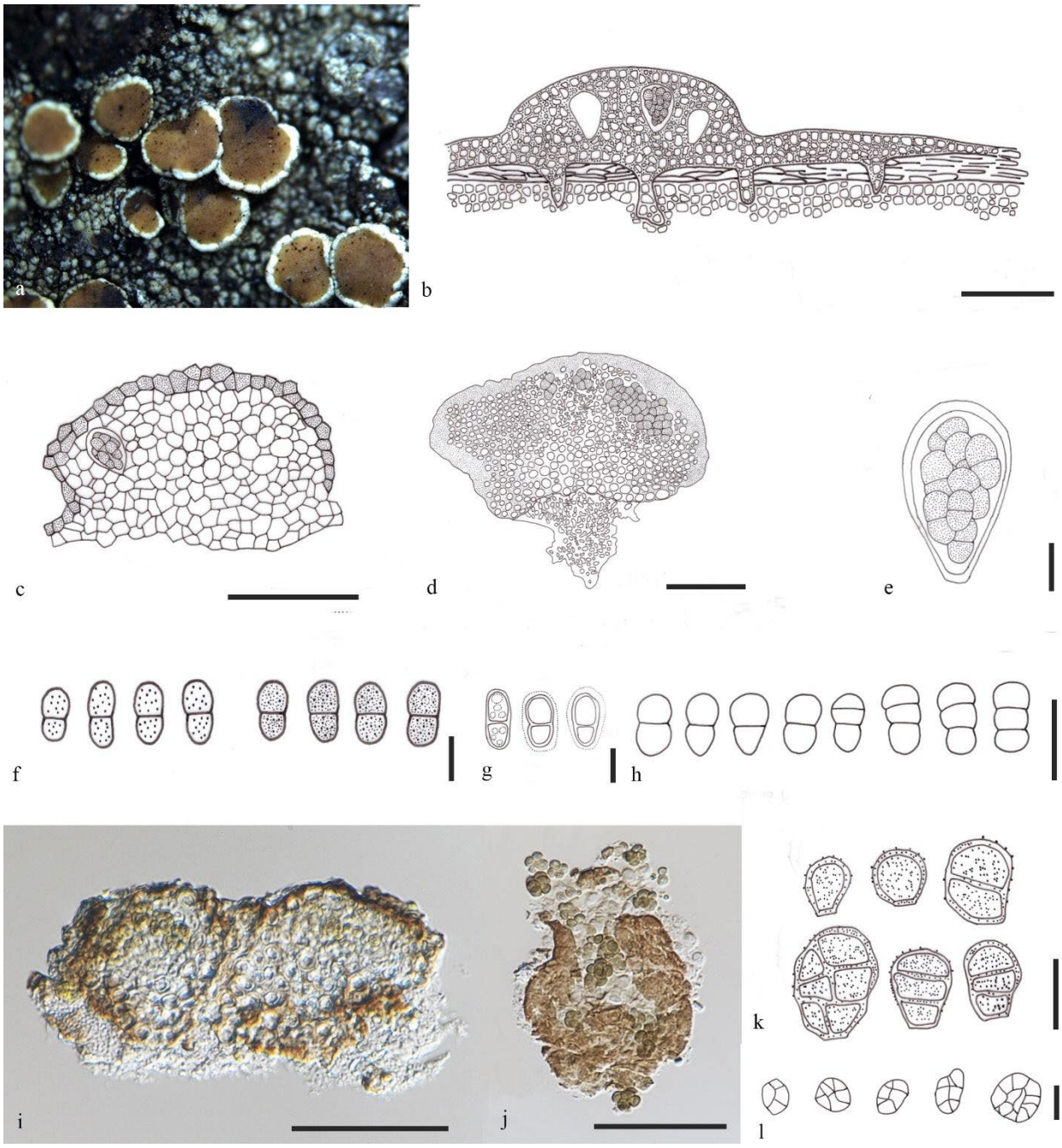


Figure 3 – Morphology of *Lichenostigmales*. a Host substrate of *Lichenostigma* sp. b Ascomata of *L. svandae*. c Ascomata of *L. iranicum.* d Ascomata of *L. rupicolaem*. e Asci of *L. rupicolae*. f–h Ascospores (f *L. iranicum*, g. *L. rupicolae,* h. *L. svandae*). i, j Conidiomata of *Lichenostigma* sp. h Macroconidia of *L. rupicola.* l Macroconidia of *L. supertegentis* (redrawn from Ihlen 2004, Vondrák & Jaroslav 2007, Fernandez-Brime et al. 2010). Scale bars: b–d, i, j = 50 µm, e–g, k, l = 10 µm, h = 20 µm.

Justification of order and problems

Lichenostigma has two subgenera; (1) subgenus *Lichenostigma* which is characterized by rounded, cushion-like ascomata and by the absence of visible vegetative hyphae or strands on the surface of the host lichens and (2) *Lichenostigma* subgenus *Lichenogramma* that is characterized by oval to elongate or irregularly shaped ascomata interconnected by superficial black hyphae or hyphal strands. In Ertz et al. (2014), the subgenus *Lichenostigma* subgen. *Lichenogramma* recovered in *Lichenotheliaceae sensu stricto* in the *Dothideomycetes* including *Lichenostigma rugosum* that do not possess the characteristic feature of superficial pigmented hyphal strands as reported in subgenus

Lichenogramma. The stromatic cells in *L. rugosum* divide by septa which is observed in cultures of *L. rugosum* while *L. maureri* (type species) divide by budding. Thus, the way of cell division has been identified as a distinguishing feature of *Lichenostigma sensu stricto* and *Lichenostigma* species belonging to the *Lichenotheliaceae*. However, *Lichenostigma* subgen. *Lichenogramma* is a heterogenous lineage which needs further studies.

Significance

Ecological and economic roles

Lichenostigmatales comprises black yeasts, lichenicolous and rock-inhabiting species (Ertz et al. 2014). *Lichenostigma rupicolae* occurs on thallus of saxicolous *Pertusaria rupicola* species. No damage was reported due to the lichenicolous *Lichenostigma* (Fernandez-Brime et al. 2010). *Phaeosporobolus usneae* was reported on various hosts such as *Bryoria*, *Evernia*, *Foraminella*, *Letharia*, *Lethariella*, *Pseudevernia*, *Ramalina* and *Usnea* with worldwide distribution (Hawksworth & Hafellner 1986). The recently introduced genus *Antarctolichenia* formed a loose association with algae and also free-living form (Muggia et al. 2021a). The members are important to understand the evolutionary link between the evolution of rock inhabiting fungi and lichen forming fungi (Ertz et al. 2014).

Chemical diversity

No chemical substances were reported in *Lichenostigmales*.

***Candelariomycetes* Voglmayr & Jaklitsch, Persoonia 42: 41 (2018)**
***Candelariales* Miadl**. **Lutzoni & Lumbsch**, **Mycological Research 111: 509–547 (2007)**

Subphylum : *Pezizomycotina*
Class : *Candelariomycetes*
Subclass : *Candelariomycetidae*

Introduction

Candelariales is a lichenized order in *Ascomycota* which comprises about 80 species assigned to six genera. The majority of the species within the order are in *Candelariella* (ca. 50 species). *Candelariales* is a single order in the class *Candelariomycetes* (Voglmayr et al. 2019b). According to molecular clock analyses (Prieto & Wedin 2013), *Candelariales* is the oldest group of lichenized fungi. The order was introduced by Hibbet et al. (2007) with *Candelaria* A. Massal. as the type. The order initially included only representatives of *Candelariaceae* Hakul. This family is primarily characterized by its pigments, comprising pulvinic acid and derivatives. These are present at least in apothecia and often also in thalli, giving the lichens a distinct and characteristic yellow to yellow-orange color (Westberg 2005). Other characteristics are the presence of lecanorine to biatorine apothecia, Candelaria-type asci, the common occurrence of polyspory (i.e. having more than 8 spores per ascus) as well as hyaline, aseptate to 1-septate ascospores (Döring & Lumbsch 1998, Miadlikowska et al. 2006, Hibbett et al. 2007, Westberg 2005, 2007a, b, c).

Phylogenetic studies supported a sister-relationship between *Candelariaceae* and *Pycnoraceae* (Bendiksby & Timdal 2013), which has led to changes in the classification of *Candelariales*. Consequently, *Candelariaceae* and *Pycnoraceae* were accepted in the order, which can be easily separated by phenotypic characters. In contrast to *Candelaricaeae*, *Pycnoraceae* possesses black lecideine apothecia with consistently 8-spored asci and simple ascospores, and produces benzyl ester (alectorialic acid).

Candelariaceae was introduced by Hakulinen (1954) with three genera, namely *Candelaria*, *Candelariella* and *Placomaronea*. Later two additional genera, namely *Candelina* (Poelt 1974b) and the recently described *Protocandelariella* (Kondratyuk et al. 2020) were added to the family. Segregation of two other genera *Candelinella* and *Opeltiella* (Kondratyuk et al. 2020) requires additional phenotypical and phylogenetic evidence (Cannon et al. 2021). The members of *Candelariales* are mostly lichenized with chlorococcoid photobionts and few are lichenicolous. A

wide range of growth form except fruticose can be found in *Candelariales*. The thallus is usually yellow to orange, also grey, brownish-grey, greenish-grey, yellowish-grey, with or without vegetative propagules. Different types of apothecia occur in *Candelariales*: lecanorine or rarely biatorine (*Candelariaceae*) or lecideine (*Pycnoraceae*), yellow to orange or black. The hypothecium is hyaline or dark brown, and hymenium amyloid. Asci are mostly clavate, with amyloid outer wall, and tholus weakly amyloid except for a darker amyloid, ring-shaped structure in the lower part, 8-spored or polyspored with hyaline, aseptate to 1-septate ascospores. The main secondary compounds are benzyl ester (alectorialic acid; *Pycnoraceae*), pulvinic acid and its derivates. The taxa are predominantly nitrophilic and distributed worldwide, with most occurring on bark, non-burned wood, rock, soil, and plant debris in undisturbed nemoral to boreal to arctic habitats as well as in urban areas (Hakulinen 1954, Westberg 2005, 2007a, b, c).

History

Studies on *Candelariales* commenced during early mycological research. These first studies focused on yellow–colored taxa. Their distinctive color is reflected in the name of one of the first representatives of the group: *Patellaria vitellina* (Hoffmann 1794) from Germany and *Lichen concolor* (Dickson 1793) from UK, which were the first described taxa in the order. These taxa were placed in *Candelaria*, which was introduced by Massalongo (1852). However, by 1860 other taxa which are presently assigned to *Candelariaceae* had been assigned to 13 different genera (Hakulinen 1954). *Candelariella* was established by Müller (1894) with *Candelariella vitellina* (Hoffm.) Müll. Arg. as the type. However, despite uniform secondary chemistry and characteristic apothecia and ascospores, the genera were divided into different families – *Candelaria* in *Parmeliaceae* and *Candelariella* in *Lecanoraceae* (Boistel 1903, Herre 1910, Zahlbruckner 1928, 1930) according to their thallus formation, including foliose and crustose respectively. Räsänen (1943) followed by Vainio (1890) included both *Candelariella* and *Candelaria* in the family *Lecanoraceae* mainly based on their lecanorine apothecia. Subsequently a close relationship with *Lecanoraceae* was suggested by Lumbsch (1994), Döring & Lumbsch (1998) and LaGreca & Lumbsch (2001), based on anatomy, ascoma ontogeny and the presence of a similar chemistry in some species of *Lecanora*. Wedin et al. (2005b) showed that *Candelariacea*e was distantly related to the core group of *Lecanorales* that was later confirmed by Hofstetter et al. (2007) and Miadlikowska et al. (2006). The third genus of the order, *Placomaronea*, was established by Räsänen (1944) for yellow, mostly peltate squamulose to umbilicate foliose, epilitic lichens distributed in Southern Hemisphere. Räsänen (1944) placed *Placomaronea* in *Acarosporaceae*, but its close relationship with *Candelariella* was later recognized by Hakulinen (1954). The major work concerning the taxonomy of the order was the monograph of Hakulinen (1954) focused on the Fennoscandian taxa in which he described *Candelariaceae* and joined genera *Candelaria* (type), *Candelariella* and *Placomaronea* based on their uniform traits such as secondary chemistry, lecanorine apothecia and simple to 1-septate ascospores. Poelt (1974b) described a new genus *Candelina* and proposed a phylogenetic system of generic relationships within *Candelariaceae*. Since that time, further data was recorded (e.g., Poelt 1958, Galun & Reichert 1960, Rondon 1966, Poelt & Reddi 1969, Filson 1975, Poelt & Vězda 1976, Harris & Buck 1978, Rogers 1982, Nimis et al. 1989, Thor & Wirth 1990, Khodosovtsev et al. 2004, Khodosovtsev 2005). Westberg (2005, 2007 a, b, c) provided a detailed monograph on the taxonomy of *Candelariella* in western North America, with the description of several new species using molecular phylogeny of ITS (Westberg et al. 2007). In the following 15 years, several new species were described (Westberg & Frödén 2007, Etayo et al. 2009, Westberg et al. 2009, 2011, Westberg & Arup 2011, Otte et al. 2013, Tripp & Lendemer 2015, McCarthy & Elix 2017b, Yakovchenko et al. 2017, Kondratyuk et al. 2017, 2018, Liu & Hur 2018, Liu et al. 2019a, Etayo et al. 2021, Kalb & Aptroot 2021, Halici et al. 2023, Yakovchenko & Davydov 2024). Revisions for the British Isles, Austria, Caucasus, and Southwest Asia were also published (Westberg & Sohrabi 2012, Neuwirth 2014, Ismailov et al. 2017, Cannon et al. 2021). Kondratyuk et al. (2020) described three new genera, namely *Candelinella*, *Opeltiella* and *Protocandelariella*. The latter one was originally proposed by Poelt (1974b) for *Candelariella subdeflexa*. However, only four genera were recognized following Lücking et al.

(2017) while Wijayawardene et al. (2022a) accepted eight genera including *Candelaria*, *Candelariella*, *Candelina*, *Candelinella*, *Opeltiella*, *Placomaronea*, *Protocandelariella* and *Pycnora* under *Candelariales*.

Studies on *Pycnoraceae* started in the 19th century with the introduction of two species which were described under *Lecidea* (Sommerfelt 1826, Nylander 1874) but were later moved to *Hypocenomyce* in the early 1980s (Hawksworth et al. 1980, Poelt & Vězda 1981, Timdal 1984). Timdal (1984) revised the genus *Hypocenomyce*, identified four evolutionary groups and proposed that the genus is polyphyletic. The genus *Pycnora* was established by Hafellner & Türk (2001) for *Hypocenomyce xanthococca*-group, (which does not grow on burned wood) and included three taxa. Molecular phylogenetic studies (Wedin et al. 2005b, Bendiksby & Timdal 2013) corroborated the polyphyletic nature of *Hypocenomyce sensu lato* and a sister relationship between *Pycnora* and *Candelariaceae*. Miadlikowska et al. (2014) suggested the inclusion of *Pycnoraceae* in *Candelariales*. This position remains uncertain due to the placement of *Pycnoraceae* outside of *Lecanoromycetes*. However, the current classification of *Pycnoraceae* within *Candelariales* has been accepted in recent studies (Lücking et al. 2017, Wijayawardene et al. 2017a, 2020, 2022a). *Candelariaceae* formed a basal lineage within *Lecanoromycetes* (Wedin et al. 2005b, Miadlikowska et al. 2006, Hofstetter et al. 2007, Bendiksby & Timdal 2013, Miadlikowska et al. 2014). Miadlikowska et al. (2006) proposed the introduction of '*Candelariomycetidae'*, which was formally established as a subclass within *Lecanoromycetes* by Lücking et al. (2017). However, Voglmayr et al. (2019b) established a separate class *Candelariomycetes* to accommodate *Candelariales*. *Candelariales* are phylogenetically separate from *Lecanoromycetes* and this classification has been accepted in the later publications (Wijayawardene et al. 2020, 2022a). Previously, Schoch et al. (2009a) and Prieto et al. (2013) also showed that *Candelariales* formed a phylogenetically separate clade to *Lecanoromycetes*. Thus, the class *Candelariomycetes*, including single order *Candelariales* was proposed (Voglmayr et al. 2019b), which was accepted in recent *Ascomycota* classifications (Wijayawardene et al. 2020, 2022a). Hyde et al. (2024b) accepted six genera and two families with the order.

General description

Candelariales is a poorly studied order with wide morphological variation among its representatives. *Candelariaceae* has long been known as exceptionally difficult, with few taxonomically useful characters to circumscribe individual species (Poelt 1974b, Westberg 2005). The characters thought to be taxonomically important in the *Candelariales* are summarized in several studies such as Hakulinen (1954), Poelt (1974b), Timdal (1984), Hafellner & Türk (2001) and Westberg (2005). The most important taxonomic features to define the taxa in the order are: life strategy, type and color of apothecia, number of spores per ascus, ascospores size, shape, and septation, color and texture of upper surface, thallus organization, presence or absence of vegetative propagules and their locality, secondary metabolite compounds, substrate and ecology (Westberg 2005).

The morphological variation in the *Candelariales* ranges from minute lichenicolous species outside the thallus (a few species of *Candelariella*) to species with well-developed foliose thallus (some species of *Candelaria*) while the majority of species possess crustose to squamulose thallus (Timdal 1984, Westberg 2005, 2007 a, b, c, 2010, Westberg et al. 2009). *Chlorococoid* is reported as their photobiont (Timdal 1984, Westberg 2005). The color of the upper surface varies from yellow and orange yellow (due to the presence of calicin and other pulvinic acid derivates) to grey with different tints: brownish-grey, greenish-grey, yellowish-grey. The texture of upper surface as well as presence/absence of epicortical layer are useful as additional diagnostic traits (Westberg 2005). Poelt (1974b) stated that peculiarities of thallus anatomy can be useful in species delineation. *Candelariales* taxa form apothecial ascomata which are sessile, ± roundish, plane to convex. Apothecia are usually darker than the thallus and the color of disc varies from pale (yellow to orange) with a yellow-brownish epithecium (K-/+ weakly red) in *Candelariaceae* to dark (brown to black) with a greenish epithecium (K+violet) in *Pycnoraceae*. The apothecia can be biatorine, lecanorine or

lecideine; immarginate or with thalline margin, proper margin or both. Proper margin can be indistinct to persistent and prominent, even to strongly flexuose as well as colorless to blackish-brown in section. A strongly pigmented hypothecium and excipulum is observed in *Pycnoraceae* whereas excipulum and hypothecium in *Candelaricaeae* are colorless. Asci can be clavate or cylindrical, Lecanora-type (Hafellner & Türk 2001) or with well-developed, I+, blue tholus and lateral amyloid zone (Bendiksby & Timdal 2013) or Candelaria-type (apical dome KI+blue in lower part, penetrated by broad apical cushion) with 8–32-spores (Westberg 2005). Polyspory is known in some taxa of *Candelaricaeae* whereas asci in *Pycnoraceae* are consistently 8-spored (Bendiksby & Timdal 2013). The ascospores of the majority of taxa of *Candelariaceae* and *Pycnoraceae* are mostly identical: colorless, ellipsoid, narrowly-ellipsoid and oblong with the exception of spherical, acicular, ovoid, citriform, teardrop-shaped ascospores known in *Candelariaceae* which are ranged from simple to 1-septate herewith ascospores in *Pycnoraceae* are consistently simple (Timdal 1984, Westberg 2005).

The asexual morph is reported for several genera of *Candelariales* which produce vegetative propagules - soredia and blastidia (Lendemer & Westberg 2010, Westberg & Arup 2011, Yakovchenko et al. 2017, Liu & Hur 2018, Liu et al. 2019a). Soredia in *Candelariales* are yellow and known only in yellow-colored taxa. Blastidia are yellow and grey and known both in yellow-colored and grey-colored taxa. Vegetative propagules can be laminal or marginal, irregular or organized into soralia (crateriform, rounded), discrete or coalescing into entire sorediate crust. Accordingly, the size of soredia can be farinose (up to 40 µm) or granulose (up to 70 µm), whereas blastidia are ca. 80 µm. Pycnidia are observed in all genera of the order. Pycnidia are small, one-to lobate chambered, black to yellow-orange, immersed to sessile in the thallus or in between the thallus areoles. According to Vobis (1980) the conidiophores correspond to type II-III. The conidiogenous cells are elongated and somewhat tapering and appear more or less flask-shaped (Westberg 2005). Conidia are simple, hyaline, narrowly ellipsoid to ellipsoid to oblong or rarely baciliform or globose (Hafellner & Türk 2001, Westberg 2004, 2005). Among *Candelariales*, *Protocandelariella* is unique in having conidiophores producing globose conidia on the lower side of the thallus (Poelt 1974b, Westberg 2007a, Yakovchenko et al. 2017, Kondratyuk et al. 2020).

Sexual morph: *Thallus* lacking or indistinct to crustose (areolate, granular, bullate, pulvinate, rosulate placodioid), squamulose (subsquamulose, peltate squamulose), foliose (subfoliose, umbilicate foliose). *Upper surface* greenish-yellow, yellow, orange-yellow, brownish-yellow, grey, greenish-grey, brownish-grey, yellowish-grey, yellowish-brown, smooth to pulverulent. *Prothallus* absent. *Photobiont* chlorococcoid green alga, maximum diam. 24 µm. *Medulla* white to yellow. *Ascomata* apothecial, lecanorine, biatorine, lecideine, sessile on thallus or in between areoles, widely attached to somewhat constricted at the base, crowded to scattered. *Disc* yellow, orange, greenish-yellow, brownish-yellow, dark-brown to black, rounded to irregular, plane to concave or strongly convex. *Proper margin* absent or indistinct to distinct, the same color as disc, even to strongly flexuose. *Thalline margin* absent to present, at the same level as the disc or higher, entire to slightly incised or almost lobate. *Hypothecium* hyaline to pigmented (brown). *Excipulum* well or poorly developed, hyaline to strongly pigmented (brownish-black). *Hymenium* amyloid, hyaline to faintly greenish or brownish at the base or near the epithecium. *Paraphyses* septate, simple to branched toward the tips, ± swollen at the tips. *Epihymenium* greenish (K+ violet) or yellow-brownish epithecium (K-/+ weakly red). *Asci* cylindrical to clavate, with amyloid outer wall, and tholus weakly amyloid except for a darker amyloid, ring-shaped structure in the lower part, 8 to poly-spored (ca. 32). *Ascospores* colorless, aseptate to 1-septate, ellipsoid, narrowly-ellipsoid, oblong, spherical, acicular, ovoid, citriform, teardrop-shaped. Asexual morph: *Soredia* yellow, laminal to marginal, farinose to granulose, discrete to coalescing into entire sorediate crust. *Soralia* rounded, crateriform to convex. *Blastidia* yellow to grey, laminal to marginal. *Pycnidia* roundish to elongated or irregular, one- to lobate chambered, immersed to somewhat protruding to sessile in the thallus or in between the thallus areoles, visible as orange to black dots or warts from the outside. *Conidia* simple, hyaline, narrowly ellipsoid, ellipsoid to oblong or rarely baciliform or globose (Figs 4, 5).

Families included in *Candelariales*

Candelariaceae Hakul.

Pycnoraceae Bendiksby & Timdal

Evolution

Molecular clock analyses (Prieto & Wedin 2013) showed *Candelariales* is the oldest group of lichenized fungi, but their crown diversification dates are among the most recent and reported as upper Cretaceous. Whether *Candelariales* have experienced a recent speciation or suffered a high number of extinctions is unknown and further studies are necessary to answer this question (Prieto & Wedin 2013). The phylogeny and trait evolution of *Candelariales* has not yet been resolved (Cannon et al. 2021). Poelt (1974b) proposed a tentative phylogeny of the family. In his hypothesis, *Candelariella subdeflexa* was considered as "protocandelariella" that was confirmed by later molecular studies (Westberg et al. 2007, Yakovchenko et al. 2017, Kondratyuk et al. 2020).

The first molecular phylogenetic study of *Candelariaceae* (Westberg et al. 2007) supported that the generic circumscription in the family was based on the outer morphology (i.e. growth form). This is only partly reflected in the phylogeny which was previously indicated by Miadlikowska et al. (2006). Phylogenetic results based on ITS (Westberg et al. 2007) demonstrated that the overall topology of the tree was poorly-resolved and strongly supported only at terminal clades due to several species with distinct morphology were described (Westberg 2007a, b, c). Westberg et al. (2007) concluded that the polyspored asci have evolved a limited number of times within the family and appeared within four clades including the core clade of *Candelariella*. Miadlikowska et al. (2014) confirmed the polyphyly of *Candelariella* and the necessity to revise generic circumscriptions to reflect the inferred phylogenetic structure for the family *Candelariaceae*. The following phylogenies based on nrITS also confirmed the polyphyletic nature of *Candelariella* and *Candelaria*. These are not well-resolved but are useful in specific level classification (Yakovchenko et al. 2017, Liu & Hur 2018, Liu et al. 2019a). Kondratyuk et al. (2020) added a dozen ITS sequences as well as LSU and mtSSU for a few species and provided a new phylogenetic tree. The concatenated dataset was very incomplete in terms of phylogenetic markers; all three markers were not obtained for any specimens and did not provide well-resolved results. The study showed that the overall topology of the tree was collapsed, nevertheless three new genera were described, namely *Candelinella*, *Opeltiella* and *Protocandelariella*. Among the genera, only *Protocandelariella* was morphologically and phylogenetically distinct (as previously noted by Poelt (1974b), Westberg (2007a), Westberg et al. (2007), Yakovchenko et al. (2017), Liu & Hur (2018) and Liu et al. (2019a)).

Two other genera lack as diagnostic phenotypic differences to *Candelariella* and *Candelaria* as statistically supported clades and therefore cannot be accepted. *Candelinella* is synonymized here with *Candelariella* and *Opeltiella* with *Candelaria*. Miadlikowska et al. (2014) stated that since the number of spores per ascus and thallus habit varies within and between closely related species, and the chemistry is uniform throughout the family, a new set of characters is needed to circumscribe monophyletic genera in *Candelariaceae*. Thus, due to absence of well-resolved phylogeny the major phylogenetic lineages are poorly understood and evolution of major characters within the *Candelariales* such as lifestyle history, ascomatal structure, polyspory and ascospore characters is uncertain. Broad taxon sampling with multiple genes is important to clarify the phylogenetic relationship between representatives of the *Candelariales* since morphologically similar species have shown independent phylogenetic evolution as well as cryptic taxa and the polyphyletic nature of *Candelariella* and *Candelaria*. To date, the lack of adequate molecular data means that the major phylogenetic lineages within the *Candelariales* remain highly speculative.

Justification of order and problems

There is some disagreement and incongruence about the phylogenetic placement, circumscription, and classification of *Candelariales* (Voglmayr et al. 2019b). *Candelariales* was shown to differ from *Lecanorales* by Wedin et al. (2005b) which was confirmed by Miadlikowska et al. (2006), Hibbett et al. (2007), Hofstetter et al. (2007), Bendiksby & Timdal (2013) and

Miadlikowska et al. (2014). Schoch et al. (2009a), doubted that *Candelariales* even belong in the *Lecanoromycetes*. Nevertheless, in all phylogenetic analyses (e.g., Wedin et al. 2005b, Miadlikowska et al. 2006, 2014, Hofstetter et al. 2007, Lumbsch et al. 2007a, Schoch et al. 2009a, Prieto et al. 2013), the *Candelariales* showed an isolated phylogenetic position outside the core *Lecanoromycetes* (Voglmayr et al. 2019b). Based on the phylogenetic results of both Miadlikowska et al. (2006) and Schoch et al. (2009a), Hodkinson (2012) recognized the "Subclass *Candelariomycetidae*", but no formal description has been provided. The subclass of *Lecanoromycetes* was formally established by Lücking et al. (2017). In phylogenetic results of Miadlikowska et al. (2014), *Pycnoraceae* (which were revealed as sister group of *Candelariaceae* within *Candelariales* by Bendiksby & Timdal (2013)) were placed not only outside the *Candelariales* but also outside *Lecanoromycetes*. Voglmayr et al. (2019b) stated this was connected with an insufficient outgroup selection. The phylogenetic analyses of Voglmayr et al. (2019b) confirmed the results of Schoch et al. (2009a) and Prieto et al. (2013) that the *Candelariales* are phylogenetically separate from *Lecanoromycetes*, and that *Pycnoraceae* is a sister group to *Candelariaceae*. The new class *Candelariomycetes* was introduced. However, the close association of *Candelariaceae* with *Pycnoraceae* has only phylogenetic support but lacks clear morphological and chemical characteristics (Bendiksby & Timdal 2013).

Significance

Ecological and economic roles

Candelariales has a worldwide distribution (including both the Arctic and Antarctic), mainly in Mediterranean-type, nemoral or boreal climatic conditions in undisturbed habitats as well as urban or agricultural areas (Kubiak et al. 2003, Westberg 2005, Tarasova et al. 2013, Yakovchenko et al. 2012, 2013, 2016, Urbanavichene & Urbanavichus 2019, Gagarina et al. 2020, Chesnokov & Konoreva 2022, Clerc 2022, Haughland et al. 2022, Ohmura et al. 2022, Yakovchenk et al. 2022, Yakovchenko & Davydov 2024). The order includes both lichenized (mutualistic) and non-lichenized (parasymbiotic, parasitic) taxa occurring on natural and artificial substrates. Species growing on rocks are predominant, but epiphytes on bark, terricolous and lignicolous on non-burned substrata are frequent (e.g., Hakulinen 1954, Timdal 1984, Westberg 2005). Many species prefer exposed and nitrogen-enriched localities. The species often have highly specialized habitat requirements, which makes them useful indicators for communities, conservation status and microclimatic conditions (Temina & Kidron 2015, Olech & Słaby 2016, Muchnik et al. 2018, Choe et al. 2021, Paz-Bermúdez et al. 2021, Karmacharya et al. 2022, Stepanchikova et al. 2022). Representatives of the order were used as a model object in bioindication studies (Jahns 1982, Perlmutter 2009, Bosch-Roig et al. 2013, Biazrov & Pelgunova, 2015, Rola et al. 2016, Liu et al. 2017a, Jia et al. 2018). The chemical substances produced by *Candelariales* need further investigations for beneficial applications but some results on antibacterial, anticancer and biological activities have been already published in Dias & Urban (2009), El-Garawani et al. (2019) and Sahfiee & Sohrabi (2021).

The representatives of the order are reported as pioneer species (Favero-Longo et al. 2006). Several taxa have been reported on historic buildings and stone cultural heritage sites. They are considered to be biodeterioration agents because they cause undesirable changes by their vital activities on culturally valuable structures (Sohrabi 2006, Favero-Longo et al. 2009, 2022, Rajkowska et al. 2014, Joshi et al. 2015). Plant essential oils (EOs) and laser removal are effective against biodeterioration of stone cultural heritage by lichens including *Candelariales* (Sanz et al. 2017, Sanmartín et al. 2019, Favero-Longo et al. 2022).

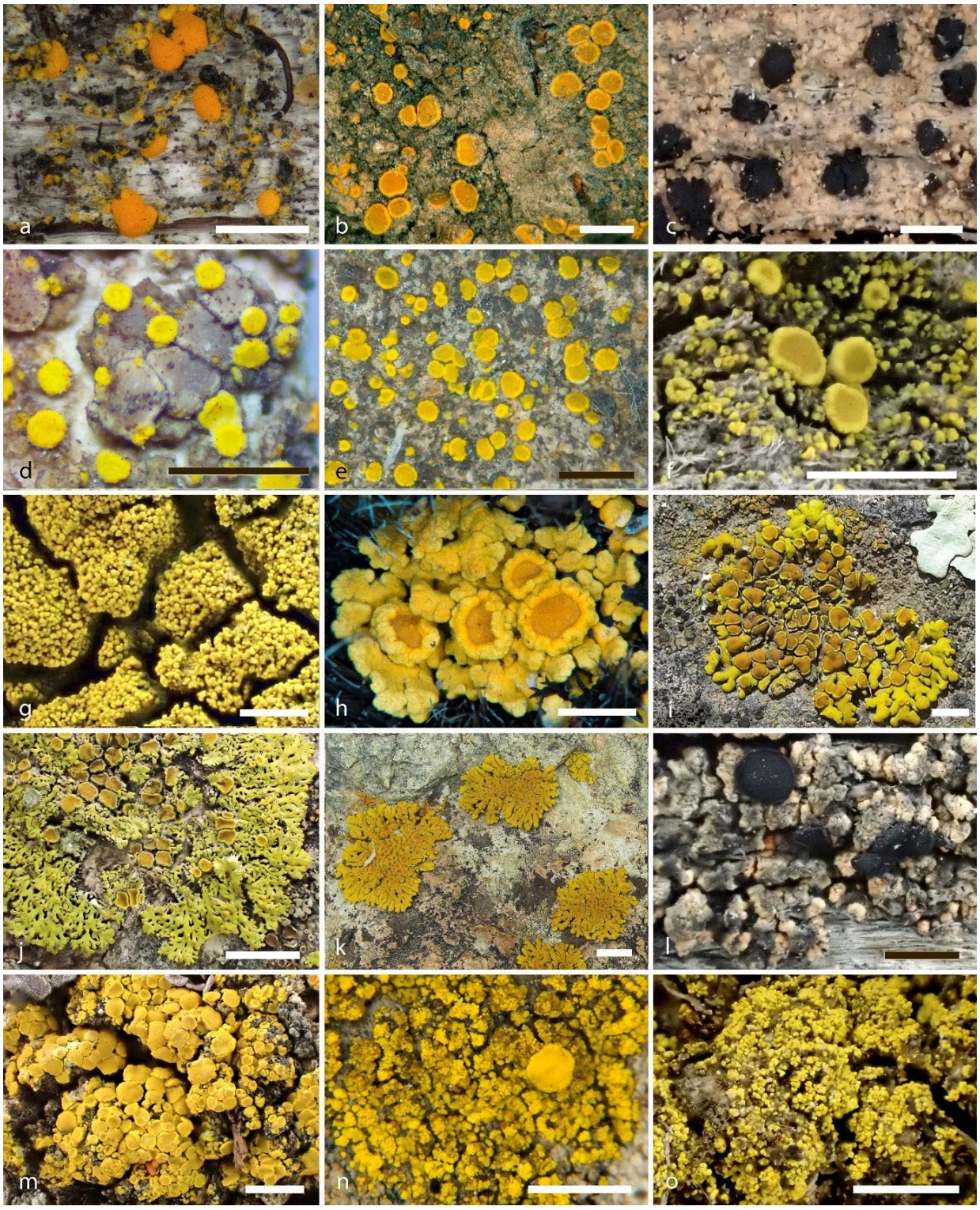


Figure 4 – Thallus morphology of *Candelariales.* a *Candelariella biatorina* (biatorine apothecia). b *Candelariella antennaria* (lecanorine apothecia). c *Pycnora xanthococca* (lecideine apothecia). d *Candelariella superdistans* (lichenicolous thallus). e *Candelariella aurella* (areolate thallus). f *Candelariella xanthostigma* (granular thallus). g *Candelariella coralliza* (pulvinate coralloid thallus). h *Candelariella placodizans* (squamulose thallus). i *Placomaronea candelarioides* (lobate thallus). j *Candelaria fibrosa* (foliose thallus). k *Placomaronea candelarioides* (umbilicate thallus). l *Pycnora xanthococca* (grey-colored thallus). m *Candelariella aggregata* (yellow-colored thallus). n *Candelariella xanthostigmoides* (sorediate thallus). o *Candelariella granuliformis* (blastidiate thallus). Scale bars: a–h, l–o = 1 mm, i = 2 mm, j, k = 2 mm. Photo: a–h, j, l-o: Davydov & Yakovchenko, i, k: J. Hollinger.

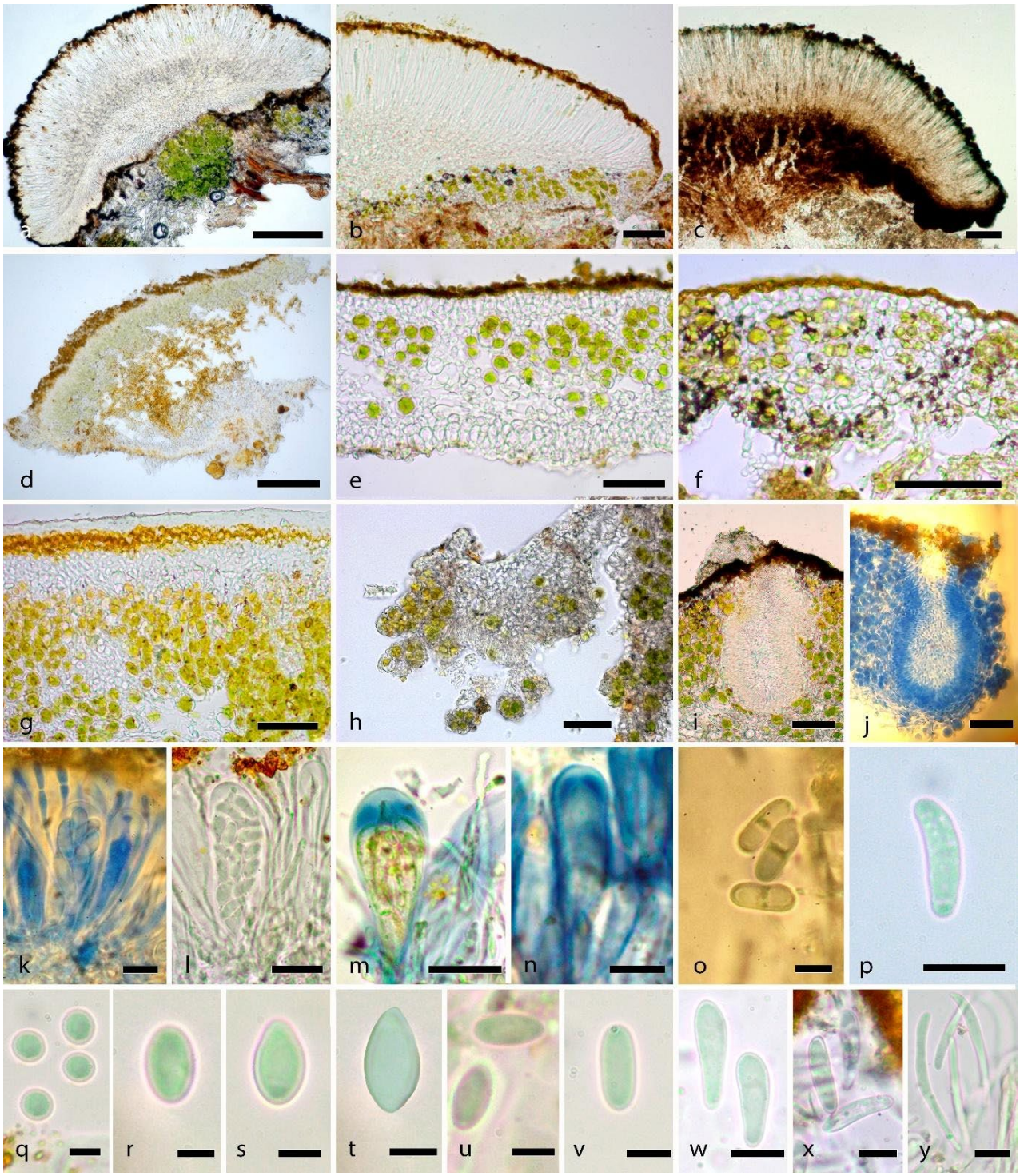


Figure 5 – Morphology of *Candelariales.* a *Candelariella biatorina* (biatorine apothecia). b *Candelariella faginea* (lecanorine apothecia). c *Pycnora xanthococca* (lecideine apothecia). d *Candelina* sp. (yellow medulla). e *Candelaria asiatica* (white medulla, presence of lower cortex). f *Candelara pacifica* (absence of lower cortex). g *Candelariella kansuensis* (presence of gelatinous epicortex). h *Protocandelariella blastidiata* (blastidia and conidiophores on the lower side). i *Candelariella rosulans* (pycnidia). j *Candelariella arctica* (pycnidia and conidia in LCB). k *Candelariella aurella* (8-spored asci and septate paraphyses with clavate tips in LCB). l *Candelariella xanthostigma* (polyspored asci). m *Candelariella kansuensis* (asci in KI). n *Pycnora xanthococca* (asci in KI). o *Candelariella vitellina* (1-septate straight ascospores). p *Candelariella rosulans* (simple curved ascospores). q *Candelariella boleana* (spherical ascospores). r *Candelariella faginea* (widely ellipsoid ascospores). s *Candelariella borealis* (ovoid ascospores). t *Candelariella citrina* (citriform ascospores). u *Pycnora xanthococca* (ellipsoid ascospores). v *Candelariella lutella*

(narrowly ellipsoid to almost oblong ascospores). w *Candelariella* sp. (oblong with narrowing at one end ascospores). x *Candelariella rosulans* (oblong ascospores). y *Candelariella spraguei* (acicular ascospores). Scale bars: a, d = 100 μm, b, c, e–j = 50 μm, k, n, w, x = 10 μm, l, m, y = 20 μm, o–v = 5 μm. Photo: a–h, j, l–o: Davydov & Yakovchenko, i, k: J. Hollinger.

Chemical diversity

Candelariales species are associated with a small range of chemical products (Mosbach 1967, Timdal 1984, Geyer 1985, Westberg 2005, Fernandes et al. 2015). Both families have different chemical composition. *Candelariaceae* has uniform chemistry within its representatives, which produce calicin, vulpinic acid, pulvinic acid and pulvinic dilactone (Geyer 1985). Exceptionally, rhizocarpic acid belonging to pulvinic acid derivates is produced by *Candelariella aggregata* (Westberg 2005). The pigments occur at least in apothecia as well as in yellow-colored thalli. Exceptionally, in medulla in *Candelina mexicana* (Westberg & Nash 2002, Westberg 2004, 2005).

Among their major substances, two chemosyndromes are distinguished which are associated with 8-spored (ChA, calicin dominate) and polyspored (ChB, equal amounts of all metabolites) species of *Candelariella* and can be useful for species taxonomy in *Candelariaceae* (Westberg 2005). The representatives of *Candelariales* often occur in open habits. Westberg (2005) noted the biological role of calicin and other cortical pigments in protecting photobionts from intense insolation. *Pycnoracea*e produce a single secondary metabolite, alectorialic acid (a type of benzyl ester) in the cortex, medulla and soralia of its representatives (Timdal 1984).

Other relevant data and future recommendations

The broad range of lifestyles, ascomatal structures and thallus differentiations as well as ecological and substrate preferences make *Candelariales* ideal model organisms for studying character evolution in lichenized fungi (Westberg et al. 2007). Most *Candelariales* species have substrate and habitat specificity, making them useful indicators for communities, conservation status, environmental and microclimatic conditions (Jahns 1982, Perlmutter 2009, Bosch-Roig et al. 2013, Biazrov & Pelgunova 2015, Temina & Kidron 2015, Olech & Słaby 2016, Rola et al. 2016, Liu et al. 2017a, Jia et al. 2018). Despite their ecological roles and production of secondary metabolites, *Candelariales* taxa are often threated by anthropogenic activities, climate change and elevated level of heavy metals (e.g., Bosch-Roig et al. 2013, Biazrov & Pelgunova 2015, Rola et al. 2016, Liu et al. 2017a). Some representatives of *Candelariales* are included or recommended for inclusion in regional Red Lists (Westberg & Arup 2010, Woods & Coppins 2012, Nascimbene et al. 2013, Tripp & Lendemer 2015, Ravera et al. 2019, Randlane et al. 2021).

The representatives of *Candelariales* are used as natural sources of dyes and biological active substances. Extracts of *Candelariella rhodax* showed significant sensitivity on some Gram-positive bacteria (Sahfiee & Sohrabi 2021). Eyupoglu et al. (2022) investigated the dyeing properties of mohair fiber dyed with natural dyes that are obtained from *Candelariella reflexa*. Dias & Urban (2009) studied biological activity of pulvinic acid derivatives from *Candelaria concolor*. El-Garawani et al. (2019) suggested a moderate to strong apoptotic anticancer potential of *Candelariella vitellina*. Despite their relevance for the preservation of biodiversity, and research efforts over the last twenty years, the taxonomy of *Candelariales* is insufficiently known at the species and genus levels. The generic and species delineation of several taxa or group of species, e.g., sorediate species, *Candelariella aurella*-group remains uncertain (Westberg et al. 2007, Lendemer & Westberg 2010, Westberg & Arup 2011).

Species which lack molecular data also need further studies for their classification. Some species have been overlooked in the field and many *Candelariales* taxa are yet to be described (Westberg et al. 2009). In Europe and North America, the type species *Candelaria concolor* had been confused with *Candelaria pacifica* (Westberg & Arup 2011). Westberg & Arup (2010, 2011) studied both species from several fresh and herbarium collections across their whole known distribution and found that they are two distinct species based on morphology, phylogeny and chemical diversity. *Candelaria pacifica* is widely distributed in Nordic countries whereas *Candelaria concolor* is a rare

and red listed species in Sweden (Westberg & Arup 2010). Thus, detailed investigation on *Candelariales* species is required for future conservation as well as better taxonomic and generic resolution.

***Coniocybomycetes* M. Prieto & Wedin, Cladistics 39(3): 305 (2013)**
***Coniocybales* M. Prieto & Wedin, Cladistics 39(3): 305 (2013)**

Subphylum : *Pezizomycotina*
Class : *Coniocybomycetes*

Introduction

Coniocybales is a recently described small order in *Ascomycota* which comprises ca. 30 species assigned to two genera (Prieto et al. 2013, Wijayawardene et al. 2020). Members of *Coniocybales* were placed for a long time in the *Caliciales sensu lato* (calicioid lichens and fungi) by having a mazaedium and passive spore dispersal. The mazaedium consists of a spore mass formed by the hymenium released from the prototunicate asci, which result is a passive dispersal of the spores. However, it has been shown that this group is polyphyletic and consists of several unrelated lineages, belonging to *Arthoniomycetes*, *Eurotiomycetes* or *Lecanoromycetes* (Tibell 1984, Gargas et al. 1995, Wedin & Tibell 1997, Wedin et al. 2000a, b, Lumbsch et al. 2009a, Prieto et al. 2013). Molecular studies have shown that *Coniocybales* is an independent lineage in *Ascomycota* (*Coniocybomycetes*) apparently closely related to the *Lichinomycetes* (Prieto et al. 2013).

The order includes *Chaenotheca* and *Sclerophora* (Middelborg & Mattsson 1987). Both genera are crustose lichens with stalked apothecia (Tibell 2001) and are characterized by aseptate, basically spherical, pale brown to brown spores. Phylogenetic studies supported the monophyly of the group including *Chaenotheca* and *Sclerophora* (Prieto et al. 2013) and, based on the similarities in general morphology and secondary chemistry between both genera (Middelborg & Mattsson 1987) they were reduced to one family, *Coniocybaceae*. Differences between *Sclerophora* and *Chaenotheca* include ascocarp morphology, spore ornamentation and ontogeny (Tibell 1984, Middelborg & Mattsson 1987). Regarding generic delimitation, fewer studies have been carried and the limited taxon sampling in Prieto et al. (2013) did not permit to test this question. Within the genus *Chaenotheca* many taxonomic problems remain, and additional species may be found in underexplored areas (Tibell et al. 2019). Members of *Coniocybales* are lichenized, distributed worldwide and epiphytic, mostly occurring on bark and wood. Some species are terricolous or fungicolous growing on polypore fruit bodies (Tibell 1999, Suija et al. 2016). Most species show preferences for high humidity and low light intensity, usually in cold areas, but they are also distributed in tropical areas.

History

Calicioid fungi were represented by a heterogeneous assemblage of taxa sharing the presence of a mazaedium (Prieto et al. 2013). Some of these fungi were treated as an order (*Caliciales sensu lato*) of the *Ascomycota* but many are now known to be nested within the *Arthoniomycetes*, *Eurotiomycetes* and *Lecanoromycetes* (Tibell 1984, 1996, Wedin & Tibell 1997, Tibell & Wedin 2000, Wedin et al. 2000a, 2000b, Lumbsch et al. 2004a, 2009a, Tehler et al. 2009) as well in the recently described Class *Coniocybomycetes* (Prieto et al. 2013).

The first species to be validly described in the *Caliciales sensu lato* (also from *Coniocybomycetes*) was *Chaenotheca furfuracea* (as *Mucor furfuraceus*) by Linnaeus in 1753. Later, Acharius (1816a) described *Coniocybe*, placed in the 'Plantae Calicioidea' together with *Calicium* and *Cyphelium*. Chevallier (1826) described *Sclerophora* and Fries (1861) gave a description of *Chaenotheca*. The family *Coniocybaceae* (as *'Coniocybeae'*) was introduced by Reichenbach (1837). Tibell (1984) placed the species belonging to *Coniocybe* in *Chaenotheca* and *Sclerophora*, and in the new genus *Cybebe*. *Sclerophora* was treated as a family of its own, the *Sclerophoraceae* and considered different to *Coniocybaceae* (Tibell 1984). Middelborg & Mattson (1987) did not find enough support for placing *Sclerophora* in the monotypic family *Sclerophoraceae* and therefore placed *Sclerophora* with *Chaenotheca* in *Coniocybaceae*. Additionally, the genus *Cybebe* was reduced to synonymy with *Chaenotheca*. Suija et al. (2023) recently added a new genus *Chaenotricha*

and consequently, Hyde et al. (2024b) accepted three genera within the single family *Coniocybaceae* and order *Coniocybales.*

General description

Lichen-forming ascomycetes with *Dictyochloropsis*, *Stichococcus*, *Trentepohlia*, or trebouxioid photobionts (Tibell 1999). As calicioid lichens or 'pin lichens' they are characterized by having stalked ascomata. They also have a mazaedium (i.e. an accumulation of spores in the ascomatal surface released from the early disintegrating asci). The color of the mazaedium depends on the color of the spores. The identified secondary substances detected are vulpinic acid, pulvinic acid, pulvinic dilactone, atranorin, baeomycesic acid and anthraquinoid pigments (Middelborg & Mattson 1987).

Sexual morph: *Thallus* crustose, superficial (farinaceous, granular, verrucose or minutely squamulose) or immersed in the substrate. *Thallus* color grey to greenish-grey, yellow or brownish. Stalked apothecia with a brown to pale mazaedium. *Capitulum* spherical to obconical. Stalk formed by periclinally arranged hyphae. *Excipulum* poorly to well developed, formed as a continuation of the stalk tissue. *Hypothecium* medium brown, with convex to flat upper surface. *Asci* cylindrical, ellipsoidal, or irregular, dissolving at an early stage, formed from ascogenous hyphae with or without croziers, either singly or in chains. *Spores* simple, spherical, or ellipsoidal, or rarely cylindrical with 1–5 septa, pale to brown, smooth or with a verrucose or cracked ornamentation (Tibell 1984, 1999, Prieto et al. 2013). Asexual morph: *Coelomycetous* anamorphs have been obtained from axenic cultures of some *Chaenotheca* species (Tibell, 1993, 1997) and are simple, asterophoma-like. Simple hyphomycetous anamorphs of several *Chaenotheca* species have also been observed in the field and obtained in axenic cultures (adapted from Honegger, 1985, Tibell, 1993, 1997) (Fig. 6).

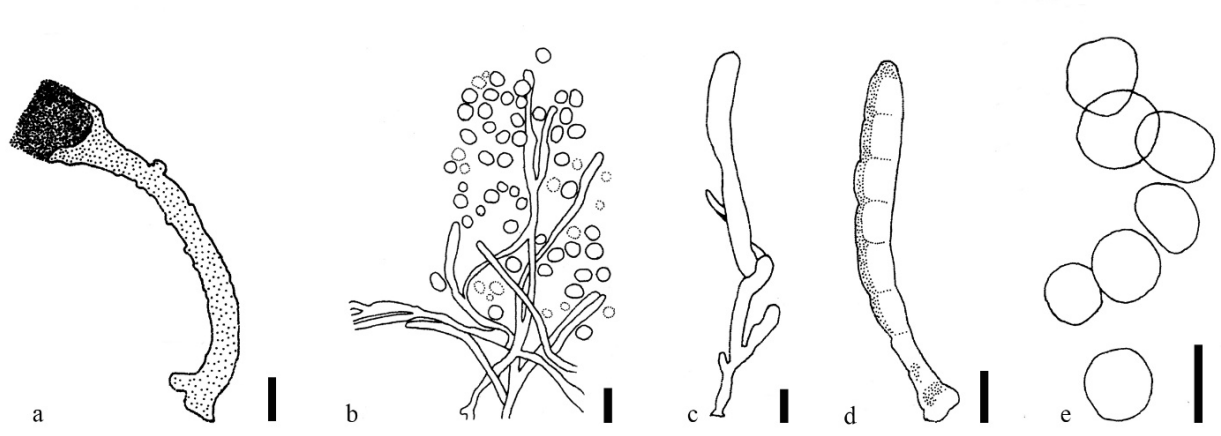


Figure 6 – Sexual morph of *Coniocybales*. a Appearance of Ascomata (*Coniocybe furfuracea*). b Developing asci, paraphyses and ascospores. c, d Ascus. e Ascospores (b–e *Chaenotricha cilians*) (drawn from Suija et al. 2023, Temu et al. 2024). Scale bars: a = 1 mm, b = 10 µm, c–e = 5 µm.

Families included in *Coniocybales*

Coniocybaceae Reichenb.

Evolution

Calicioid lichens and fungi have been shown to be a polyphyletic group belonging to different classes in *Ascomycota* as *Arthoniomycetes*, *Coniocybomycetes*, *Eurotiomycetes* and *Lecanoromycetes* based on phylogenetic analyses (Tibell 1984, Gargas et al. 1995, Wedin & Tibell 1997, Wedin et al. 2000a, b, Lumbsch et al. 2009a, Prieto et al. 2013). Based on ancestral state reconstruction analysis several independent gains of the mazaedium have been shown in *Ascomycota* revealing that this character is highly homoplastic (Prieto et al. 2013, 2021). Prieto et al. (2013)

corroborates the hypothesis that passive spore dispersal resulting from prototunicate asci and mazaedia have been acquired multiple times from ancestors with an apical dehiscence apparatus and active spore dispersal (Berbee & Taylor 1992c, Wedin & Tibell 1997, Wedin et al. 2000 a, b, Grube 2001, Schoch et al. 2009a).

Justification of order and problems

Phylogenetic studies showed *Coniocybales* as an independent lineage in *Ascomycota*, closely related to *Lichinomycetes* (Prieto et al. 2013). This result is supported by genomic data (Díaz-Escandón et al. 2022). However, in this latter study, it is proposed to consider several classes of *Ascomycota* (including *Coniocybomycetes*) as a more broadly circumscribed *Lichinomycetes* which in our opinion is not justified as it includes a wide variety of morphologies, ecologies and trophic modes and it is only justified by the presence of small genomes with reduced metabolic arsenals. Although both genera (*Chaenotheca* and *Sclerophora*) were shown to be monophyletic in Prieto et al. (2013), the taxon sampling was very limited and further studies should be carried out. In *Chaenotheca*, a high variability and some problems in species delimitation have been reported (Tibell 1999, Rikkinen 2003a, Suija et al. 2016).

Significance

Ecological and economic roles

Although Calicioid fungi are not a natural group, they have been treated together by ecologists, because of their ecology, and their importance for bioindication and conservation (Puntillo & Puntillo 2009). Some species of *Coniocybales* occur in habitats with long forest continuity and high species diversity, often associated with mature and old-growth trees and forests (Tibell 1992, Selva 1996). Some species are sensitive to air pollution and fire (Puntillo & Puntillo 2009). Thus, they have been used to assess environmental continuity (Rose 1976) and been reported as bioindicators, key species or indicator species (Tibell 1992, Kruys & Jonsson 1997, Puntillo & Puntillo 2009) in forests and other habitats with high conservation values due to specific ecological requirements. Additionally, several species have been included in Red Lists in both Hemispheres (e.g., Thor 1998, Martínez et al. 2003, Liška et al. 2008, de Lange et al. 2012, Lõhmus et al. 2019). Five *Chaenotheca* fossils have been found enclosed in Bitterfeld and Baltic amber (Rikkinen et al. 2018), and one of them used as a minimum age constraint for *Chaenotheca* (*Coniocybales*) in dating studies (Prieto & Wedin 2013, Beimforde et al. 2014).

Chemical diversity

In *Chaenotheca,* vulpinic and pulvinic acids and pulvinic dilactone occur as a pruina in the ascomata and rarely in the thallus. Also, b-orcinol depsides atranorin, baeomycesic and squamatic acid occur in the thallus and rarely pseudoplacodiolic acid (Tibell 1984, 1999). In *Sclerophora*, anthraquinoid pigments have been identified in the apothecia (Middelborg & Mattson 1987).

Other relevant data and future recommendations

Many species of *Chaenotheca* are known to be morphologically plastic and several species complexes occur which may contain multiple morphologically cryptic species (Tibell 1999, Tibell & Beck 2002, Tibell et al. 2019). Within these, those fungicolous species growing on polypore fruit bodies (Tibell 1999) are remarkable, particularly on the annual wood-rotting species *Trichaptum abietinum* (Dicks.) Ryvarden (*Polyporaceae*). Four *Chaenotheca* species have been reported on *Trichaptum abietinum*: *C. brunneola* (Fries 1865, Tibell 1999, Hawksworth et al. 2014), *C. gracillima* (Spribille et al. 2010), *C. trichialis* (Selva 2014) and *C. balsamconensis* (Allen & McMullin 2015). Fries (1865) noticed a variant of *Chaenotheca brunneola* (called variety *cilians)* growing on *Trichaptum*. Suija et al. (2016) studied the variability of several species growing on polypores and found that those *Chaenotheca* species externally similar to *C. brunneola* but growing on *Trichaptum* basidiomata formed a separate evolutionary lineage representing a case of convergent evolution and cryptic speciation. Further studies are being carried to understand these relationships and the variability of these species (Prieto & Wedin in prep).

Tibell (2001) studied the photobionts associated with *Chaenotheca* showing that the studied species consistently harbored only one photobiont. Also, a partial congruence between photobiont association and cladogenesis in the genus was found. This was proposed for infrageneric classification as species with closely related photobionts were believed to be closely related. Based on these results, Tibell (2001) excluded the possibility of an opportunistic photobiont association based on the availability of photobionts at a particular time and location. However, further studies should be carried out widening the taxon sampling (more individuals and more sites) to test the evolutionary relationships in relation with photobiont and the intraspecific variability.

***Dothideomycetes* O.E. Erikss. & Winka, Myconet 1(1): 5 (1997)**
***Abrothallales* Pérez-Ort. & Suija, Fungal Diversity 64(1): 302 (2013) [2014]**

= *Lichenoconiales* Diederich, Lawrey & K.D. Hyde
Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Abrothallales was introduced by Pérez-Ortega et al. (2014) to accommodate a single family *Abrothallaceae* with a monotypic genus *Abrothallus* based on six genes (SSU, LSU, mtSSU, RPB1, RPB2 and TEF1-α) phylogenetic analyses along with morphology. The order formed a monophyletic clade and sister to *Jahnulales* within the subclass *Pleosporomycetidae* (Pérez-Ortega et al. 2014).

History

Abrothallales was originally introduced to accommodate a single genus *Abrothallus*. *Abrothallus* was introduced for a single species *A. bertianus* (De Notaris 1845) and was identified as a lichenized fungus and was placed in the tribe *Coccocarpiae* of the order *Gymnocarpi* (Montagne 1851) or suborder *Biatorinae* of *Lecideaceae* (Körber 1855, Lindsay 1857). Shortly, its lichenicolous nature was established (De Notaris 1846, Tulasne 1852, Montagne 1856). However, its taxonomic placement changed over time including the order *Bulgariacei* (= *Bulgariaceae*, *Helotiales*) (Montagne 1856) or suborder *Phacidiae* (= *Phacidiaceae*, *Helotiales*) (Saccardo 1889b), *Patellariaceae* (then *Dermatales*) (Rehm 1896), and *Arthoniales* (tribe *Arthoniae*) (Jatta (1911). Notably, Fink (1935), synonymized *Abrothallus* with *Buelliella* based on having dark-colored ascospores. Later, the genus was treated as *Ascomycetes incertae sedis* (Lumbsch & Huhndorf 2010).

The asexual morph was described under the name *Vouauxiomyces* (Hawksworth & Dyko 1979). Pérez-Ortega et al. (2011b) established the connection between the sexual and asexual morphs and adopted the name *Abrothallus* over *Vouauxiomyces* according to dual nomenclature. Pérez-Ortega et al. (2014) provided a detailed study of the genus based on molecular data by establishing its own order *Abrothallales*. Liu et al. (2017b) found the sister clade relationship between *Abrothallales* and *Lichenoconiales*. A lichenicolous order *Lichenoconiales* was introduced to accommodate *Lichenoconium* and the order formed a distinct clade within *Dothideomycetes*. Diederich et al. (2018) synonymized *Lichenoconiales* with *Abrothallales* and tentatively *Lichenoconiaceae* with *Abrothallaceae*. Hongsanan et al. (2020a) formally synonymized *Lichenoconiaceae* over *Abrothallaceae* since *Lichenoconiaceae* is the older name and this is followed in Wijayawardene et al. (2022a) and Hyde et al. (2024b).

General description

The sexual members of *Abrothallus* are characterized by apothecioid ascomata, often covered with green or golden pruina, bitunicate asci with four to eight, 2–4-celled brown asymmetric ascospores with clear ornamentation, ramified-anastomosed interascal filaments and epiphymenial layer with granulose pigments, which commonly dissolve in potassium hydroxide. The presence of apothecial disc with pruina is also used to identify the species in the field. The asexual members of *Abrothallus* and *Lichenoconium* are characterized by pycnidial anamorph (Suija et al. 2015a, Pérez-

Ortega et al. 2014) but *Lichenoconium* lack sexual morph (Hyde et al. 2013). Both sexual and asexual morphs are associated with some species while others are mainly reported as asexual morphs (Tulasne 1852, Suija et al. 2015a).

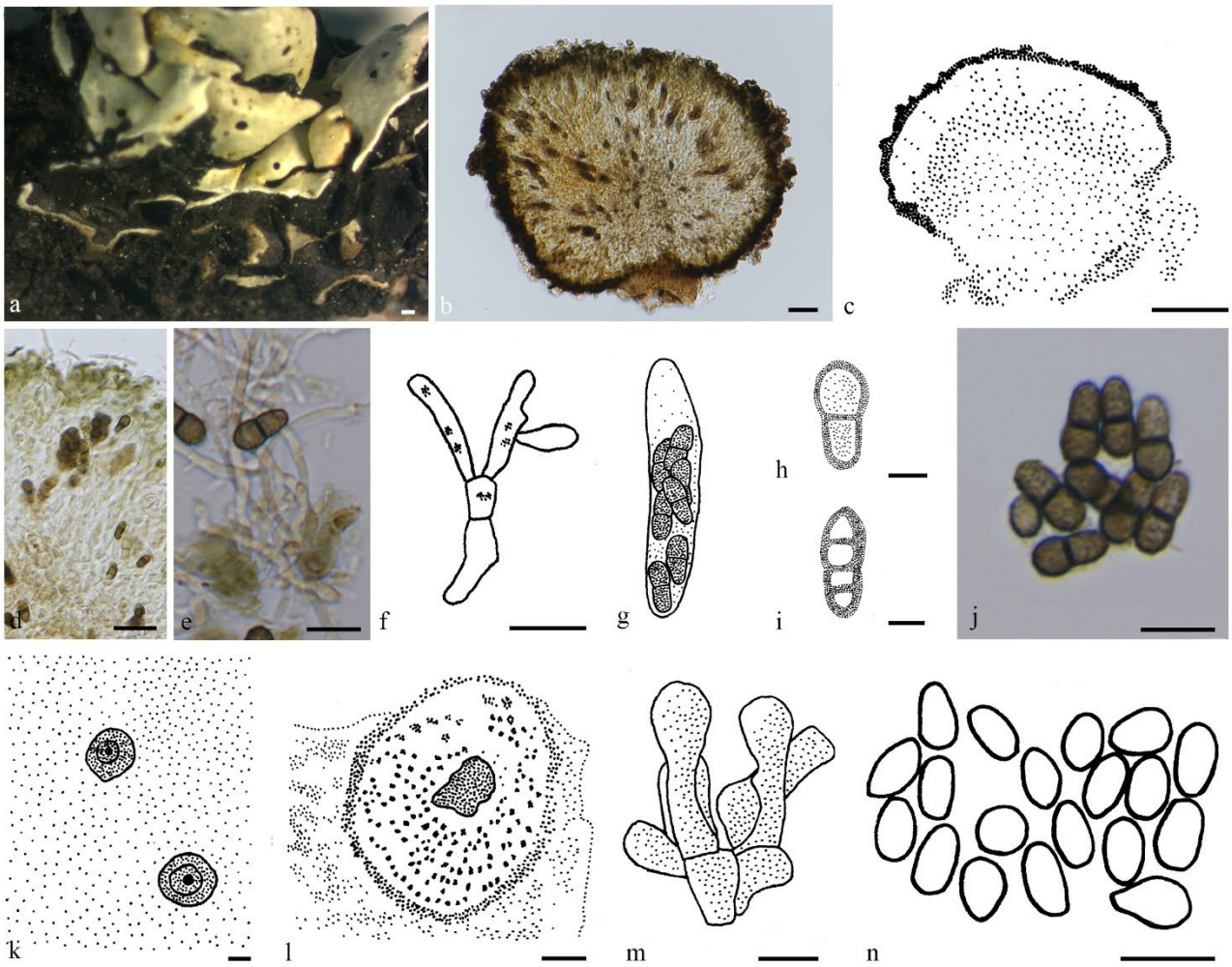


Figure 7 – Sexual and asexual morph of *Abrothallales.* a *Abrothallus* sp. on host lichen. b Cross section of *Abrothallus* sp. c Cross-section of the apothecium of *A. acetabuli*. d Ascus and paraphyses of *Abrothallus* sp. e Paraphyses of *Abrothallus* sp. f Paraphyses of *A. parmeliarum*. g Ascus of *Abrothallus* sp. h Ascospore with one septum in *A. bertianus*. I Ascospore with three septa in *A. suecicus*. j Ascospores of *Abrothallus* sp. k Surface view of pycnidia of *A. bertianus* on the thallus of *Melanelixia fuliginosa*. l Cross-section of a pycnidium of *A. bertianus* observed by scanning electron microscopy. m Cross-section of a pycnidium of *A. bertianus* observed by scanning electron microscopy. n Conidiospores of *A. bertianus* (drawn from Pérez-Ortega et al. 2014). Scale bars: a, b = 20 µm, c, k = 100 µm, d–g, j = 10 µm, m, h, I, n = 5 µm.

Sexual morph: *Ascomata* apothecioid, solitary or in groups, superficial, rounded, convex to almost globose, rarely fattened, black or dark brown, some species with greenish pruina, at least in young stages. *Proper exciple* thin, usually disappearing when mature, composed of radiating hyphae. *Hymenium* hyaline or greenish in upper part, covered with light to dark brown or reddish granules dissolving in KOH. *Hypothecium* light to dark brown, composed of isodiametric cells (*textura angularis*-type). *Hamathecium* comprising septate, anastomosed and irregularly dichotomously branching interascal filaments. *Asci* 4–8-spored, thick-walled, bitunicate, functionally fissitunicate, ovate to clavate, apedicellate, with a distinct ocular chamber, I-. *Ascospores* irregularly or 2-seriately arranged within the ascus, ellipsoid to broadly ellipsoid, light to dark brown, 1–3-septate, asymmetric and soleiform, splitting into part-spores within the ascus in some species, wall fnely ornamented to

verrucose. Asexual morph: *Coelomycetous*, pycnidium immersed, semi-immersed or almost superficial, black, with a small ostiole. *Pycnidial wall* thick-walled, comprises isodiametric cells (*textura angularis*-type). *Conidiophores* reduced. *Conidiogenous cells* percurrently proliferating, ampulliform to lageniform, lining the cavity of the pycnidium, hyaline, smooth-walled. *Conidia* holoblastic, clavate to obpyriform or almost roundish, hyaline to dark brown, smooth to slightly echinulate, usually embedded in mucilage (adapted from Hongsanan et al. 2020a, Pem et al. 2024) (Fig. 7).

Families included in *Abrothallales*

Lichenoconiaceae Diederich & Lawrey (= *Abrothallaceae* Pérez-Ort. & Suija)

Evolution

The divergence time for *Abrothallales* is estimated as 204 million years ago (MYA) (stem age, Hongsanan et al. 2020b). Broad taxon sampling can help to understand the evolutionary processes such as host switching, co-evolutionary processes, and geographical barriers (Suija et al. 2015a).

Justification of order and problems

The number of species remains uncertain due to numerous single collections reported on unusual hosts, which may potentially represent new species. In addition, there are only a few collections available from certain regions, further complicating the species diversity (Hongsanan et al. 2018, Suija et al. 2018).

Significance

Ecological and economic roles

Members of *Abrothallus* are reported on all continents except Antarctica and inhabit a wide variety of foliose and fruticose lichen families such as *Cladoniaceae*, *Lobariaceae*, *Nephromataceae*, *Pannariaceae Parmeliaceae*, *Ramalinaceae* and *Stereocaulaceae* (Pérez-Ortega et al. 2014). All members are lichenicolous and occur as parasitic or parasymbiotic on host thalli. Some *Lichenoconium* species are host-specific (Hyde et al. 2013) while others occur in disparate genera worldwide (Lawrey et al. 2011).

Chemical diversity

No relevant studies are available for the chemistry of *Abrothallales* species.

***Acrospermales* Minter, Peredo & A.T. Watson, Boletín de la Sociedad Argentina de Botánica 42(1-2): 112 (2007)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Acrospermales was introduced by Minter (2007) to accommodate the previously known family *Acrospermaceae* which was introduced by Fuckel (1870). Previously, *Acrospermaceae* members were listed under different orders by different authors (Hongsanan et al. 2020a). Currently, this order is listed under *Dothideomycetes* and comprises only one family, *Acrospermaceae* with six genera (Wijayawardene et al. 2022a, Hyde et al. 2024b). *Acrospermaceae* members are reported as saprobic, epiphytic, or symbiotic on herbaceous plants (Hudson et al. 2019, Hongsanan et al. 2020a, Pem et al. 2024). The taxa are mainly characterized by having fattened, club-shaped to conoid, with a short stipe and ostiolate ascomata that are erect and elongate in stromata with smooth or sometimes rough surfaces (Hongsanan et al. 2020a, Pem et al. 2024). The hamathecium of these members comprises narrow, long, hyaline, filiform pseudoparaphyses. Asci of *Acrospermaceae* are typically 8-spored, bitunicate, long, narrowly cylindrical, pedicellate, and apically rounded with an ocular chamber. Ascospores are fasciculate, filiform, hyaline, multi-septate, almost as long as the asci, smooth-walled,

and typically intertwined in a fascicle within the ascus (Hongsanan et al. 2020a, Pem et al. 2024). Asexual morphs of *Acrospermaceae* are hyphomycetous with micronematous, pale brown, septate, branched, or unbranched conidiophores (Hongsanan et al. 2020a). Conidiogenous cells are holoblastic, sympodial with denticles, pale brown, and smooth-walled (Hongsanan et al. 2020a). Conidia are cylindrical, long ellipsoid, pale yellow, 1–3-septate, and smooth-walled (Hongsanan et al. 2020a).

Acrospermaceae was listed under *Hysteriales*, *Dothideales*, *Ostropales*, *Clavicipitales*, *Xylariales*, and *Pyrenulales* by different authors (Minter et al. 2007). The close relationship of *Acrospermaceae* with *Coryneliales*, *Pseudosphaeriales*, and *Clavicipitales* was also discussed in the history (Minter et al. 2007). However, *Pyrenulales*, *Dothideales*, and *Hysteriales* differ from the *Acrospermaceae* in having two functional wall layers in their asci (Minter et al. 2007). Unlike *Acrospermaceae*, *Hysteriales* members typically open by an elongated apical split and are black and very brittle. *Dothideales* differ from *Acrospermaceae* by having longitudinally asymmetrical ascospores constricted at the primary septum (Hawksworth et al. 1995). *Acrospermaceae* is excluded from *Pyrenulales* because of their non-lichenized occurrence and their ascomata are often immersed and rather flattened in the horizontal plane (Hawksworth et al. 1995). *Coryneliales* also have two functional wall layers, of which the outer splits at a very early stage in development which differs from *Acrospermaceae* (Johnston & Minter 1989). *Acrospermaceae* is largely superficial and perithecial compared to *Ostropales* members (Sherwood 1977b). *Clavicipitales* (= *Hypocreales*) differ from *Acrospermaceae* by having asci with very characteristic thickened apices. *Xylariales* have free-ended paraphyses unlike those of the *Acrospermaceae* (Eriksson & Hawksworth 1991a).

History

Fuckel (1870) introduced *Acrospermaceae* with *Acrospermum* as the type species. Later, Rehm (1887) placed this family under *Hysteriales* based on having compressed fructifications and elliptical ostioles. Ellis & Everheart (1892) transferred this family from *Hysteriales* to *Hypocreales* due to the texture and coloration of most of the species. Again, Lindau (1896) incorporated *Acrospermaceae* in *Hysteriales*. Höhnel (1917c) considered *Acrospermum* as pyrenomycetous and placed it in *Sordariaceae* of *Sphaeriales*. Riddle (1920) suggested placing this family under *Hypocreales* based on internal structure studies. Arnaud & Les Asterinees (1930) considered these members as Caliciees (a discomycete group). Clements & Shear (1931) considered *Acrospermaceae* as a member of *Hypocreales*. Notably, Brandriff (1936) considered that it was connected to the *Coryneliales* or *Pseudosphaeriales*. In Luttrell's (1955) classification, *Acrospermaceae* was placed in *Coryneliales* with *Coryneliaceae* due to their morphological similarities. Sherwood (1977b) speculated the relationship with *Clavicipitales*. Eriksson (1982) doubtfully placed this family in *Pyrenulales*. Barr (1990b) stated its ordinal position in more detail and placed it in the *Xylariales*.

In the 9th edition of Ainsworth & Bisby's Dictionary of the Fungi (Kirk et al. 2001), and in the preceding edition, *Acrospermaceae* was listed as of uncertain affinity. In the 1st and 2nd editions, *Acrospermaceae* was listed in *Hysteriales* or *Dothideales* and in the 3rd to 5th editions it was listed in the *Dothideales* (Minter et al. 2007). In the 6th edition, the family was placed in *Ostropales* and the 7th, it was placed tentatively in the *Clavicipitales* (Minter et al. 2007). In all the editions of "Outline of the Ascomycetes" in Systema Ascomycetum, the *Acrospermaceae* is listed as a family of uncertain affinity (Minter et al. 2007). Based on the morphological comparison of *Acrospermaceae* members with the above orders, Minter et al. (2007) introduced a new order namely *Acrospermales* to accommodate *Acrospermaceae*.

General description

Ascomata are superficial or immersed in stromata with club-shaped to conoid, with a short stipe and ostiolate. Hamathecium consists of long, hyaline, filiform pseudoparaphyses. Asci of these members are bitunicate, very long, and apically rounded with an ocular chamber.

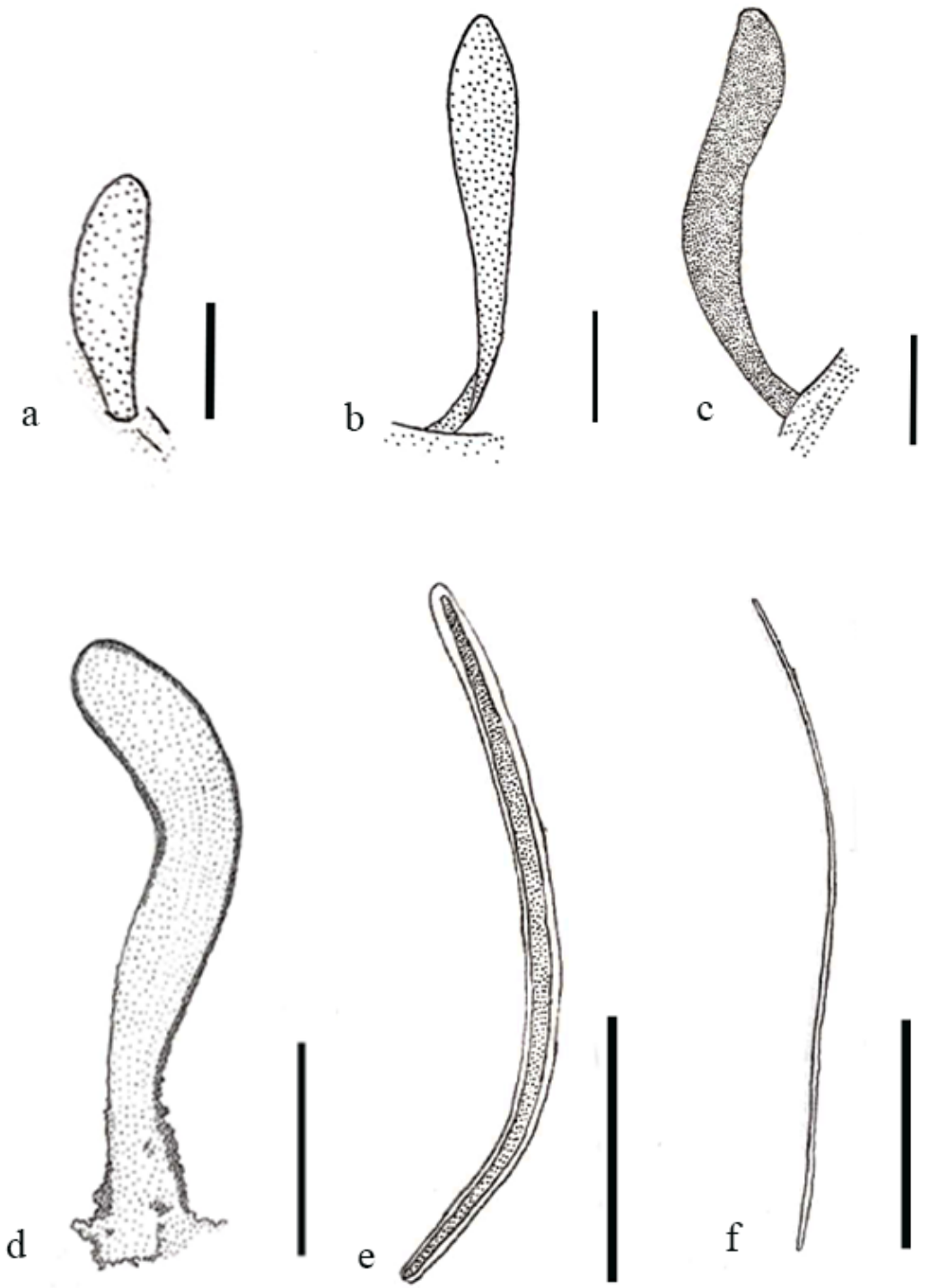


Figure 8 – Sexual morph characters of *Acrospermales*. a Ascomata of *Acrospermum urticae* on host surface. b, c Ascomata of *Acrospermum chilense* on host surface. d vertical section of ascoma of *Acrospermum urticae*. e Ascus of *Acrospermum urticae*. f Ascospore of *Acrospermum urticae* (drawn from Minter et al. 2007, Hongsanan et al. 2020a). Scale bars: a–d = 500 μm, e = 100 μm, f = 50 μm.

Ascospores are multi-septate, almost as long as the asci, smooth-walled, and typically intertwined in a fascicle within the ascus (Minter et al. 2007, Hongsanan et al. 2020a). Asexual morphs were reported as hyphomycetous with micronematous, septate, branched, or unbranched conidiophores. Conidiogenous cells are holoblastic, sympodial with denticles and conidia are cylindrical, long ellipsoid, septate with smooth-walled (Hongsanan et al. 2020a).

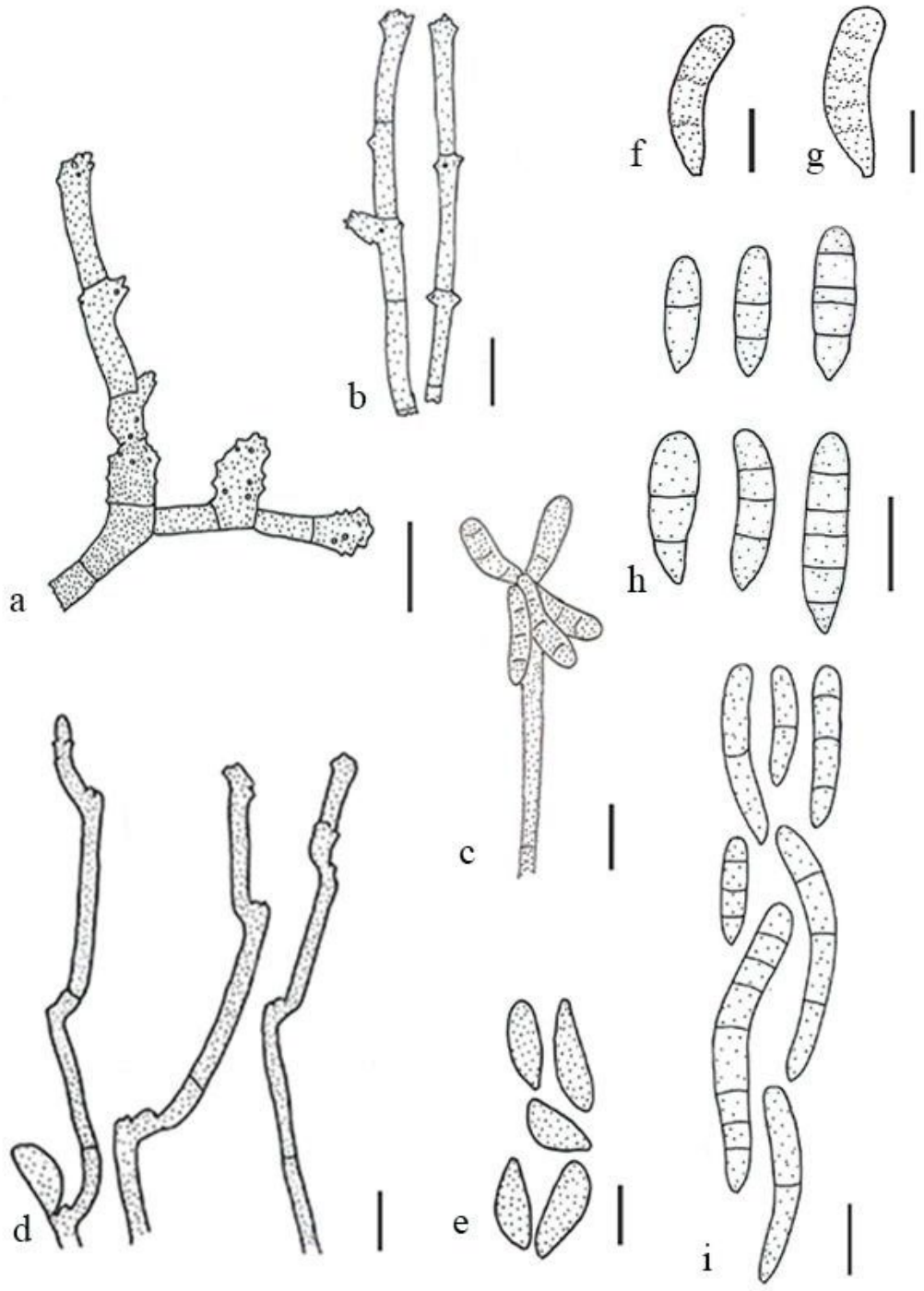


Figure 9 – Asexual morph characters of *Acrospermales*. a–d Conidiophore morphology of *Acrospermales* (a, b *Gonatophragmium mori,* c *Pseudoacrospermum goniomae,* d *Pseudovirgaria hyperparasitica*). e–i Conidia morphology of *Acrospermales* (e *Pseudovirgaria hyperparasitica*, f, g *Pseudoacrospermum goniomae,* h, i *Gonatophragmium mori*) (redrawn from Deighton 1969, Arzanlou et al. 2007, drawn from Crous et al. 2021c). Scale bars: a–i = 10 µm.

Sexual morph: *Ascomata* solitary or gregarious, superficial or immersed in stromata, erect, elongate, dark brown to black, fattened, smooth or rough-surfaced, club-shaped to conoid, with a short stipe, swelling when moist, ostiolate. *Peridium* consists of 2-3 layers, the outer layer is composed of dark brown cells of *textura angularis*, the central layer is composed of hyaline, sometimes pale brown tissue of elongated cells intertwined, and the inner layer is composed of dense tissue of small, light brown cells. *Hamathecium* consists of narrow, long, hyaline, filiform pseudoparaphyses. *Asci* bitunicate, long, narrowly cylindrical, pedicellate, generally 8-spored,

apically rounded with an ocular chamber. *Ascospores* fasciculate, filiform, hyaline, multi-septate, long as the asci, smooth-walled, not fragmenting, and typically intertwined in a fascicle within the ascus. Asexual morph: *Hyphomycetous*. *Conidiophores* micronematous, pale brown, septate, branched, or unbranched. *Conidiogenous cells* are holoblastic, sympodial with denticles, pale brown, and smooth-walled. *Conidia* cylindrical, long ellipsoid, pale yellow, septate or aseptate, smooth and thin-walled (adapted from Hongsanan et al. 2020a) (Figs. 8, 9).

Families included in *Acrospermales*

Acrospermaceae Fuckel

Evolution and fossil records

Several estimations of divergence periods in fungi have been provided using fossil evidence from ascomycetes (Mapook et al. 2016b, Pérez-Ortega et al. 2016). The Permian-Triassic extinction event (252 MYA) has been related to ancient fungal spore records, and several marine and terrestrial fungi are thought to have evolved during this time (Visscher et al. 1996, Shen et al. 2011). Based on the results of the molecular clock and divergence time estimates of Mapook et al. (2016b), the divergence estimate is at 319 MYA (247−400), in the Carboniferous for *Dothideomycetes* and *Lecanomycetes*. The estimated crown dates of *Acrospermales* in the Cretaceous of 124 MYA (90−160) and it shares the most common ancestor with *Pleurotremataceae*, *Palawaniaceae*, and *Muyocopronales* at 215 MYA (164−272) in the late Triassic.

Justification of order and problems

Previously, the placement of *Acrospermales* in *Ascomycota* was uncertain, and Stenroos et al. (2010) placed it within the lineage that contains *Dothideomycetes* and *Arthoniomycetes*. Based on the results of phylogenetic analysis, Pang et al. (2013) suggested that *Acrospermales* is nested within the *Dothideomycetes* with a weak posterior probability (0.56) value and again Hudson et al. (2019) proved it with fairly strong support (posterior probability = 0.87). However, *Acrospermales* remains *incertae sedis* within the *Dothideomycetes* other than being a sister-group relationship with the *Dyfrolomycetales* due to weak support along the branches that cross clade contains *Dyfrolomycetales* and *Acrospermales* (Hudson et al. 2019). Increasing genomic sampling will be required to provide a robust understanding of the relationship between the *Acrospermales* and *Dyfrolomycetales* and the remaining orders of *Dothideomycetes*.

Significance

Ecological and economic roles

Acrospermaceae members were reported as saprobes, necrotic and epibiotic species living on fungi, ferns, and angiosperms (Hudson et al. 2019). Members of this order reported worldwide with different host plants (Hongsanan et al. 2020a). *Acrospermum* shows a specific relationship with the fern family *Polypodiaceae* which contains approximately 45 neotropical species of ferns (Hudson et al. 2019). However, more extensive studies are needed to determine the nature of the relationship between *Acrospermum* and their fern hosts.

***Arthrocatenales* Piątek, Stryjak-Bogacka & Czachura, MycoKeys 108: 57 (2024)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Dothideomycetidae*

Introduction

Arthrocatenales was recently introduced to accommodate the monotypic family *Arthrocatenaceae,* which has two genera: *Arthrocatena* and *Hyphoconis* (Piątek et al. 2024).

History

Arthrocatena and *Hyphoconis* were introduced as rock-inhabiting fungi (Egidi et al. 2014) and the genera formed a close clade within *Capnodiales sensu lato*. However, these genera were accepted under *Capnodiales incertae sedis* and *Mycosphaerellales* genera *incertae sedis* by Hongsanan et al. (2020a) and Wijayawardene et al. (2022a), respectively. Piątek et al. (2024) isolated sooty moulds on leaves and the multigene phylogenetic analyses showed that the new strains (CBS 150721, CBS 150720) grouped with type and additional strains of *Capnobotryella antalyensis* (MA 4659 and MA 4775) and they together formed a sister clade to *Arthrocatena tenebrosa*. The newly generated sequences and *Capnobotryella antalyensis* showed high genetic diversity and moderate bootstrap support but no distinguishing micromorphological features were observed. Thus, *Capnobotryella antalyensis* is synonymized under *Arthrocatena antalyensis* and all the strains are considered as the same species *Arthrocatena antalyensis*. *Capnobotryella antalyensis* was originally introduced by Sert et al. (2007), as a second species to *Capnobotryella*. The species formed a close clade to *Anguillispora rubescens* with the type species *C. renispora* in the phylogenetic analyses. However, in the subsequent studies (Zucconi et al. 2012, Isola et al. 2016, De Leo et al. 2022), *Capnobotryella antalyensis* formed a distinct lineage within *Neodevriesia*. However, these authors used different strains (MA 4615, MA 4624, MA 4766MA) that were not generated during the establishment of the species by Sert et al. (2007) and are reported as rock inhabiting fungi. Thus, Piątek et al. (2024) assumed that these strains could presumably be undescribed species of *Neodevriesia* and transferred *Capnobotryella antalyensis* to *Arthrocatena*. The monotypic genus *Hyphoconis* formed a sister clade to *Arthrocatena* and these genera formed a close clade to *Cladosporiales* and *Comminutisporales*. Thus, a new order *Arthrocatenales* and family *Arthrocatenaceae* were established to accommodate the genera based on multi-locus phylogenetic analyses (ITS-LSU-SSU-RPB2- TEF1) along with morphological characterizations (Piątek et al. 2024).

General description

Arthrocatenales members are known only from sterile mycelia and *Arthrocatena* specifically produce arthroconidia and chlamydospores (Piątek et al. 2024).

Sexual morph: Not observed. Asexual morph: Colonies erumpent, spreading, with elevated and folded center, greenish olivaceous, forming concentric rings, margin smooth, entire or undulate. Reverse black. *Mycelium* composed of branched, septate, pale brown or brown, smooth, straight, flexuose or torulose, thin-walled hyphae. *Arthroconidia* ellipsoid or broadly ellipsoid, rarely barrel-shaped, brown, smooth, one-septate, intercalary or on side branches, single or in chains. *Chlamydospore-like cells* spherical, brown, smooth, aseptate, intercalary, in simple or branched chains. *Chlamydospores* spherical, brown, smooth, muriformly septate, intercalary, single (adapted from Piątek et al. 2024) (Fig. 10).

Families included in *Arthrocatenales*

Arthrocatenaceae Piątek, Stryjak-Bogacka & Czachura

Evolution

The order has been recently introduced and further studies are needed to understand their evolutionary relationship.

Justification of order and problems

Piątek et al. (2024) discussed the morphological and habitual similarities and dissimilarities with the closely related orders *Cladosporiales* and *Comminutisporales*. More taxon sampling especially on sooty moulds and communities can provide a wider understanding between members.

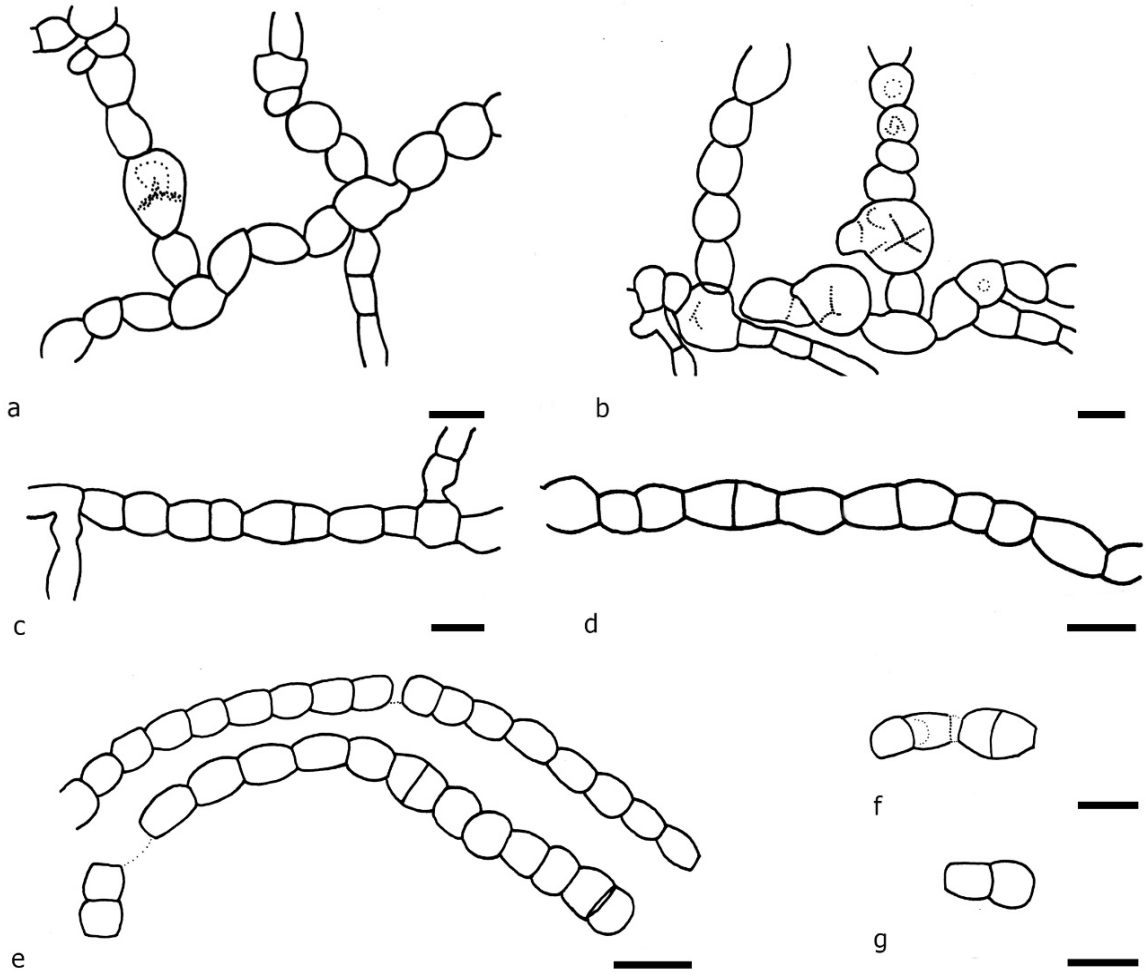


Figure 10 – Asexual morph of *Arthrocatenales* (*Arthrocatena antalyensis*). a, b Chlamydospore-like cells and muriformly septate chlamydospores. c, d Arthroconidia. e Disintegrating chains of arthroconidia. f Disintegrated arthroconidia (drawn from Piątek et al. 2024). Scale bars: a–g = 10 µm.

Significance

Ecological and economic roles

The members of *Arthrocatena* have been found in various environments including the gut of feather mites in Spain, plants in China, Estonia and Italy, indoor dust in the USA, tsetse fly in Tanzania or rocks in Antarctica and sooty mould communities on the leaves of *Tilia cordata* and needles of *Pinus nigra* in southern Poland whereas *Hyphoconis* is reported from rock in Spain (Egidi et al. 2014, Wu et al. 2019, Cox et al. 2022).

Chemical diversity

No relevant studies are available for the members of *Arthrocatenales*.

***Aulographales* Crous, Spatafora, Haridas & I.V. Grig. Studies in Mycology 96: 151 (2020)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Aulographales was established by Haridas et al. (2020) to accommodate two families *viz*. *Aulographaceae* and *Rhizodiscinaceae*.

History

Aulographum was introduced by Libert (1834) for *Aulographum hederae* and is characterized by longitudinally splitting ascomata, peridial wall appressed by mycelium with bright-colored at the margin (Hyde et al. 2013). *Aulographaceae* was introduced by Luttrell (1973) based on the tribe *Aulographées* without Latin diagnosis. Kirk et al. (2001) validated this family with a Latin diagnosis. The family was characterized by possessing a longitudinal slit at maturity which exposes the asci (Sierra 2006). It was placed in *Microthyriales* based on having thyriothecial ascomata (Kirk et al. 2008a). The members of *Aulographaceae* were transferred to other families, including *Asterinaceae*, *Elsinoaceae*, *Leptopeltidaceae* and *Lophiostomataceae*. Hyde et al. (2013) accepted *Aulographum*, *Echidnodella*, *Echidnodes*, *Lembosina*, *Morenoina* and *Thyriopsis* within *Aulographaceae*, and was placed under *Asterinales*, without the support of molecular data. Hongsanan et al. (2014) initially provided the molecular data for *Aulographum hederae* and they excluded this family from *Asterinales* based on morpho-molecular evidence and placed it in *incertae sedis*. The family formed a distinct clade to *Asterinaceae* and varied in having linear or X- or Y-shape of thyriothecium, hyphae without appressoria, with hyaline ascospores. Within *Asterinaceae*, the thyriothecia are globose, hyphae with appressoria, ascospores are hyaline when immature and become brown at maturity (Hongsanan et al. 2014). *Aulographum*, *Echidnode*s, *Lembosiella*, *Lembosina*, *Morenoina* and *Thyriopsis* were accepted under *Aulographaceae* (Hongsanan et al. 2014). Crous et al. (2019b) provided the first molecular data for *Lembosina* and found that it formed a distinct lineage next to *Lichenoconiales* and thus was later transferred to *Lembosinales*. Hongsanan et al. (2020a) established a new family within *Asterinales* to accommodate *Morenoina* based on the morphological characters with phylogenetic analyses. Consequently, Hongsanan et al. (2020a) and Wijayawardene et al. (2022a) accepted four genera including *Aulographum*, *Echidnodes*, *Lembosiella* and *Thyriopsis* within the family. Lini et al. (2021) transferred *Echidnodes* to *Lembosiaceae* based on having colonies spread on the host surface, superficial thyriothecia, globose asci and 1-septate ascospores. *Rhizodiscinaceae* was recently introduced to accommodate a single genus *Rhizodiscina* (Haridas et al. 2020). Hafellner & Poelt (1976) introduced *Rhizodiscina* as a monotypic genus and suggested placing it within *Patellariaceae* and was characterized by ascomata, massive exciple and bitunicate asci (Kutorga & Hawksworth 1997, Yacharoen et al. 2015). The order presently comprises *Aulographum*, *Lembosiella*, *Thyriopsis* and *Rhizodiscina;* which are accepted under *Aulographaceae* and *Rhizodiscinaceae*.

General description

The members of *Aulographales* can have both apothecial to thyriothecial, apothecial ascomata and pycnidial conidiomata. For *Thyriopsis halepensis*, the pycnidia give rise to thyriothecia and asci developing under layer of conidiophores which suggest that conidia may be acting as spermatia and remnants of conidiophores, giving the appearance of paraphyses (Ouellette 1966).

Sexual morph: *Ascomata* apothecial to thyriothecial, globose to ellipsoidal, superficial, black, simple or branched, scattered to loosely clustered. *Hamathecium* dissolving early, or of branched, hyaline, septate, anastomosing pseudoparaphyses. *Asci* clavate or globose to subglobose, 8-spored, bitunicate, with or without pedicel. *Ascospores* obovoid to narrowly clavate, irregularly arranged, hyaline to brown, constricted at the septum, smooth-walled, with or without remnants of mucilage (adapted from Haridas et al. 2020). Asexual morph: *Pycnidia* roundish to elongate, black, amphigenous, subcuticular, covering the layer of isodiametric, brownish, thick-walled cells, opening by clefts, *Conidiophores* originating from a thin layer of hyphae next to substratum, hyaline, cylindrical to obclavate, from 15–30 × 1.5–3 becoming septate. *Conidia* hyaline, oval to cylindrical (adapted from Ouellette 1966) (Fig. 11).

Families included in *Aulographales*

Aulographaceae Luttr. ex P.M. Kirk, P.F. Cannon & J.C. David

Rhizodiscinaceae Crous, Spatafora, Haridas & Grigoriev

Evolution

The evolution of *Aulographales* is poorly studied and needs further investigation.

Justification of order and problems

Both *Lembosiella* and *Thyriopsis* lack molecular data. Further investigation with molecular data is required to confirm their phylogenetic placement (Hongsanan et al. 2020a).

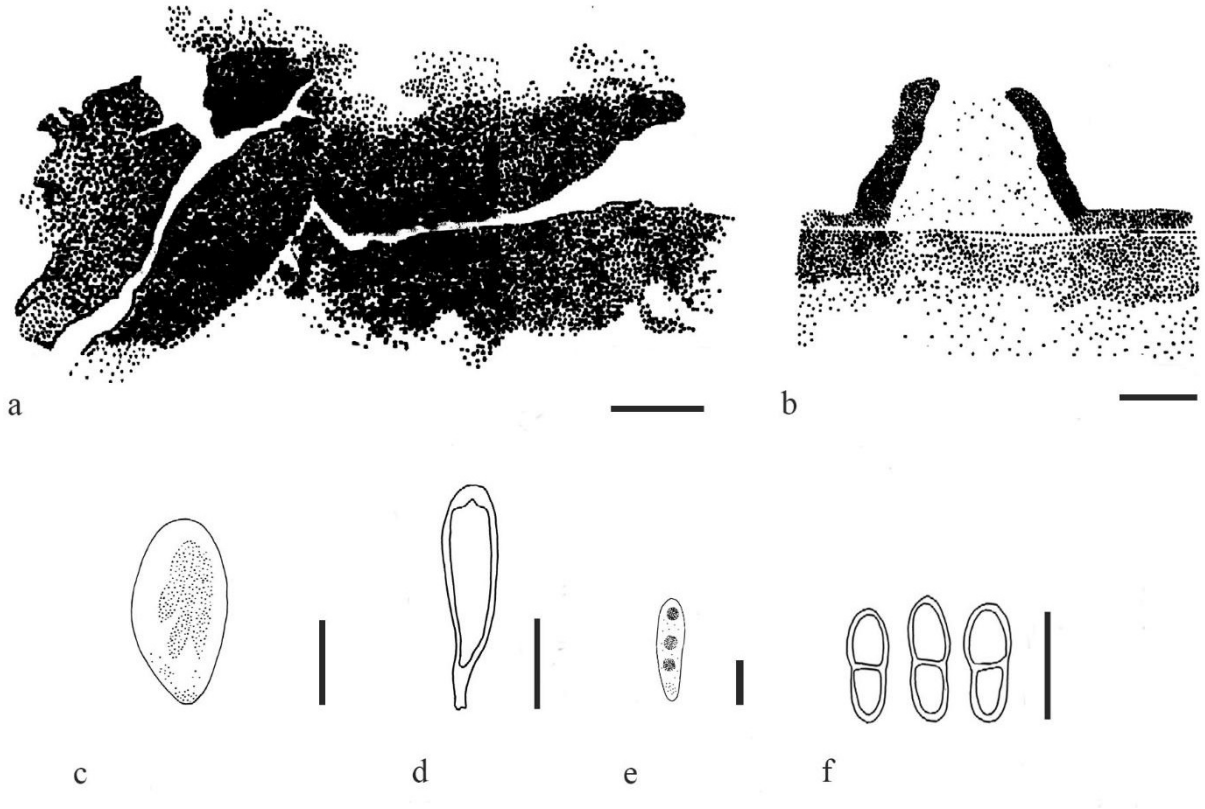


Figure 11 – Sexual morph characters of *Aulographales*. a Ascomata on host substrate of *Aulographum hederae*. b Section through ascoma of *A. hederae*. c, d Ascus (c *A. hederae*, d *Rhizodiscina lignyota)*. e, f Ascospore (e *A. hederae*, f *R. lignyota*) (redrawn from Kutorga & Hawksworth 1997, Hongsanan et al. 2020a). Scale bars: a = 50 µm, b, c = 20 µm, d = 20 µm, e = 5 µm, f = 10 µm.

Significance

Ecological and economic roles

Aulographaceae are mainly reported as saprobic on dead leaves. *Rhizodiscina lignyota* was recorded on *Basidiomycetes* and dead wood (Uzun & Kaya 2018). *Thyriopsis halepensis* was associated with chlorotic spots on living needles of jack pine in its asexual morph. However, it is unknown whether this species causes any injuries to its host pine tree (Ouellette 1966).

Chemical diversity

There is no report about chemical diversity for the species in *Aulographales*.

***Asterinales* M.E. Barr ex D. Hawksw. & O.E. Erikss. Systema Ascomycetum 5(1): 177 (1986)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Asterinales was introduced by Barr (1976) without a Latin diagnosis and was subsequently validated by Hawksworth & Eriksson (1986) to accommodate *Asterinaceae*. Based on phylogenetic analysis using LSU sequence data (Hongsanan et al. 2014, 2020a, Marasinghe et al. 2022a, b, Hyde et al. 2024b), this order represents a distinct clade within *Dothideomycetes*. However, adding all available sequence data indicated that *Asterina* species are segregated into two unrelated clades with *Dothideomycetes* (Ertz et al. 2016, Hyde et al. 2016b, Liu et al. 2017b, Dai et al. 2018). *Asterinales* is identified as a distinct order due to its unique morphological characteristics. Most of the species in this order are considered to be host, genus or family specific, although this has not yet been confirmed. Currently, this order comprises 11 families which are *Asterinaceae*, *Asterotexaceae*, *Brunneofissuraceae*, *Cylindrohyalosporaceae*, *Hemigraphaceae*, *Lembosiaceae*, *Melaspileellaceae*, *Morenoinaceae*, *Neobueliellaceae*, *Oblongohyalosporaceae*, and *Stictographaceae* (Wijayawardene et al. 2022a, Marasinghe et al. 2023).

History

Asterinales was formally established by Hawksworth & Eriksson (1986), based on the type family *Asterinaceae* (Hyde et al. 2013, Hongsanan et al. 2014, 2020a). Molecular analyses also confirmed that *Asterinales* is a distinct order within *Dothideomycetes* with good support (Hofmann et al. 2010, Wu et al. 2011, Hyde et al. 2013, Hongsanan et al. 2014, 2020a). Wu et al. (2011) further proposed the inclusion of *Aulographaceae* and *Parmulariaceae* in this order, and this was subsequently accepted by Hyde et al. (2013). The order was revised by Hongsanan et al. (2014), however, the classification of *Asterinales* has encountered challenges due to insufficient sequence data. Phylogenetic trees have shown that the sequence data of *Asterinales* cluster into two distinct clades (Ertz et al. 2016, Hyde et al. 2016b, Liu et al. 2017b). The clade containing *Asterotexis cucurbitacearum* was initially treated as *Asterotexiales* (Ertz et al. 2016), but later, Hyde et al. (2016b) synonymized it under *Asterinales sensu stricto*, as most strains of *Asterinales* were found in this clade. Conversely, the clade that includes species of *Parmulariaceae* was treated as *Asterinales sensu lato* (Liu et al. 2017b), and *Parmulariaceae* was segregated into its own order, *Parmulariales*, by Dai et al. (2018).

Despite the inclusion of the type species *Asterina melastomatis* and other similar taxa within *Asterinales sensu lato* clade (Ertz et al. 2016, Hyde et al. 2016b), Hongsanan et al. (2020a) excluded these from their analysis based on the need for re-evaluation of asterinales-like taxa in *Asterinales sensu lato*, particularly because other hyphomycetous strains were also placed in this clade, raising questions about their actual classification. However, the addition of more sequence data from asterinaceous fungi such as species of *Asterina*, *Batistinula*, *Lembosia* and *Prillieuxina*, has since supported the reliability of the clade containing the type species (*A. melastomatis*), especially sequence data obtained from pure cultures provided by Firmino & Pereira (2021). *Asterinales sensu stricto* consisted of the families *Asterinaceae* and *Parmulariaceae* in Johnston & Park (2019), Phookamsak et al. (2019) and Firmino & Pereira (2021). However, recent classifications have assigned *Parmulariaceae* to a distinct order, *Parmulariales* (Marasinghe et al. 2022b, 2023, Hyde et al. 2024b). In this study, we follow the treatment of Marasinghe et al. (2023) and Hyde et al. (2024b) by maintaining *Parmulariales* as a distinct order, but strongly recommend that future research is conducted on the status of *Parmulariales*, and phylogenetic analyses should include both clades of *Asterinales* (*sensu stricto* and *sensu lato*) to clarify their classification. *Thyrinulaceae* was introduced to accommodate a clade related to *Parmulariales* (= *Asterinales sensu lato*), with *Thyrinula* as the generic type, adhering to the rules of nomenclatural priority. Hongsanan et al. (2014) initially synonymized *Lembosiaceae* under *Asterinaceae*. However, with the addition of more sequence data for *Lembosia*, it was suggested that *Lembosia* should be raised to a family in *Asterinales* (Hongsanan et al. 2020a). Consequently, Hongsanan et al. (2020a) retained *Lembosiaceae* in the order and introduced *Morenoinaceae* and *Neobuelliellaceae* to accommodate the clades of *Morenoina* and *Neobuelliella*, respectively. Further expanding the order, Tennakoon et al. (2021) introduced two new families, *Cylindrohyalosporaceae* and *Oblongohyalosporaceae*, and Marasinghe et al. (2022a)

established a new family *Brunneofissuraceae* based on phylogeny and morphological characteristics. However, Marasinghe et al. (2023) excluded four lichenicolous families (*Hemigraphaceae*, *Melaspileellaceae Neobuelliellaceae* and *Stictographaceae*) and considered families with epifoliar taxa in the monograph of epifoliar fungi. We herein accepted 11 families in *Asterinales*; *Asterinaceae*, *Asterotexaceae*, *Brunneofissuraceae*, *Cylindrohyalosporaceae*, *Hemigraphaceae*, *Lembosiaceae*, *Melaspileellaceae*, *Morenoinaceae*, *Neobuelliellaceae*, *Oblongohyalosporaceae* and *Stictographaceae*. Pem et al. (2024) treated the genera in the order, however, the classification of *Asterinales* is questionable and needs more morphological and molecular data to clarify its phylogenetic relationship.

General description

Morphological characteristics of *Asterinales* include both sexual and asexual morphs. The appearance of its sexual morph and coelomycete state on host surface show microthyrium-like, with flattened thyriothecia or longitudinal thyriothecia, a lack of obvious ostioles, opening by stellate fissures, with or without superficial hyphae with appressoria (Hongsanan et al. 2014, 2020a).

Sexual morph: *Superficial hyphae* present with appressoria or absent. Sometimes external mycelium present. *Thyriothecia* or *Ascomata* superficial or erumpent, solitary or scattered, circular to longitudinal, x- or y-shaped, flattened, with stellate or longitudinal dehiscence. *Upper walls* or peridium brown, comprising radial, septate cells of *textura angularis* or *prismatica*. *Asci* 8-spored or 4–6-spored, bitunicate, globose to subglobose, ellipsoid or cylindrical, usually thickened at the apex, with or without pedicels. *Hamathecium* with cellular pseudoparaphyses and hymenium present or absent. *Ascospores* 2–5-seriate or fasciculate or conglobate, fusoid to ellipsoid, hyaline to dark brown, mostly 1-septate, with or without guttules, smooth-walled or toughened, sometimes bearing appendages (Adapted from Hongsanan et al. 2020a). Asexual morph: *Hyphomycetous*, without conidiomata or sporodochia then gelatinous, pale; *Coelomycetous* pycnothyria, scattered, flattened, dimidiate, radiate, orbicular or rounded to oval, brown to black, stellately dehisced at the centre. *Conidiophores* branched or unbranched, hyaline or brown. *Upper wall* comprising an irregular arrangement of dark cells, cells at margin branching and forming superficial hyphae. *Conidiogenous cells* monoblastic or percurrent, hyaline or brown, or evanescent. *Conidia* ovate to oblong, cylindrical with obtuse ends, pyriform, angular, or wall straight to sinuate, unicellular, hyaline to brown (Adapted from Hongsanan et al. 2020a, Tennakoon et al. 2021) (Figs. 12, 13, 14, 15, 16).

Families included in *Asterinales*

Asterinaceae Hansf.
Asterotexaceae Firmino, O.L. Pereira & Crous
Brunneofissuraceae Marasinghe, Hongsanan & K.D. Hyde
Cylindrohyalosporaceae Tennakoon, C.H. Kuo, S. Hongsanan & K.D. Hyde
Hemigraphaceae D.Q. Dai & K.D. Hyde
Lembosiaceae Hosag.
Melaspileellaceae D.Q. Dai & K.D. Hyde
Morenoinaceae Hongsanan & K.D. Hyde
Neobuelliellaceae Hongsanan & K.D. Hyde
Oblongohyalosporaceae Tennakoon, C.H. Kuo, S. Hongsanan & K.D. Hyde
Stictographaceae D.Q. Dai & K.D. Hyde

Asterinales genera *Incertae sedis*
Calothyriopsis Höhn.
Caribaeomyces Cif.
Caudella Syd. & P. Syd.
Discopycnothyrium Hongsanan & K.D. Hyde
Dothidasteromella Höhn.
Hazslinszkya Körb.

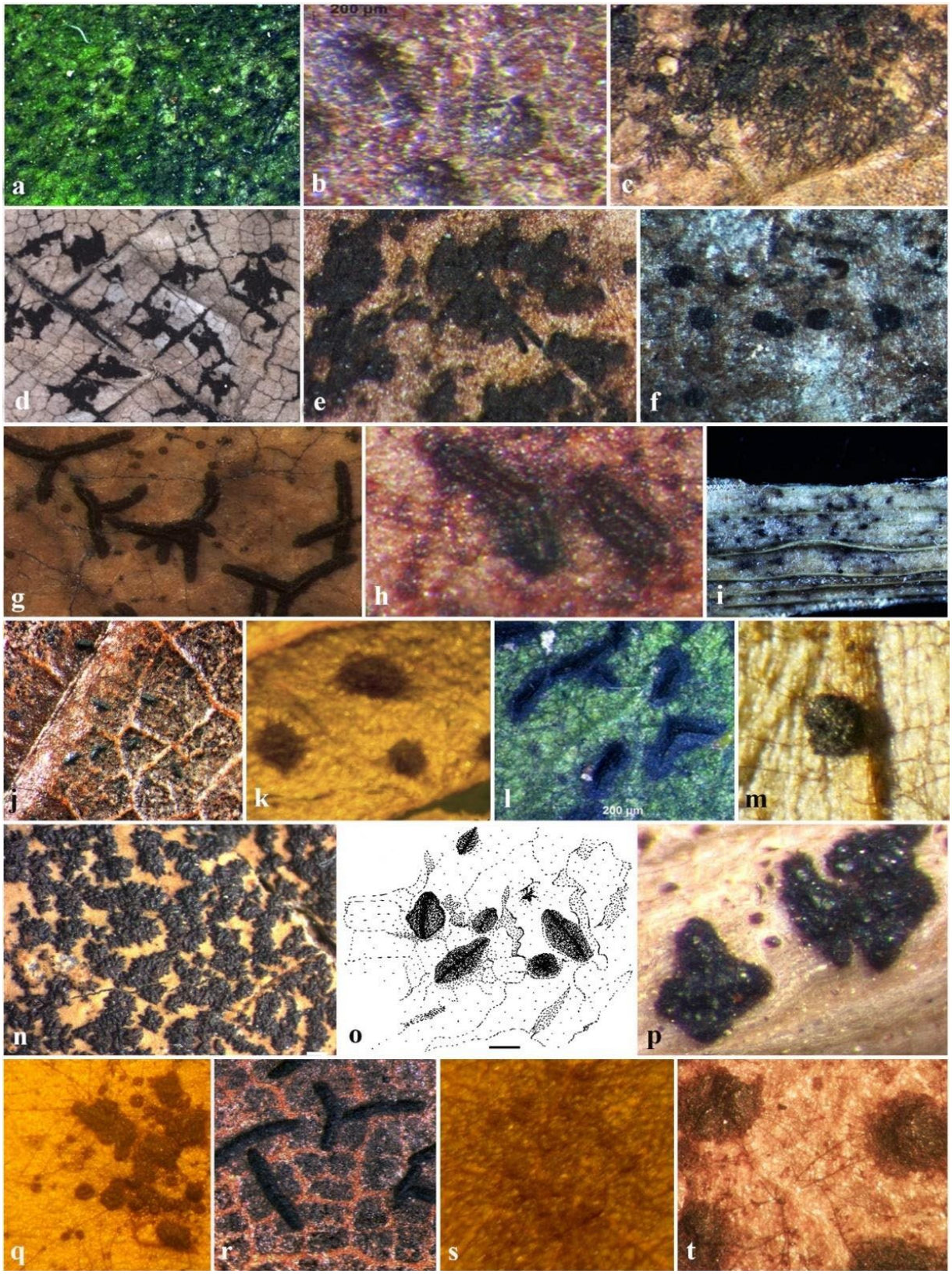


Figure 12 – Thyriothecial morphology of *Asterinales*. a *Asterina* sp. b *Batistinula* sp. c *Meliolaster* sp. d *Asterotexis* sp. e *Uleothyrium* sp. f *Cylindrohyalospora* sp. g *Brunneofissura* sp. h *Echidnodella* sp. i *Oblongohyalospora* sp. j *Cirsosia* sp. k *Halbania* sp. l *Lembosia* sp. m *Schenckiella* sp. n *Hemigrapha* sp. o *Stictographa* sp. p *Morenoina* sp. q *Prillieuxina* sp. r *Echidnodes* sp. s *Trichasterina* sp. t *Pycnocarpon* sp. (adapted from Hongsanan et al. 2014, 2020a, Tennakoon et al. 2021, Marasinghe et al. 2022a, 2023). Scale bars: o = 300 µm.

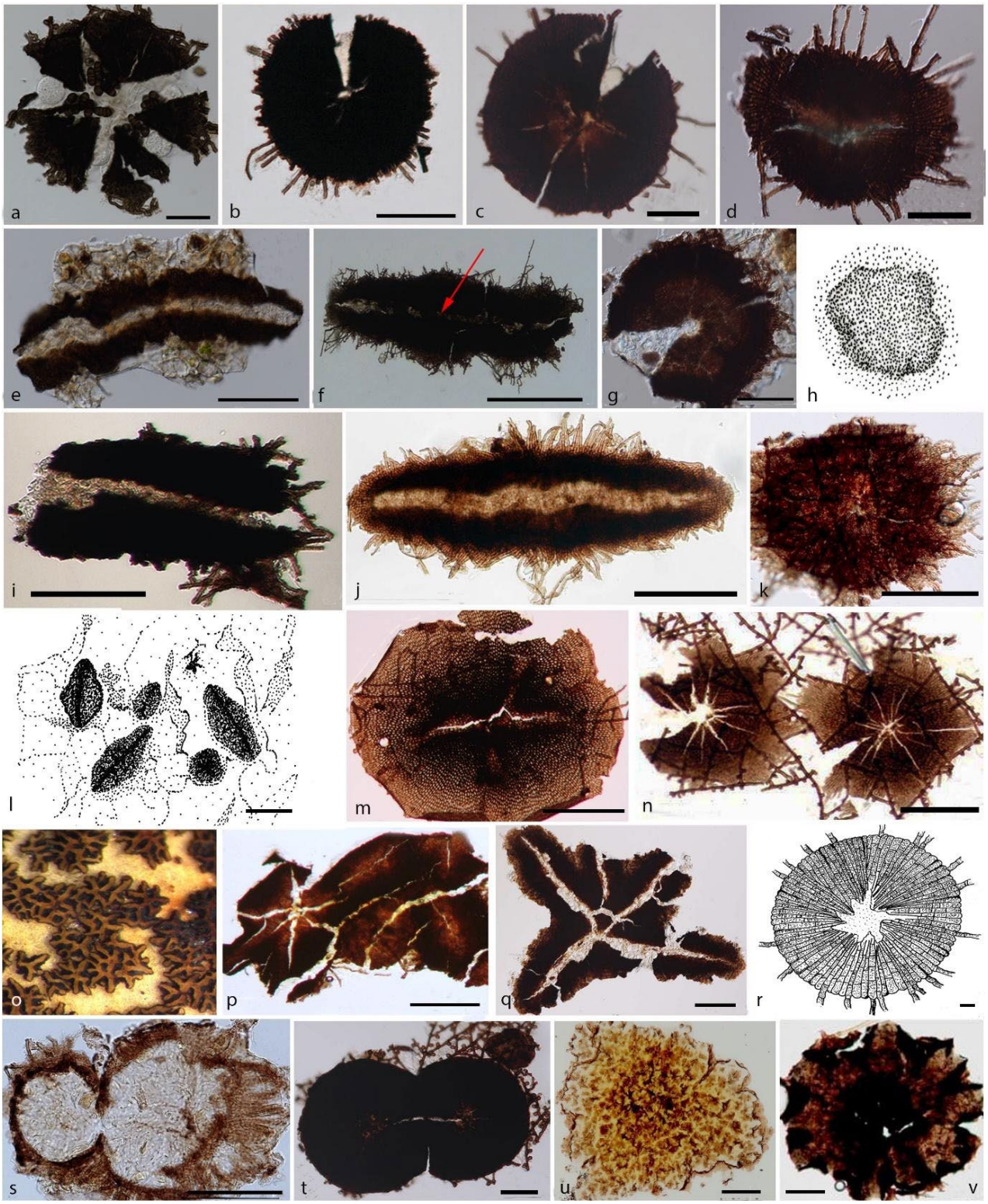


Figure 13 – Thyriothecial morphology of *Asterinales*. a *Asterina* sp. b *Batistinula* sp. c *Meliolaster* sp. d *Cirsosia* sp. e *Brunneofissura* sp. f *Lembosia* sp. g *Uleothyrium* sp. h *Neobuelliella* sp. i *Echidnodella* sp. j *Echidnodes* sp. k *Halbania* sp. l *Stictographa* sp. m *Pycnocarpon* sp. n *Trichasterina* sp. o *Hemigrapha* sp. p *Prillieuxina* sp. q *Morenoina* sp. r *Vishnumyces* sp. s *Parasterinopsis* sp. t *Meliolaster* sp. u *Asterotexis* sp. v *Inocyclus* sp. (adapted from Hongsanan et al. 2014, 2020a, Boonmee et al. 2017, Doilom et al. 2018, Tennakoon et al. 2021, Marasinghe et al. 2022a,b, 2023). Scale bars: a, d, p, r = 50 µm, b, m = 200 µm, c, e, f, i–k, n, q, s–v = 100 µm.

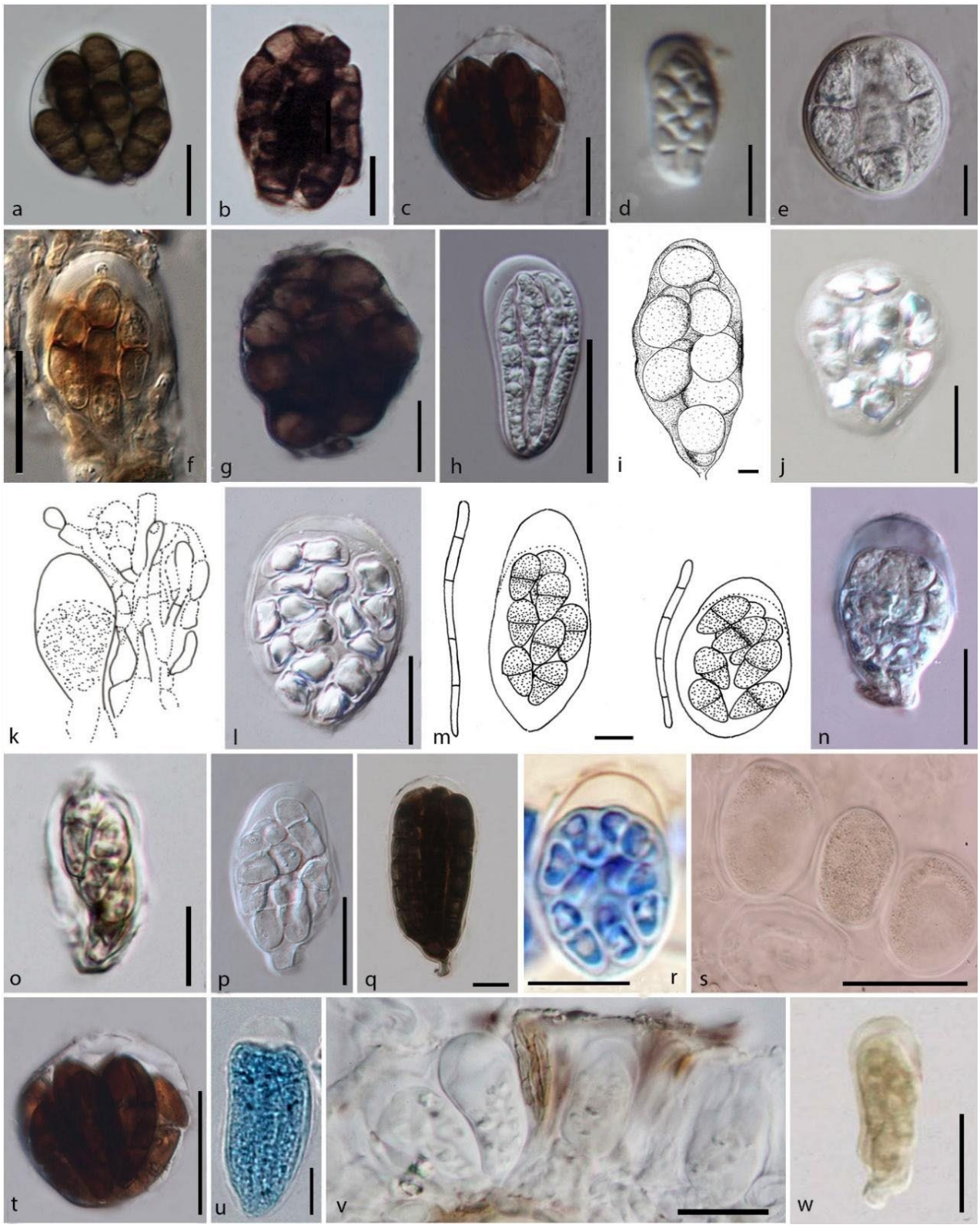


Figure 14 – Asci morphology of *Asterinales*. a *Asterina* sp. b *Batistinula* sp. c *Meliolaster* sp. d *Brunneofissura* sp. e *Cirsosia* sp. f *Echidnodella* sp. g *Lembosia* sp. h *Uleothyrium* sp. i *Vishnumyces* sp. j *Prillieuxina* sp. k *Neobuelliella* sp. l *Trichasterina* sp. m *Stictographa* sp. n *Halbania* sp. o *Morenoina* sp. p *Asterotexis* sp. q *Schenckiella* sp. r *Echidnodes* sp. s *Pycnocarpon* sp. t *Meliolaster* sp. u *Parasterinopsis* sp. v *Hemigrapha* sp. w *Inocyclus* sp. (adapted from Hongsanan et al. 2014, 2020a, Boonmee et al. 2017, Doilom et al. 2018, Tennakoon et al. 2021, Marasinghe et al. 2022a, b, 2023). Scale bars: a, b, e–h, j, l, o–q = 20 µm, c, n, t = 50 µm, d, r, u = 10 µm, i = 5 µm, r, u = 10 µm, s = 100 µm.

Inocyclus Theiss. & Syd.
Melanographa Müll. Arg.
Parasterinopsis Bat.
Pirozynskiella S. Hughes
Schenckiella Henn.
Spiralomyces
Uleothyrium Petr.
Vishnumyces Hosag.
Vizellopsis Bat. J.L. Bezerra & T.T. Barros

Evolution

The evolution of *Asterinales* clade, which includes *Asterotexiales* and related families within the same order, is estimated to date back approximately 221 MYA (Hongsanan et al. 2020a), indicating a deep evolutionary history within the *Dothideomycetes*. However, Hongsanan et al. (2020a) did not include the *Asterinales* clade that comprises *Asterina melastomatis* in their analysis. Future evolutionary studies are needed to analyze both the *sensu stricto* and *sensu lato* clades. A key feature of *Asterinales* species is their flattened thyriothecia found on their host plants. This character is similar to the genera of *Microthyriales* (*Dothideomycetes*) and *Micropeltidales* (*Eurotiomycetes*). This resemblance leads to interesting questions about how these thyriothecial species evolved and developed across different classes. Studying these structures offers insights into how fungal shapes and ways of living have changed over time. Furthermore, *Asterinales* includes some lichenicolous species, which live and behave differently from most species in the order. By exploring these evolutionary connections, we could gain deeper insight into the historical development of *Asterinales* and enhance our knowledge of the diverse adaptation strategies and variety of fungi across diverse habitats.

Justification of order and problems

The classification of *Asterinales*, initially based on morphological traits such as the distinct flattened thyriothecia on host plant surfaces, faces challenges due to similar features evolving in unrelated species. Therefore, phylogenetic analyses based on DNA have been crucial in shedding light on the evolutionary relationships within the order. A major difficulty in classifying *Asterinales* is the lack of extensive sequence data for many species. This shortage is partly due to the difficulty in culturing most species of this order on media and easily contamination cultures or DNA from non-targeting fungi on the same leaf surface. Insufficient molecular data slows down attempts to accurately identify, classify and better understand their evolutionary relationships. Firmino & Pereira (2021) provided guidelines for isolating and obtaining pure cultures of species within this order. However, sequence data indicated that *Asterinales* formed two distinct clades (Hyde et al. 2016b, Liu et al. 2017b). Additional sequence data are therefore needed to clarify the classification of these clades.

The debate over the classification of *Asterinales* is further complicated by the observed host-specificity of many species, particularly within *Asterinaceae* (Hongsanan et al. 2014, 2020a). Numerous species have been identified based solely on the host species they inhabit, even if they show only a few distinct characteristics. This approach has led to questions about the true diversity and specificity of these fungi, adding another layer to the ongoing debate and study in fungal taxonomy (Phukhamsakda et al. 2022, Hyde et al. 2024b).

Significance

Ecological and economic roles

Most of the species within *Asterinales* are pathogenic biotrophs, which play crucial ecological and economic roles, particularly in tropical and subtropical regions. The ability of *Asterinales* to adapt to a wide range of host families, including herbs, trees, weeds, and economically important plants, indicates their ecological adaptability and potential impact on various plants (Vishnu et al. 2017, Marasinghe et al. 2022a, 2023).

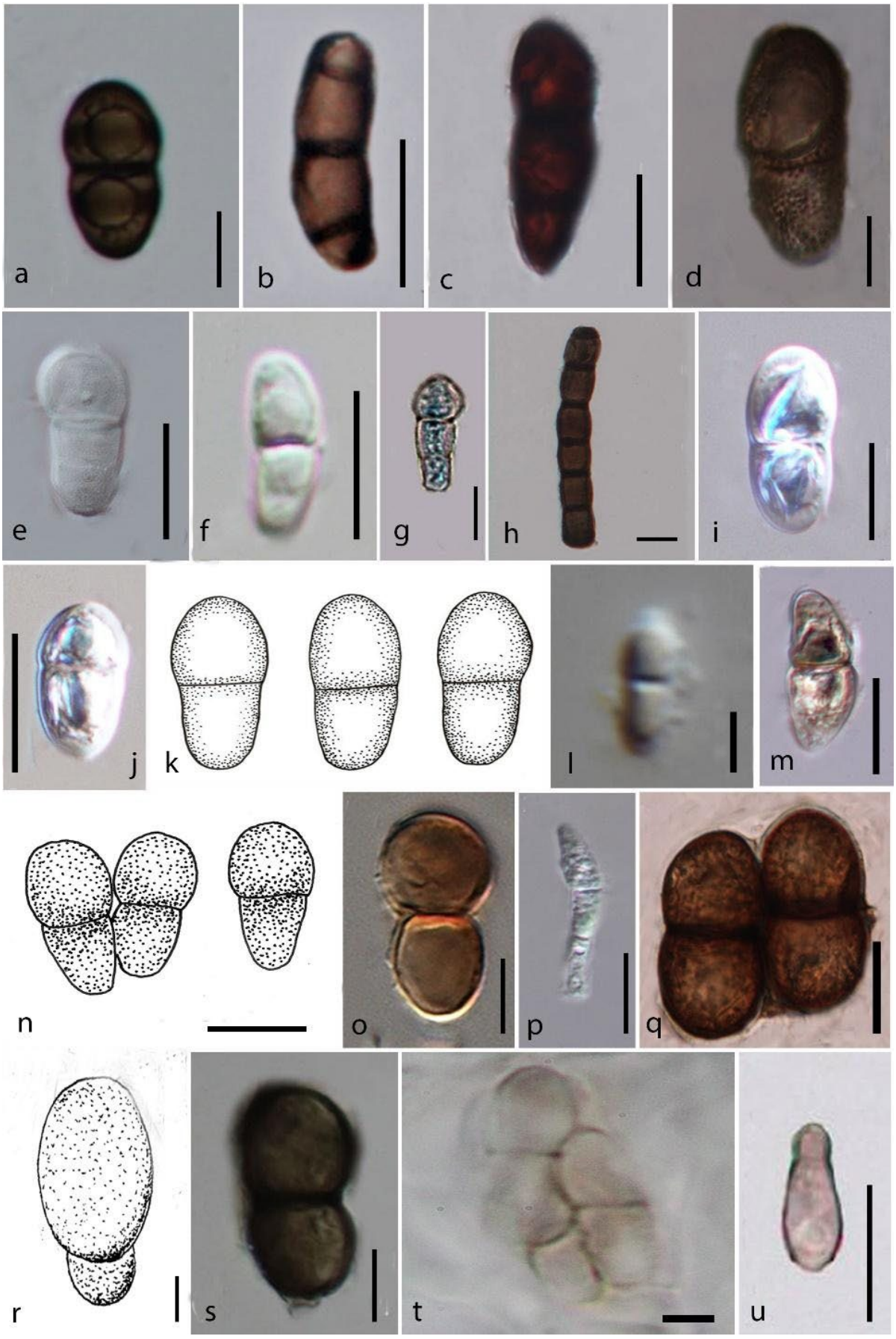


Figure 15 – Ascospores morphology of *Asterinales*. a *Asterina* sp. b *Batistinula* sp. c *Meliolaster* sp. d *Cirsosia* sp. e *Asterotexis* sp. f *Morenoina* sp. g *Parasterinopsis* sp. h *Schenckiella* sp. i Trichasterina sp. j *Prillieuxina* sp. k *Neobuelliella* sp. l *Brunneofissura* sp. m *Halbania* sp. n

Stictographa sp. o *Echidnodella* sp. p *Uleothyrium* sp. q *Pycnocarpon* sp. r *Vishnumyces* sp. s *Lembosia* sp. t *Hemigrapha* sp. u *Inocyclus* sp. (adapted from Hongsanan et al. 2014, 2020a, Boonmee et al. 2017, Doilom et al. 2018, Tennakoon et al. 2021, Marasinghe et al. 2022a, b, 2023). Scale bars: a, b, e, g, i, l–o, s, u = 10 µm, c, f, h, j, p, q = 20 µm, r, t = 5 µm.

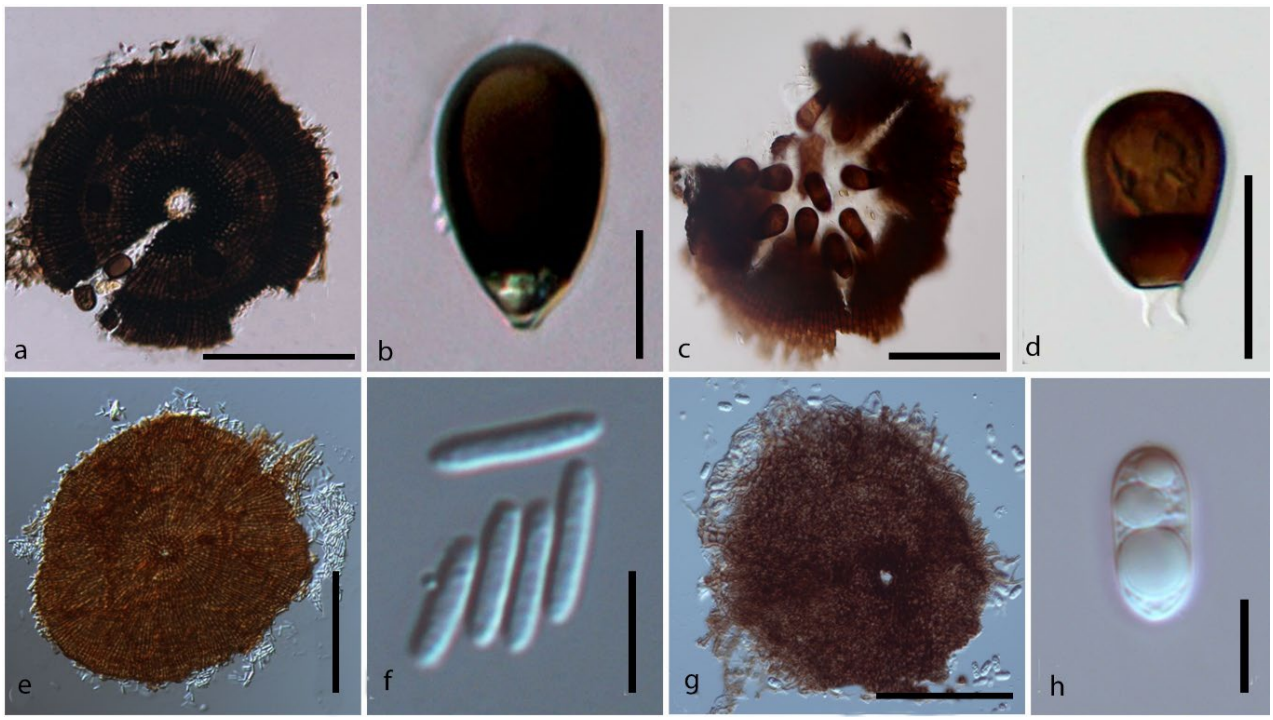


Figure 16 – Asexual morphs of *Asterinales*. a, b *Discopycnothyrium* sp. c, d *Prillieuxina* sp. e, f *Cylindrohyalospora* sp. g, h *Oblongohyalospora* sp. (adapted from Hongsanan et al. 2014, 2016a, Tennakoon et al. 2021). Scale bars: a = 100 µm, b = 10 µm, c, g = 50 µm, d, e = 20 µm, f, h = 5 µm.

Economically, their role as pathogenic biotrophs on crops and other economically valuable plants can lead to agricultural losses, necessitating effective management and control measures. Nevertheless, these organisms may adversely impact the process of photosynthesis in plants and potentially compromise host defense mechanisms. For instance, research conducted in India revealed that *Asterina congesta* negatively affected the photosynthetic activity of sandal trees. This was attributed to the extensive growth of black colonies, which hindered the entry of light and led to a reduction in chlorophyll content in the leaves (Hosagoudar et al. 1997b). Furthermore, Hosagoudar et al. (1997b) reported that the infection of *A. congesta* on sandal trees increased the production of cyclic compounds, such as proline, indicating high-stress levels in the host.

On the other hand, their unique biological characteristics may offer potential in biotechnological applications, such as in the development of biocontrol agents or pharmaceuticals. However, research on the potential uses of *Asterinales* is limited because they are hard to grow on artificial media. Firmino & Pereira (2021) recently cultured asterinaceous fungi using *in vitro* by the ascospores ejection technique and suggested the importance of cultivation technique and not on the medium used.

Even though more research is needed to confirm it, the fact that *Asterinales* often infect specific host plants leads to interesting questions regarding how they have evolved together with these plants (co-evolution) and the implications for variety of crops and their ability to resist diseases. Understanding and managing the ecological and economic impacts of *Asterinales* thus remains a significant challenge and area of study in both ecological conservation and agricultural productivity.

Chemical diversity

There is no report about chemical diversity for the species in *Asterinales*.

Other relevant data and future recommendations

In addition to the taxonomic and ecological aspects, future research on *Asteriales* should focus on their host-specific interactions, which can provide valuable insights into co-evolutionary processes, host-pathogen aspects, and developing isolation techniques in laboratory settings, which currently poses a significant challenge. Additionally, expanding ecological, taxonomic and evolutionary studies will provide a better understanding of *Asterinales*, potentially uncovering new species, potential industrial applications and shedding light on their evolutionary and coevolutionary trends.

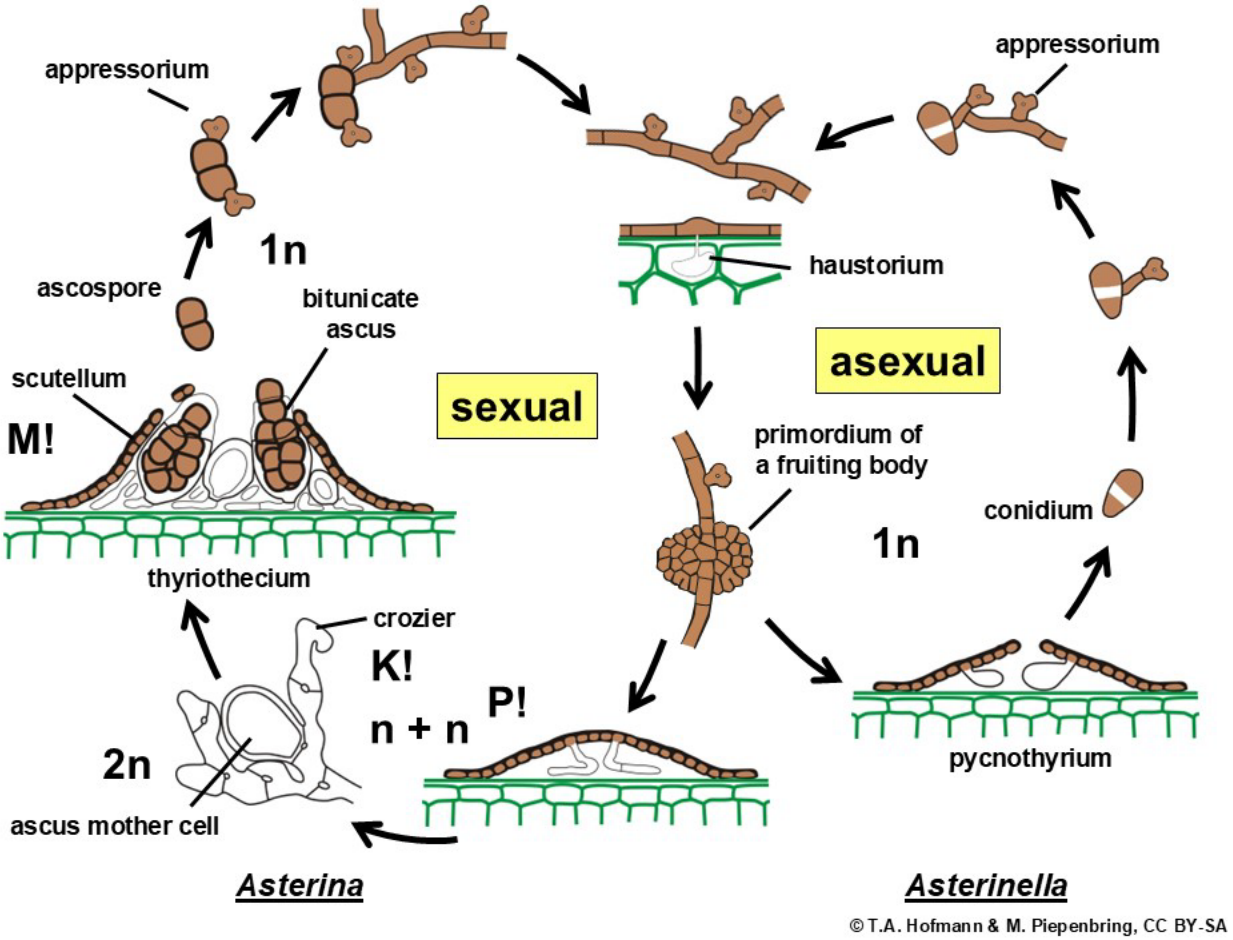


Figure 17 – Sexual and asexual life cycles of *Asterinales* (From Mycological teaching diagrams by Meike Piepenbring (2023)). Abbreviations: 1n = haploid, 2n = diploid, P! = plasmogamy, K! = karyogamy, M! = meiosis. Black and white circles represent haploid nuclei of different mating types, circles of both colors represent diploid nuclei.

Aureoconidiellales **Hern.-Restr. & Crous, Fungal Systematics and Evolution 6: 2 (2020)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Dothideomycetidae*

Introduction

Aureoconidiellales is a monotypic order in *Dothideomycetes*. It was introduced to accommodate *Aureoconidiella foliicola* Hern.-Restr. & Crous, delimited based on multi-locus phylogeny of the LSU sequence data and morphological signatures such as unbranched conidiophores, cicatrised and sympodial conidiogenous cells with thickened scars, subglobose, verruculose, and golden-brown conidia. It is phylogenetically closely related to *Asterinales* and *Cladoriellales* but differs in the asexual morphology (Hernández-Restrepo et al. 2020).

Aureoconidiella foliicola, the type species, has been recorded in South Africa on leaves of *Syzygium cordatum* (Hernández-Restrepo et al. 2020).

History

Aureoconidiellales is a relatively new order of fungi introduced by in Hernández-Restrepo et al. (2020). Since its introduction, it has remained a monotypic order.

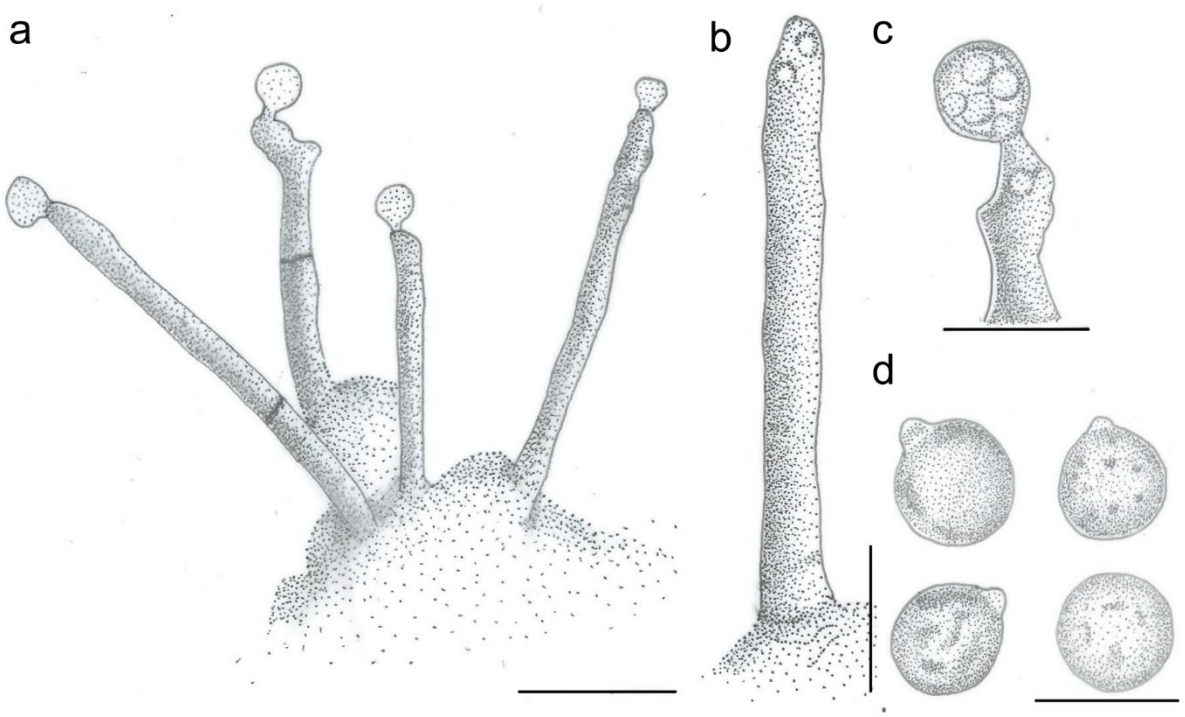


Figure 18 – Morphology of *Aureoconidiella foliicola* (CBS 145943). a Conidiophores. b Conidiophore with conidiogenous cell. c Conidiogenous cells giving rise to conidia. d Conidia (drawn from Hernández-Restrepo et al. 2020). Scale bars: a = 20 µm, b, c, d = 10 µm.

General description

Aureoconidiellales is characterised only by *Aureoconidiella* asexual morph.

Sexual morph: Unknown. Asexual morph: Conidiophores macronematous, simple, septate, and brown conidiophores. *Conidiogenous cells* integrated, terminal, polyblastic, with thickened scars, brown to pale brown. *Conidia* rising from the conidiogenous cells are globose to subglobose with an apiculate base, initially subhyaline, golden brown at maturity, and verrucose (Fig. 18).

Families included in *Aureoconidiellales*

Aureoconidiellaceae Hern.-Restr. & Crous

Justification of order and problems

Aureoconidiellales was introduced to accommodate a lineage with singular morphology. Even though it is phylogenetically related to *Asterinales* and *Cladoriellales*, they differ in the morphology of the asexual morphs. *Aureoconidiellales* is characterised by unbranched conidiophores, producing cicatrised and sympodial conidiogenous cells with thickened scars and subglobose, verruculose, and golden-brown conidia (Hernández-Restrepo et al. 2020), *Asterinales* are coelomycetes with pycnothyrial conidiomata (Guatimosim et al. 2015a, Jaklitsch et al. 2016a). *Cladoriellales* resembles cladosporium-like hyphomycetous producing conidia that remain attached in acropetal chains (Crous et al. 2006, 2017a).

Significance

Ecological and economic roles

Aureoconidiellales has been solely reported from living leaves of *Syzygium cordatum* (*Myrtaceae*) from South Africa, indicating it can be a pathogen in this crop, which may lead to damage and loss of production. This interaction can be highly species-specific, often determined by the unique interplay between plant receptors, defense-related proteins, and specific molecules derived from the fungus (Zeilinger et al. 2016). This can lead to a wide or narrow host range of this fungus; however, sampling should be done to reveal its real specificity and/or diversity.

Chemical diversity

No relevant studies are available for the members of *Aureoconidiellales*.

Botryosphaeriales C.L. Schoch, Crous & Shoemaker, Mycologia 98(6): 1050 (2007) [2006]

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Botryosphaeriales (*Dothideomycetes*) introduced by Schoch et al. (2006) to accommodate *Botryosphaeriaceae*. It has diverse distribution in wide range of hosts and habitats (Schoch et al. 2006, Phillips et al. 2013a, 2019, Abeywickrama et al. 2023). Members of *Botryosphaeriales* found as endophytic, and saprobic lifestyles (Schoch et al. 2006, Ekanayaka et al. 2016, Phillips et al. 2019), as well as are associated with die back and cankers, fruit and root rots, and leaf spots (Slippers & Wingfield, 2007, Phillips et al. 2013a, b, Jami et al. 2014, Slippers et al. 2014, Trakunyingcharoen et al. 2015). Associated hosts and substrates include leaves, twigs, woody stems and branches, grass culms of monocots and dicots, and also thalli of lichens (Barr 1987b, Denman et al. 2000, Mohali et al. 2007, Lazzizera et al. 2008, Marincowitz et al. 2008b). De Hoog et al. (2000) found some members are causing opportunistic infections in humans. Taxa of *Botryosphaeriales* are mainly characterized by having uni- or multiloculate ascostromata, aseptate or septate ascospores sometimes with a mucilaginous sheath and septate pseudoparaphyses (Phillips et al. 2013). Molecular phylogenetics using combined ITS, LSU, SSU, TEF1-α, TUB2 and RPB2 were recognized in generic-level delimitation of *Botryosphaeriales* (Phillips et al. 2013a, b, 2019). To date there are six families including 35 genera and 8 genera *incertae sedis* (Hyde et al. 2024b) accepted in *Botryosphaeriales*. *Botryosphaeriaceae* is the largest monophyletic family accommodating 23 genera (Hyde et al. 2024b) with more than 100 species (Species Fungorum 2025). Wu et al (2021) has published a website dedicated to the order.

History

Schoch et al. (2006) introduced *Botryosphaeriales* to accommodate *Botryosphaeriaceae*, based on SSU, LSU, TEF1-α and RPB2 data. *Botryosphaeriaceae* included *Botryosphaeria*, *Phaeobotryon* and *Dibotryon* which failed to group within any order of *Dothideomycetes* (Schoch et al. 2006) leading to the inception of *Botryosphaeriales*. Based on molecular phylogeny, Minnis et al. (2012) introduced *Planistromellaceae* as a distinct family within *Botryosphaeriales*. *Phyllostictaceae* accommodating *Phyllosticta* (= *Guignardia*) species was restored in *Botryosphaeriales* by Wikee et al. (2013). Slippers et al. (2013) added three new families, *Aplosporellaceae*, *Melanopsaceae* and *Saccharataceae* to the order. Wyka & Broders (2016) established *Septorioideaceae* to accommodate *Septorioides* while Yang et al. (2017c) introduced *Endomelanconiopsisaceae* and *Pesudofusicoccumaceae* to accommodate *Endomelanconiopsis* and *Pseudofusicoccum* species, respectively. Wijewardene et al. (2018) accepted nine families within *Botryosphaeriales*. Phillips et al. (2019) synonymized *Endomelanconiopsisaceae*, *Pseudofusicoccaceae*, and *Septorioideaceae* under *Botryosphaeriaceae*, *Phyllostictaceae* and *Saccharataceae*, respectively. According to the latest revisions *Alanphillipsia*, *Barriopsis*, *Botryobambusa*, *Cophinforma*, *Diplodia*, *Dothiorella*,

Endomelanconiopsis, *Eutiarosporella*, *Lasiodiplodia*, *Macrophomina*, *Marasasiomyces*, *Mucoharknessia*, *Neodeightonia*, *Neofusicoccum*, *Neoscytalidium*, *Oblongocollomyces*, *Sakireeta*, *Sardiniella*, *Sphaeropsis* and *Tiarosporella* are accommodated within *Botryosphaeriaceae* increasing the number of genera to 23 (Phillips et al. 2019, Zhang et al. 2021a, Hyde et al. 2024b). *Kellermania* and *Umthunziomyces* were accommodated in *Planistromellaceae* (Phillips et al. 2019). *Pseudofusicoccum* was included in *Phyllostictaceae* (Slippers et al. 2013, Phillips et al. 2019) and *Pileospora* was introduced while synonymizing *Septorioides* under *Saccharataceae* (Phillips et al. 2019). *Aplosporellaceae* presently accommodates *Alanomyces* and *Aplosporella* as the only accepted genera (Phillips et al. 2019, Zhang et al. 2021a). Morphology of *Botryosphaeriaceae*, *Planistromellaceae* and *Phyllostictaceae* played a crucial role in their inclusiveness within the order yet DNA-based phylogeny delimited the entire six families within *Botryosphaeriales*. Presently, *Botryosphaeriales* contains 35 genera distributed in six families (Phillips et al. 2019, Zhang et al. 2021a, Dissanayake et al. 2021a, Wijayawardene et al. 2022a). Several recent papers have introduced new species and provided new records of members of *Botryosphaeriales* (Senanayake et al. 2023).

General description

Families within *Botryosphaeriales* have varying morphologies both in their sexual and asexual morphs. Sexual morph characters include uni- or multi loculate ascostromata, ascospores with or without a mucilaginous sheath, aseptate, narrow, filiform pseudoparaphyses and septate hyaline or pale golden brown ascospores are distinctive features in delimiting families within the order. Another unique feature is the occurrence of large fruiting bodies bearing both sexual and asexual morphs within the same stroma. Large ascospores and fusiform conidia are also distinctive in *Botryosphaeriales*. Asexual morph characters include pigmented or hyaline, septate or aseptate conidia with or without a mucilaginous sheath. The occurrence of sexual morphs of *Botryosphaeriales* are rarely documented for all the genera compared to asexual morphs, thus delimitation of families within the order is based mainly on key asexual morph features (Phillips et al. 2013a, b, 2019).

Sexual morph: *Ascostromata* uni- or multi loculate, rectangular locules, individual or gregarious, brown to black, subglobose, pseudothecial, immersed to partially or fully erumpent, pulvinate. *Ostiole* central or periphysate, papillate, epidermal clypeus, thick-walled or multi layered dark brown cells of *textura angularis*, frequently or infrequently embedded in stromatic tissue arising solitary or as clusters. *Pseudoparaphyses* hyaline, broad, filiform, cylindrical, thin-walled, hyphal like, branched or non-branched, septate, constricted, or non-constricted at the septa, intermixed with asci, abundant or deliquescing at maturity. *Asci* 8-spored, bitunicate, fissitunicate, fasciculate containing thick endotunica, sessile or stalked, clavate, cylindric to clavate, short pedicellate or short stipitate, rounded at the apex with well-developed apical chamber. *Ascospores* 1–3 seriate, hyaline or pigmented, guttulate or granular, fusoid, ellipsoid to ovoid or rhomboid to obovoid, limoniform, smooth to verruculose, septate or aseptate, 1–2 transverse septate, mucoid appendages, mucilaginous sheath, or caps present or absent. Asexual morph: *Conidiomata* uni- or multi-loculate, pycnidial or acervular, solitary or gregarious, globose, dark brown, separate to aggregated, with a central ostiole, mostly or infrequently embedded in stromatic tissue or subepidermal, 3–6 layers of brown *textura angularis* cells. *Paraphyses* present or absent, hyaline, smooth walled, septate, branched or unbranched, hyphal-like arising between the conidiogenous cells. *Conidiophores* hyaline, subcylindrical, smooth, 1–2-septate, branched or not, sometimes reduced to *conidiogenous cells*. *Conidiogenous cells* hyaline, smooth, subcylindrical to ampulliform or doliiform, phialidic, branched or unbranched, discrete, 1–2-septate, smooth, percurrent proliferation or internally giving rise to periclinal thickening at apex, with or without collarettes, frequently covered in mucilaginous sheath.. *Conidia* ellipsoid to subcylindrical, fusoid to obovoid, ovoid or obclavate, hyaline or pigmented, muriform, septate or aseptate or multi-septate, thin or thick-walled, outer surface rough, spinulose, smooth, striate or verruculose, guttulate or granular, mucoid appendages or sheath present or absent, with or without single mucilaginous apical appendage. *Synasexual morph* coelomycetous or hyphomycetous. *Microconidiomata* separate or in same conidiomata with asexual morph.

Microconidiogenous cells ampulliform to lageniform or subcylindrical, hyaline, smooth, phialidic. *Microconidia* developing in conidiomata or spermatogonia, hyaline, smooth, granular,subcylindrical or dumbbellshaped, with rounded ends. *Synasexual conidia* pigmented, thick and small walled, finely verruculose, ellipsoid or oval, aseptate (adapted from Phillips et al. 2013a, b, 2019) (Fig. 19)

Families included in *Botryosphaeriales*

Aplosporellaceae Slippers, Boissin & Crous
Botryosphaeriaceae Theiss. & H. Syd. (= *Endomelanconiopsidaceae* Tao Yang & Crous)
Melanopsaceae Phillips A.J.L. Slippers, Boissin & Crous
Phyllostictaceae Fr. (= *Pseudofusicoccumaceae* Tao Yang & Crous)
Planistromellaceae M.E. Barr
Saccharataceae Slippers, Boissin & Crous (= *Septorioideaceae* Wyka & Broders)

Botryosphaeriales genera *Incertae sedis*
Auerswaldiella Theiss. & Syd.
Coccostromella Petr.
Mycosphaerellopsis Höhn.
Leptoguignardia E. Müll.
Metameris Theiss. & Syd.
Phyllachorella Syd.
Pilgeriella Henn.
Sivanesania W.H. Hsieh & Chi Y. Chen
Vestergrenia Rehm

Evolution

According to Phillips et al. (2019), the origin of *Botryosphaeriales* crown age lies within 110 (99–119) MYA which corresponds to the early Cretaceous period. The late epoch of the Cretaceous period was when the simultaneous diversification of flowering plants occurred by replacing the conifers (Coiffard et al. 2012). Woody angiosperms evolved around the end of the late Cretaceous and the start of the Paleogene period and are assumed to be the main hosts of the members of *Botryosphaeriales* (Coiffard et al. 2012). The divergence of the predecessors of *Botryosphaeriales* occurred presumably around this period whereas the present six lineages evolved during the end of the late epoch of the Cretaceous period and persisted towards the start of the Paleogene Period (66 MYA). The mass extinction is assumed to have occurred around 66 MYA and the six lineages survived, adapted, and diversified on the surviving hosts during the Eocene epoch of the Paleogene period. Subsequently, the six lineages that were presumably identified as the families of *Botryosphaeriales* diverged into present-day genera and species on specialized hosts (Slippers et al. 2013, Phillips et al. 2019). The time ranges considered appropriate as *Dothideomycetes* evolution also occurred within 100-220 MYA (crown age) (Liu et al. 2017b) verifying the evolution of *Botryosphaeriales* within these time ranges (Phillips et al. 2019).

The latest study on evolution and ancestral character reconstruction for *Botryosphaeriales* was carried out by Rathnayaka et al. (2023). Asexual morphology, such as conidal color and septation together with the nutritional mode of the taxa were considered in divergence time estimation within the order. The study confirmed the origin of *Botryosphaeriales* around 109 MYA in the early epoch of the Cretaceous period whereas six families evolved during the late epoch of the Cretaceous period (66–100 MYA) confirming the previous studies conducted by Phillips et al. (2013a, b, 2019), and Slippers et al. (2013). The diversification of the families occurred during Paleogene and Neogene periods in the Cenozoic era (Rathnayaka et al. 2023). The establishment and diversification of *Botryosphaeriaceae* and *Phyllostictaceae* occurred in the Cretaceous period while *Melanopsaceae*, *Planistromellaceae*, *Saccharataceae* and *Aplosporellaceae* diversified in the Paleogene and Neogene periods in the Cenozoic era (0–66 MYA) (Rathnayaka et al. 2023). The diversification of asexual morph characters, such as conidial color and septation, occurred during the Eocene of the Paleogene

period (33.9–56 MYA). Hyaline to pigmented and aseptate to septate conidial diversification occurred confirming that common ancestral characters are hyaline aseptate conidia for the taxa within the order. Evolution of the basic nutritional mode for the order is pathogenic/endophytic and occurred around 136 MYA. It evolved into a pathogenic/saprobic ancestral nutritional mode during 109 MYA which later became endophytic/pathogenic/saprobic during the late epoch of the Cretaceous period (100 MYA) resulting in multiple lifestyle switches among the taxa within the order. The pathogenic/saprobic life mode was confirmed as the ancestral character in *Botryosphaeriales* due to the lack of evidence for pathogenic/endophytic life mode (Rathnayaka et al. 2023).

Among the taxa in *Botryosphaeriales*, so far, the fossil records have been observed for *Diplodia* from permineralized chert from the Deccan Intertrappean bed, India (Mahabale 1968). *Diplodia intertrappea* was morphologically identified as two-celled spores, thick-walled with oval pycnidia (Taylor et al. 2015b). *Diplodites rodei* (≡ *Diplodia rodei*) and *Diplodites sahnii* (≡ *Diplodia sahnii*) fossils belonging to the late Cretaceous period were documented from the Mohgaonkalan locality in Chhindwara District, Madhya Pradesh, India (Saxena et al. 2021). The morphological characters observed indicated 1-septate dark brown or aseptate light brown conidia similar the extant fungi of *Diplodia*, *Dothiorella* and *Macrophoma* thus providing evidence towards the presence of *Diplodia* ancestors in the late Cretaceous period (Kalgutkar et al. 1993, Saxena et al. 2021).

Justification of order and problems

Circumscribed members of *Botryosphaeriales* have undergone numerous taxonomic revisions based on their morphology, phylogeny, evolutionary relationships and ancestral character reconstructions throughout the recent years (Liu et al. 2012b, Phillips et al. 2013a, 2019, Slippers et al. 2013, Crous et al. 2015d, Yang et al. 2017c, Rathnayaka et al. 2023). So far, many species have been introduced yet plasticity in morphological characters makes it difficult to effectively delimit species within the order (Slippers et al. 2014, 2017, Zhang et al. 2021a). Inferring phylogenetic relationships towards species circumscription lacks consensus due to the unavailability of common gene regions and loci that can clearly define species boundaries within the order (Phillips et al. 2013a, b, 2019, Slippers et al. 2014, Zhang et al. 2021a). Furthermore, studies conducted with insufficient taxon sampling have resulted in incorrect phylogenies (Phillips et al. 2013a, b, 2019). Phillips et al. (2013) revisited *Botryosphaeriales* and accepted six families within the order based on DNA sequence data. Phillips et al. (2013a, 2019) also utilized sexual morphology and evolutionary relationships to define and validate the families accepted within the order. Rathnayaka et al. (2023) contributed significantly to this matter by analyzing ancestral characteristics of taxa based on conidial characters and nutritional mode thus verifying the evolutionary relationships and time-scales of *Botryosphaeriales* accordingly.

Significance

Ecological and economic roles

Members of *Botryosphaeriales* have cosmopolitan distribution, occurring in various life modes from endophytic pathogenic to saprobic, mainly as plant-associated fungi (Slippers et al. 2014, Slippers et al. 2017, Zhang et al. 2021a, Abeywickrama et al. 2023). The majority of taxa are reported on monocots and dicots associated with woody plants, preferably on trunks and branches (Phillips et al. 2013, Lawrence et al. 2017, Scarlett et al. 2018, Zhu et al. 2018). *Botryosphaeriales* species are associated with grapevine trunk diseases all around the world. Some taxa are reported on lichens and leaves as host substrates (Arx 1987, Barr 1987b, Denman et al. 2000, Mohali et al. 2007). *Botryosphaeria*, *Diplodia*, *Dothiorella*, *Lasiodiplodia*, *Neofusicoccum*, *Phyllosticta*, *Pseudofusicoccum* and *Saccharata* are commonly identified endophytes thriving on asymptomatic healthy tissues for longer durations (Zhang et al. 2021a). *Lasiodiplodia* and *Neofusicoccum* are endophytes in green manure crops (Abeywickrama et al. 2023). Some members of *Botryosphaeriales*, such as *Botryosphaeria* and *Lasiodiplodia*, are economically important phytopathogens causing destructive blight, wood canker, and dieback (Luo et al. 2019a, Phillips et al. 2019), avocados, citrus, grapevines and olives (Michailides 1991, McDonald et al. 2009,

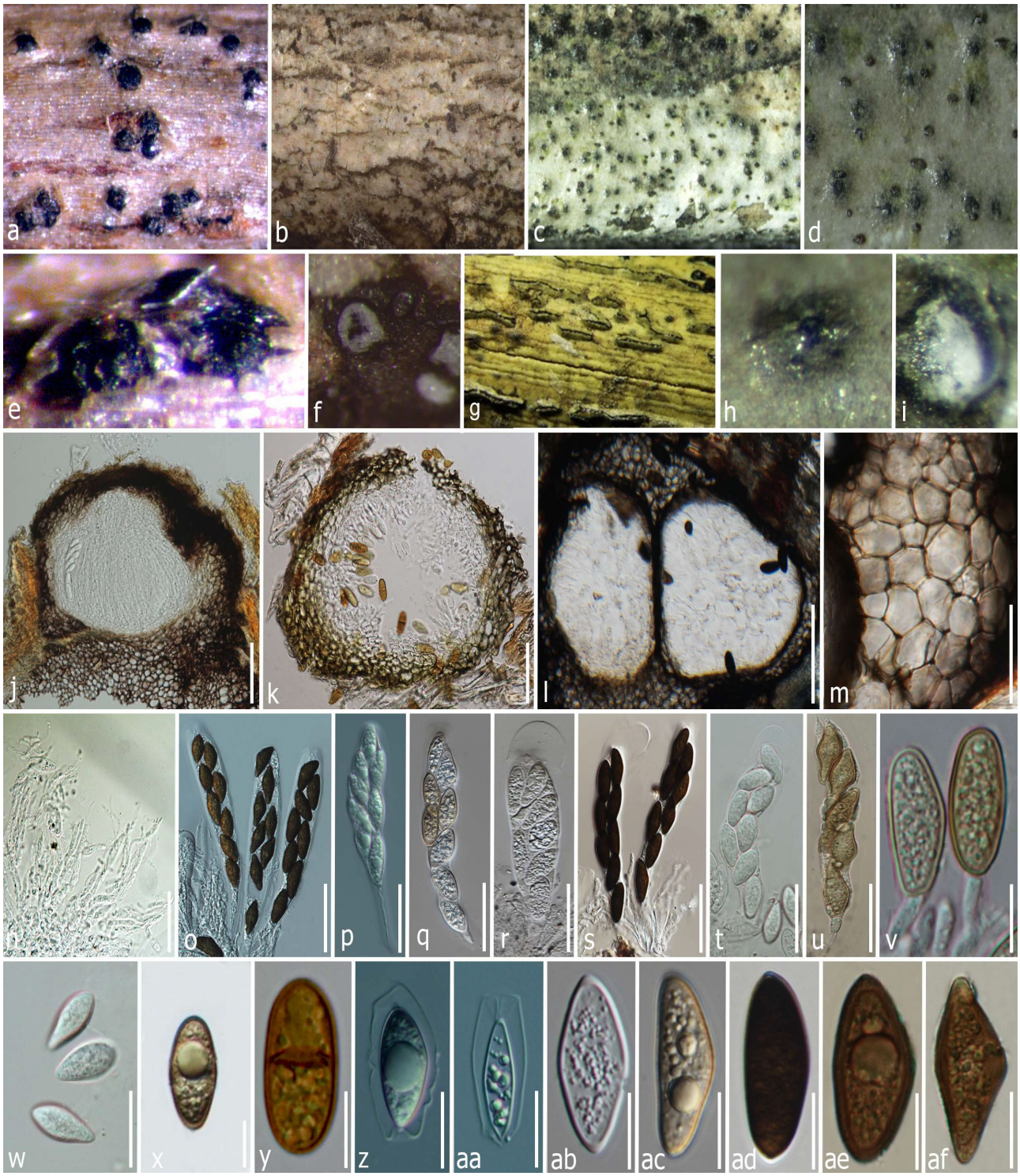


Figure 19 – Morphology of *Botryosphaeriales*. a, e Conidiomata of *Dothiorella sarmentorum*. b, f, g Ascomata of *Botryobambusa guizhouensis*. c, d, h, i. Ascomata of *Neodeightonia arengae*. j Cross section through an ascoma of *Botryosphaeria fabicerciana*. k Cross section through conidioma of *Dothiorella sarmentorum*. l Cross section through an ascoma of *Sphaeropsis eucalypticola*. m Cross section through peridium of *Sphaeropsis eucalypticola*. n Cross section through hamathecium of *Botryosphaeria fabicerciana*. o, u Asci of *Barriopsis archontophoenicis*. q, r, s Asci of *Sphaeropsis eucalypticola*. p Asci of *Neodeightonia arengae*. t Asci of *Botryosphaeria fabicerciana*. v Conidiogenous cells of *Dothiorella sarmentorum*. w, x Ascospores of *Barriopsis tectonae*. y Conidium of *Dothiorella sarmentorum*. z, aa Ascospore of *Neodeightonia arengae*. ab, ac, ad Ascospore of *Sphaeropsis eucalypticola*. ae, af Ascospore of *Barriopsis archontophoenicis*. Scale bars: j, k = 50 µm, l, m = 10 µm, n = 20 µm, o–v = 20 µm, w–af = 15 µm.

Inderbitzin et al. 2010, Luque et al. 2010, Urbez-Torres 2011, Gramaje et al. 2012, Phillips et al. 2012, Úrbez-Torres et al. 2013, Chen et al. 2014, Linaldeddu et al. 2015, Nouri et al. 2018, Galarneau et al. 2019, Nouri et al. 2019, Holland et al. 2020). Saprobic *Lasiodiplodia* species, such as *Lasiodiplodia magnoliae* and *L. pseudotheobromae*, were recorded from dead twigs of *Magnolia candolii* (de Silva et al. 2019). Few members are known to cause human infections, but some examples are known in *Lasiodiplodia* and *Neoscytalidium* (Dionne et al. 2015, Zhang et al. 2021a).

Chemical diversity

The families of *Botryosphaeriales* including *Phyllostictaceae*, *Aplosporellaceae*, and *Botryosphaeriaceae*, are recognized as prolific sources of bioactive compounds due to their notable chemical diversity. *Phyllosticta* species, especially those inhabiting mangrove environments, produce a wide array of metabolites, such as isocoumarins, pyrone derivatives, polyketides, alkaloids, and terpenoids, which exhibit cytotoxic, antibacterial, antifungal, and antioxidant activities (Xu et al. 2019). Similarly, *Pseudofusicoccum* sp. has been identified to produce compounds of diketopiperazines such as cyclo (L-Pro-L-Val) and cyclo (L-Leu-L-Pro), which are known for their antibacterial, antifungal, and antioxidant activities (Alves et al. 2025). *Aplosporellaceae* members, including *Alanomyces manoharacharyi* and *Aplosporella javeedii*, synthesize unique compounds like alanomycins and sulfur-containing alkaloids (aplospojaveedins) with potential applications in the pharmaceuticals and cosmetic industries (Gao et al. 2024). Comparatively, the genera of *Botryosphaeriaceae* are reported to accommodate the highest chemical diversity among the families within the order. *Dothiorella* produce a diverse range of metabolites, including 6-methylpyridione analogues, benzofuran derivatives, sesquiterpenes, steroids, and cytosporone derivatives possessing antifungal, antibacterial, and anti-inflammatory properties (Salvatore et al. 2024a).

Endomelanconiopsis endophytica produces metabolites like endomelanconins, tenuazonic acid, and fumonisin, demonstrating antifungal, antibacterial, and antioxidant activities (Sun et al. 2016). *Eutiarosporella dactylidis* produces dactylidins with antifungal, antibacterial, and cytotoxic activities, while *E. tritici* produces triticins that suppress plant immune responses (Thynne et al. 2019). Furthermore, *Alanphillipsia* is notable in its biosynthesis of silver nanoparticles (AgNPs) (Shahim et al. 2019). *Cophinforma*, *Diplodia*, *Botryosphaeria*, *Lasiodiplodia*, *Macrophomina*, *Melanops*, *Neodeightonia*, *Neofusicoccum*, *Neoscytalidium*, *Phaeobotryon*, *Sphaeropsis*, and *Tiarosporella* are reported to synthesize diverse polyketide and terpenoid-derived compounds with notable biological activities, particularly antimicrobial and phytotoxic properties, highlighting their potential in agricultural and medicinal applications (Krzysiak 2006, Salvatore et al. 2020a,b, 2021a, 2024b, Nagel et al. 2021, Xu et al. 2021, Mosunova et al. 2022, Al-Khayri et al. 2023, Derviş & Özer 2023, Dhillon et al. 2024, Gurgel et al. 2024). These diverse fungal genera represent a rich reservoir of novel bioactive compounds. Their diverse biosynthetic pathways and unique chemical structures offer promising avenues for developing new drugs, biocontrols for agriculture, and derived applications.

Other relevant data and future recommendations

Botryosphaeriales species have a wide range of distribution, occurring on various host substrates (Zhang et al. 2021a). Slippers et al. (2017) highlighted difficulties in the use of morphological features among the taxa for correct species identification. Due to a lack of molecular tools, most of the earlier studies were based on single locus phylogenetic placements (Zhang et al. 2021a). Sequence-based molecular phylogeny occupying ITS, TEF1-α, TUB2, and RPB2 is shown to be useful together with morphological characters in delimiting species boundaries within *Botryosphaeriales* (Phillips et al. 2013a, b). It is vital to reassess the culture collection isolates occupying multi-gene phylogenies; thus, this in turn will aid towards reassessing species boundaries among taxa of *Botryosphaeriales* (Zhang et al. 2021a).

***Capnodiales* Woron. Annales Mycologici 23(1/2): 177 (1925)**

Subphylum : *Pezizomycotina*

Class : *Dothideomycetes*
Subclass : *Dothideomycetidae*

Introduction

Capnodiales was established based on *Capnodiaceae* Höhn. ex Theiss. and introduced to encompass the sooty mould fungi that are members of the families *Antennulariellaceae*, *Capnodiaceae*, and *Coccodiniaceae* (Woronichin 1925). Phylogenetic analyses placed *Coccodiniaceae* outside *Capnodiales*, and divided sooty mould fungi in two different lineages residing in *Capnodiales*/*Dothideomycetes* and *Chaetothyriales*/*Eurotiomycetes* (Geiser et al. 2006, Schoch et al. 2006, 2009b). Systematic studies, mostly based on rDNA sequence data, over time broadened the concept of the *Capnodiales* to accommodate morphologically and ecologically diverse fungal groups with different lifestyles and modes of nutrition distinct from the sooty moulds associated with sugary exudates of insects (Crous et al. 2007a, 2009c, 2016b, 2018a, Quaedvlieg et al. 2014, Hongsanan et al. 2017b, Lücking et al. 2017, Videira et al. 2017, Doilom et al. 2018, Trovão et al. 2019).

In a recent study on the *Capnodiales* including a large collection of sooty moulds, phylogenetic analyses of rDNA (LSU and ITS) and protein-coding (TEF1-α and RPB2) sequence data together with morphology and ecology revealed that the *Capnodiales* is a polyphyletic group and was split into seven orders, namely *Capnodiales sensu stricto*, *Mycosphaerellales* and five new orders *Cladosporiales*, *Comminutisporales*, *Neophaeothecales*, *Phaeothecales* and *Racodiales* (Abdollahzadeh et al. 2020). Furthermore, ancestral state reconstruction analysis of various lifestyles in *Capnodiales* recognized the epiphytic lifestyle as a character state more recently evolved and restricted to sooty mould taxa in *Dothideomycetes*. Thus, sooty mould fungi were restricted to *Capnodiales sensu stricto* as a distinct clade supported by sequence data and their unique morphology, ecology and mode of nutrition (Abdollahzadeh et al. 2020).

History

Since *Capnodiales sensu lato* has been split to seven orders including *Capnodiales sensu stricto* we hereafter use the term *Capnodiales* in the strict sense referring to dothideomycetous sooty moulds, epiphytic fungi that usually grow on leaf surfaces as a black colonies in association with honeydew of insects. Historically the sooty moulds date back to Woronichin (1925), who introduced *Capnodiales* to accommodate the sooty moulds in three families, *Antennulariellaceae*, *Capnodiaceae* and *Coccodiniaceae*. The above-mentioned sooty moulds were shown to belong to *Dothideomycetes* and *Eurotiomycetes*. These two groups of sooty moulds are found in the same niches but can be distinguished morphologically and ecologically as explained by Chomnunti et al. (2011).

Capnodiales is based on *Capnodiaceae* with *Capnodium* as type genus. Several mycologists have paid attention to the taxonomy of sooty mould fungi including *Dothideomycetes*, which have been reviewed in several studies (Hughes 1976, Chomnunti et al. 2011, 2014). In last two decades phylogenetic studies based on DNA sequence data have contributed to the taxonomy of these fungi (Crous et al. 2009c, Chomnunti et al. 2011, 2014, Abdollahzadeh et al. 2020). Through the years, dothideomycetous sooty moulds have been classified within *Capnodiales* in four families namely, *Antennulariellaceae*, *Capnodiaceae*, *Euantennariaceae* and *Metacapnodiaceae*. Recently, Abdollahzadeh et al. (2020) recognized two new families, *Neoantennariellaceae* and *Readerielliopsidaceae*, and increased the number of families to six. Of these, DNA sequence data are available only for *Capnodiaceae*, *Neoantennariellaceae* and *Readerielliopsidaceae*. To provide an updated classification which reflects the phylogenetic relationships of these fungi, it is necessary to include representative taxa for *Antennulariellaceae*, *Euantennariaceae* and *Metacapnodiaceae*. However, no DNA sequence data are presently available for the majority of families included in these studies. In the recent outline, Hyde et al. (2024b) accepted seven families within *Capnodiales.*

General description

Most commonly being associated with honeydew producing insects, forming a thin and black layer of hyphae or pseudoparenchymatous crust on the surface of leaves, fruits, branches and stems

or trunks. The outer wall surface of the hyphae is commonly encased in mucilage. Frequently sooty mould taxa show high levels of pleomorphy, and grow intermixed in an apparent harmony on the substrate surface (Hughes 1976, Crous et al. 2009c, Chomnunti et al. 2011, Abdollahzadeh et al. 2020).

Sexual morph: *Ascomata* develop superficially on the mycelium; subglobose to globose, with or without setae, dark brown, with a central ostiole. *Pseudoparaphyses* absent. *Asci* fasciculate, bitunicate, saccate, with a short pedicel, lacking an ocular chamber. *Ascospores* multiseptate or muriform, hyaline to brown. Asexual morph: hyphomycetous or pycnidial coelomycetous along with hyphomycetous synasexual morphs or spermatogonia (adapted from Hughes 1976, Crous et al. 2009c, Chomnunti et al. 2011, Abdollahzadeh et al. 2020) (Fig. 20).

Families included in *Capnodiales*

Antennulariellaceae Woron.
Capnodiaceae Höhn. ex Theiss.
Euantennariaceae S. Hughes & Corlett
Johansoniaceae Doilom, Phook. & K.D. Hyde
Piedraiaceae Viégas ex Cif., Bat. & S. Camposa
Neoantennariellaceae Abdollahz. & Crous
Readerielliopsidaceae Abdollahz. & Crous

Capnodiales genera *incertae sedis*
Anariste Syd.
Catenulomyces Egidi & de Hoog
Perusta Egidi & Stielow
Plurispermiopsis Pereira-Carv., Inácio & Dianese
Pseudoepicoccum M.B. Ellis
Racoleus R. Sant. & D. Hawksw.
Ramimonilia Stielow & Quaedvl.
Rosaria N. Carter
Stigmatodothis Syd. & P. Syd.
Stomiopeltis Theiss.

Evolution

Evolutionary studies on fungi have revealed that the saprobic lifestyle is a primitive and ancestral ecological character within *Dothideomycetes* and that several transitions have occurred to evolve a diverse set of lifestyles from saprobic to pathogenic, parasitic, ectophytic, endophytic, epiphytic and lichenized lifestyles (Ametrano et al. 2019a, Haridas et al. 2020). However, Bhunjun et al. (2024) provided strong arguments that most fungi have evolved from endophytic ancestors. In *Capnodiales sensu lato* the ancestral state reconstruction analysis based on multigene sequence data recognized the saprobic lifestyle as the ancestral character state, from which pathogenic, ectophytic, epiphytic and lichenised lifestyles have evolved (Abdollahzadeh et al. 2020). Among these, Adollahzadeh et al. (2020) recognized the epiphytic lifestyle as a derived or synapomorphic character state more recently evolved in the sooty mould fungi restricted to *Capnodiales sensu stricto*. In terms of morphology, as we have no sequence data for members of three sooty mould families, *Antennulariellaceae*, *Euantennariaceae* and *Metacapnodiaceae*, and many taxa within *Capnodiaceae*, it is too early to illustrate a clear evolutionary trend within *Capnodiales sensu stricto*.



Figure 20 – Insects and sooty mould growth on a leaf surface (*Capnodiales*). b Ascoma with setae of *Phragmocapnias betle*. c Asci and ascospores of *Phragmocapnias betle*. d Ascoma with 3-septate brown ascospores of *Chaetocapnodium insulare*. e, f Conidiomata with conidia of *Phaeoxyphiella phylicae*. g Conidioma of *Chaetocapnodium thailandense*. h Conidioma of *Chaetocapnodium tanzanicum*. i Conidioma of *Scolecoxyphium phylicae*. j Conidioma of *Phragmocapnias betle*. k Conidioma of *Scolecoxyphium leucadendri*. l Conidiomata of *Capnodium gamsii*. m Conidiomata of *Scorias aphidis*. n, o Conidiomata of *Conidiocarpus* sp. p Conidioma of *Leptoxyphium citri*. Scale bars: c, d, f, g, i–k = 20 µm; b, h, l, p = 25 µm; e, m–o = 50 µm.

Justification of order and problems

The high diversity in morphology, ecology, lifestyle, and mode of nutrition within *Capnodiales sensu stricto* which was established for *Capnodiaceae* sooty moulds with epiphytic lifestyles associated with honeydew of insects, questioned the monophyly of this order of *Dothideomycetes* (Crous et al. 2009c, Abdollahzadeh et al. 2020). Although phylogenetic studies based on ribosomal DNA sequence data shed more light on the phylogenetic relationships in *Capnodiales sensu stricto*, these studies suffered by producing poorly supported backbone phylogenies, and having an insufficient number of representative taxa for study (Crous et al. 2009c). Accordingly, Abdollahzadeh et al. (2020) used a combination of rDNA and protein-coding loci and a large collection of strains representing *Capnodiales sensu lato*.

Based on the sequences of four nuclear loci (LSU, ITS, TEF1-α and RPB2), this order was recognized as polyphyletic, and split into seven well supported clades/orders including *Capnodiales sensu stricto* restricted to the *Dothideomycetes* sooty moulds. This new concept for *Capnodiales* is also supported by two unique characters; the association with insect honeydew exudates, and an epiphytic lifestyle, which recently evolved in sooty moulds. The two main challenges facing the systematics of sooty moulds remain mixed infections on plant surfaces, and pleomorphy (Hughes 1976, Chomnunti et al. 2014). More than one asexual morph has commonly been observed on the plant surfaces, and reported in association with a single sexual morph, for which the connection was never confirmed in culture (Hughes 1972, 1976, Seifert et al. 2011).

Significance

Ecological and economic roles

Although the possibility of sooty mould nourishment from leachates and glandular secretions in the phyllosphere has been raised by researchers (Ruinen 1956, Hughes 1976), these fungi have no parasitic relationship with plants and are not known as pathogens. They reduce the photosynthetic ability of plants and marketability of plant products by producing a black, thick hyphal layer on the plant surface (Nelson 2008), but may also "smother" trees, leading to a gradual decline and reduced fruit production. Little information is available about the ecology, physiology and application of sooty moulds. Commonly, no plant preferences have been detected for sooty moulds, but few reports indicated some species are associated with certain or a few related plants (Yamamoto 1955, Hughes 1976). Sooty moulds derive nutrients from honeydew of insects and other secretions on plants and rocks and soil below infected plants (Boedijn 1931, Ruinen 1956, Barr 1987b). They are commonly foliicolous fungi found in tropical, subtropical and temperate climates (Chomnunti et al. 2014). They grow in extreme, unstable and complex hostile environments exposed to ozone, UV radiation and atmospheric fluctuations in competition with a dynamic microbiome which is probably related to their ability to produce some unique fungal metabolites with potential applications in agriculture, industry and medicine. Sooty mould fungi exhibited a significant potency in accumulation of atmospheric air pollutants associated with polycyclic aromatic hydrocarbons (PAHs) and heavy metals on leaves of deciduous trees (Jouraeva et al. 2006), which implies their potential to be exploited for bioremediation and environmental sustainability.

Chemical diversity

Limited studies can be found on the chemical aspects and properties of sooty moulds. Analysis of non-volatile metabolites of sooty moulds (e.g., *Capnodium*, *Leptoxyphium*) confirmed antioxidant and antifungal activity of their crude extracts comprised phenolic compounds, flavonoids and proteins against plant pathogens (Haituk et al. 2022). Schumacher et al. (2022) characterized the structure of two new lactone lipids of *Scorias spongiosa* with antimicrobial activity against pathogenic fungi (*Candida albicans*, *C. glabrata*, *C. krusei*, *Cryptococcus neoformans*) and bacteria (*Staphylococcus aureus*, methicillin-resistant *S. aureus*).

Other relevant data and future recommendations

Chomnunti et al. (2014) have explained the methods to work with sooty moulds, and the challenges facing the systematic studies on these fungi, which are strongly recommended to be

employed by students and researchers. Briefly, to improve the systematics of sooty moulds it is important to re-examine the type materials using molecular methods if they are available and suitable for DNA sequencing. Since they are pleomorphic and found together with other fungi to provide a natural classification system and update their systematics it is recommended to work with purified isolates via single spore isolation methods. Most of the few molecular studies on sooty moulds are based on rDNA sequence data, thus employing multigene phylogeny using protein-coding genes (e.g., RPB2) combined with rDNA data is a necessity. Even though RPB2 provides highly resolved phylogenies at different taxonomic level from species to families within this order, amplification and sequencing of this locus using the existing primers are difficult and time-consuming to obtain high quality sequences. Thus, it is recommended to develop sequences for other genes commonly used in fungal systematics (e.g., ACT1, TEF1-α, TUB2, CaM). Because of the unique ecology of sooty moulds, it is recommended to collect more isolates worldwide, and pay more attention to investigate their phylogeny, potential as biocontrol and bioremediation agents, and other possible applications in agriculture, industry and medicine.

Catinellales **Ekanayaka, K.D. Hyde & Ariyawansa, Fungal Diversity 105: 66 (2020)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

The order *Catinellales* is one of the four orders in *Dothideomycetes* that produce apothecial ascomata (Hongsanan et al. 2020a, Lestari et al. 2023). The order was established by Hongsanan et al. (2020a) with its sole family and type family, *Catinellaceae* Ekanayaka, K.D. Hyde & Ariyawansa, to accommodate the genus *Catinella* Boud based on multi-gene phylogeny, which was transferred from *Leotiomycetes*. Being a monospecific family, *Catinella* represents the type genus of *Catinellaceae* and comprises three accepted saprobic species (Hongsanan et al. 2020a, Wijewardene et al. 2022a), though four species are listed in the Index Fungorum (2024). The *Catinella* taxa are characterized by discoid, cupulate, flattened and sessile apothecia, attached to the substratum through radiating, dark fibres. The apothecial discs exhibit a fleshy and somewhat gelatinous texture when fresh, transitioning to a friable consistency when dry. The hymenium comprises an excipulum composed entirely of parenchymatous cells, exhibiting a deep violet hue in response to ionomidotic reaction with KOH. The asci of *Catinella* are inoperculate, comprising one-celled, pale brown, uniseriately arranged eight ascospores. The ascal tips do not exhibit blue in iodine and agglutinated with paraphyses to form an epithecium (Durand 1922, Hongsanan et al. 2020a). Members of this order are commonly found on the underside of damp, well-decayed hardwood logs, typically in areas predominantly concealed by moss and soil. This specific habitat preference contributes to the infrequency of reports for these taxa (Pomerleau 1980, Keizer 1990, Spooner & Legon 1999, Greif et al. 2007).

History

Since its introduction by Boudier (1907), the identification and taxonomic placement of *Catinella* taxa have been subjects of controversy. The genus was initially established to accommodate *Peziza olivacea*, which was transferred due to its inoperculate asci and intense ionomidotic reaction with KOH, differentiating them from other taxa in *Pezizaceae* (Durand 1922). *Catinella* taxa were transferred from *Pezizaceae* to *Dermateaceae* in *Helotiales* and were accepted based on their distinctive morphological characters, such as the presence of a hymenium supported within a blackish-olive discoid receptacle, comprising an excipulum of large, thin-walled, deeply pigmented, subangular to globose cells, which produced an intense response to ionomidotic reaction with KOH, inoperculate, 8-spored asci that show a negative reaction in iodine, and uniseriate, darkly pigmented, one-celled ascospores (Durand 1922, Seaver 1961, Korf 1973, Eriksson et al. 2004). Later, Spooner & Legon (1999) also suggested that *Catinella* taxa may be better aligned with the characters of

Leotiaceae, *Helotiales* based on the gelatinous layer that overlies the hymenium. These initial studies that placed *Catinella* taxa in the *Leotiomycetes* have relied on the observations of mature, field-collected apothecia and the structure of the ascal tip. However, the interpretations of the ascal tip structure can be ambiguous in older specimens (Greif et al. 2007); therefore, the reliability of older specimens might be biased.

In a later study, Strödel (1984) showed melanized ascospores of *Catinella* taxa with minutely verrucose walls, suggesting their affinities with *Dothideomycetes* rather than *Leotiomycetes*. In addition, these members followed an apothecial formation pattern commonly observed in *Dothideomycetes*, wherein the tissues destined to enclose the ascogenous system develop prior to the emergence of gametangia and ascogenous initials (Barr & Huhndorf 2001, Lindemuth et al. 2001, Greif et al. 2007). The apothecioid fruiting bodies with anchoring hyphae of *Catinella* taxa are similar to the ascomata of *Patellariales* taxa (Kutorga & Hawksworth 1997, Greif et al. 2007) and some subicular tissue prominent in some taxa in *Dothideomycetes* (Dennis 1977, Eriksson 1981, Greif et al. 2007). *Catinella* taxa also show similarities with some dothideomycetous taxa by having unitunicate asci, non-bluing ascal tips, and an ocular chamber along with the prominent bivalvate split, which indicates bitunicate taxa in *Dothideomycetes* (Eriksson 1981, Barr & Huhndorf 2001, Greif et al. 2007).

Greif et al. (2007) confirmed the affinity of *Catinella* taxa within *Dothideomycetes* rather than the *Leotiomycetes* using the combined LSU and SSU phylogeny of its type species; however, the study could not resolve the ordinal placement of the type species within *Dothideomycetes*. This is mainly due to the lack of sequence data for morphologically similar taxa, i.e. patellariales-like and karschia-like (Greif et al. 2007). Considering the morphological, developmental and phylogenetic characteristics, Hongsanan et al. (2020a) introduced the order *Catinellales*, along with the family *Catinellaceae*, to accommodate *Catinella* taxa, and confirmed the taxonomic disposition using the combined LSU, RPB2, SSU and TEF1-α based multi-gene phylogeny and divergence time analyses (Hongsanan et al. 2020b).

General description

As *Catinellales* comprises a single genus with only three described species, the morphological characters of this order are very narrow. Only the sexual morphs of the order have been described, and no asexual morphs have been described yet for *Catinella* (Fig. 21).

Sexual morph: *Apothecia* discoid, solitary or two or three together, initially greenish-yellow, becoming darker green to blackish-olive when matured, fleshy, sometimes gelatinous when fresh, becomes olive-black, exterior brownish, somewhat furfuraceous or vertically striate, friable when dry, sessile, attached to the substrate by numerous, thick, radiating, brownish hyphae, spherical when young, becoming cup- to saucer-shaped and finally applanate, with an upturned margin at maturity. *Excipulum* comprising *textura angularis* to *textura globose*, dark brown, parenchymatous ectal cells, becoming smaller towards the hymenium. *Hymenium* smooth, yellowish-olive to brownish-olive, producing a deep violet hue in response to ionomidotic reaction with KOH. *Hamathecium* comprises cylindric, septate, and paraphyses. *Paraphyses* septate, cylindrical, rarely branched, somewhat longer than the asci, slightly swollen and agglutinated at the tips. *Asci* 8-spored, narrowly cylindric-clavate, rounded and non-bluing (J-) apex, inoperculate with an ocular chamber, J-. *Ascospores* uniseriate, ellipsoidal, slightly narrowed near the middle, light brown to brownish, smooth. Asexual morph: Undetermined (adapted from Greif et al. 2007, Akata et al. 2016, Hongsanan et al. 2020a).

Families included in *Catinellales*

Catinellaceae Ekanayaka, K.D. Hyde & Ariyaw.

Evolution

Hongsanan et al. (2020b) conducted the first and only evolutionary analysis for the class *Dothideomycetes* using divergence time estimates based on the combined sequence data of LSU, RPB2, SSU and TEF1-α. Based on the maximum clade credibility tree obtained from the Bayesian approach, the order *Catinellales* has a divergence time of 163 MYA.

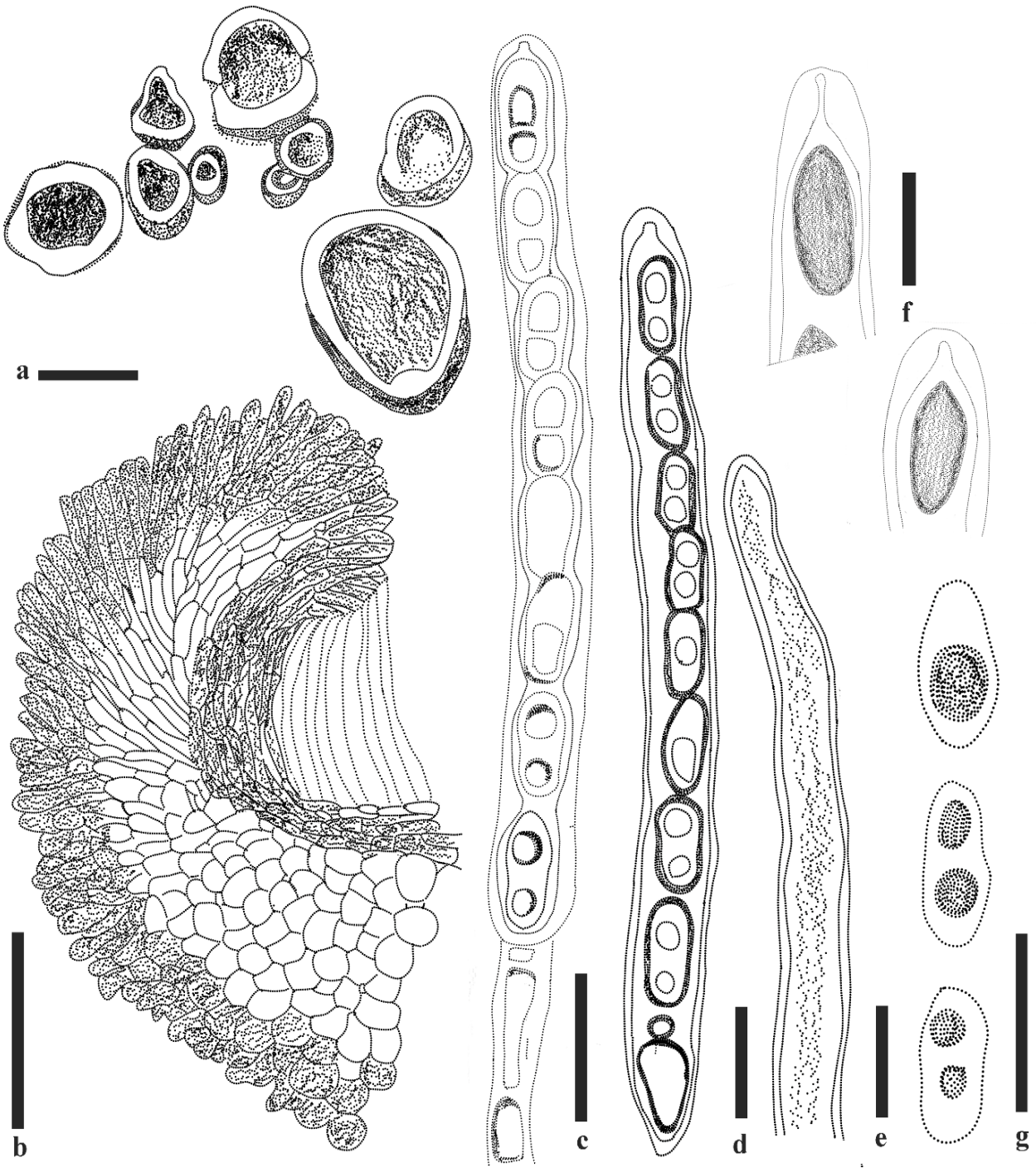


Figure 21 – Morphological characters of the type species *Catinella olivacea*. a Apothecia. b Section of the mature ascoma; The hymenium was covered by a dark pseudoepithecium. c, d Ascus with a single wall layer and a thickened apex. e Anchor hyphae. f Close-up of the ascal tips with clearly visible ocular chambers. g Mature ascospores (redrawn from (b= Hongsanan et al (2020a), a, c–e, g = Akata et al (2016), f = Greif et al. (2007))). Scale bars: a, c–e = 20 μm, b, g = 10 μm, f = 7 μm.

Justification of order and problems

Even though Greif et al. (2007) showed the affinity of *Catinella* taxa within *Dothideomycetes*, the ordinal placement of the genus was not resolved. Members of *Catinella* differ from *Holmiellales* and *Homortomycetales* in having apothecial, discoid ascomata, excipulum composed of angularis to globose cells and cylindric, septate, paraphyses. The differences in the multi-gene phylogenies and significant morphological differences observed among the phylogenetically-related *Homortomyces*, *Catinella*, *Holmiella* and *Botryosphaeriales* make the separation into four orders (*Homortomycetales*,

Catinellales, *Holmiellales*, and *Botryosphaeriales*) straightforward. Therefore, Hongsanan et al. (2020b) established the order *Catinellales* to accommodate the *Catinella* taxa.

Significance

Ecological and economic roles

All the *Catinellales* taxa identified so far are terrestrial saprobes and have been identified from Canada on *Pinus resinosa* (Ginns 1986) and *Populus tremuloides* (Greif et al. 2007), China on decaying wood (Zhuang & Wang 1998), Sweden on *Popolus* sp. (Eriksson 2014), Ukraine on *Fagus sylvatica* (Dudka et al. 2004), and the United Kingdom on *Fagus* sp., *Fraxinus* sp., *Popolus* sp., *Salix* sp., *Ulmus* sp. (Dennis 1986). They play a role in the decomposition and recycling of organic matter (Durand 1922, Akata et al. 2016, Hongsanan et al. 2020a).

Chemical diversity

No studies reported on the chemical diversity of the taxa in *Catinellales*.

Other relevant data and future recommendations

Given the limited study, sparse species representation, and insufficient molecular data available for the *Catinellales* taxa in question, it is strongly recommended to prioritize and invest in comprehensive research efforts. Establishing a thorough investigation involving increased taxon sampling, thorough species documentation, and the generation of more molecular data is crucial. This approach will not only enhance our understanding of these poorly studied *Catinella* taxa but also contribute to a more accurate and robust classification system for *Catinellales* and closely related orders.

Cladosporiales **Abdollahz. & Crous, Studies in Mycology 95: 390 (2020)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Dothideomycetidae*

Introduction

Members of *Cladosporiales* were previously treated in *Capnodiales*. *Cladosporiales* was introduced by Abdollahzadeh et al. (2020), which belongs to *Dothideomycetes*. *Cladosporiales*, similar to *Dothideomycetes*, can be found in a variety of lifestyles and environments (Iturrieta-González et al. 2021). *Cladosporiales* contains a single family, *Cladosporiaceae*, which includes eight genera: *Acroconidiella*, *Cladosporium*, *Davidiellomyces*, *Graphiopsis*, *Neocladosporium*, *Rachicladosporium*, *Toxicocladosporium* and *Verrucocladosporium* (Wijayawardene et al. 2022a). Members of the *Cladosporiaceae* are generally saprobic and endophytic, with a few fungicolous, lichenicolous, or plant and animal pathogenic species (Heuchert et al. 2005, Heuchert et al. 2014, Sandoval-Denis et al. 2015). Although some *Cladosporiales* species reverted to parasitism, saprobes were the primitive lifestyle of all *Cladosporiales* (Abdollahzadeh et al. 2020).

History

Nannizzi (1934) introduced *Cladosporiaceae* in *Capnodiales* to accommodate *Cladosporium* which is one of the largest genera of dematiaceous hyphomycetes. Lindquist & Alippi (1964) proposed *Acroconidiella* to accommodate *Acroconidiella tropaeola*, which is now accepted in *Cladosporiaceae*, *Cladosporiales*. Based on DNA data, Braun et al. (2003) established a new genus *Davidiella* in *Mycosphaerellaceae* and confirmed it as the sexual morph of *Cladosporium*. Further, *Cladosporium malorum* was transferred to *Alternaria*, which is supported by its distinct conidiogenesis (Braun et al. 2003). Aptroot (2006) indicated the differences in ascospores of *Davidiella* and *Mycosphaerella*. Subsequently, phylogenetic analysis of combined LSU, SSU, RPB2 and TEF1-α sequence data was carried out and introduced *Davidiellaceae* in *Capnodiales* as a new family to accommodate *Davidiella* and its *Cladosporium* asexual morphs (Schoch et al. 2006). Crous et al. (2007b) also agreed that several cladosporium-like genera are phylogenetically unrelated to

Cladosporium and placed in *Davidiellaceae*, *Capnodiales*. Crous et al. (2007b) introduced *Toxicocladosporium*, *Rachicladosporium*, *Verrucocladosporium* in the genera *incertae sedis*, whereas *Rachicladosporium*, and *Verrucocladosporium* formed a separate clade from *Toxicocladosporium* species. Bezerra et al. (2017b) introduced *Neocladosporium* in *Cladosporiaceae* as five other isolates formed a distinct phylogenetic clade. *Davidiellomyces* was introduced to accommodate *Davidiellomyces australiensis*. Following the identification of many non-dictyoconidial taxa as belonging to *Alternaria*, Ferreira & Barreto (2019) investigated *Acroconidiella tropaeoli* using multi-gene phylogeny and transferred *A. tropaeoli* to *Alternaria*. Since the type species of *Acroconidiella* was transferred to other genus, the placement of other *Acroconidiella* species is uncertain. Abdollahzadeh et al. (2020) carried out the taxonomic reconstruction of *Capnodiales*, including taxa from 11 families and two *incertae sedis* genera and separated the new order *Cladosporiales* from the *Capnodiales* based on molecular data (Abdollahzadeh et al. 2020).

General description

Cladosporium species produce olive-brown to black colonies, and have dark-pigmented conidia that are formed in simple or branching chains. They have velvet texture culture like other molds. Fungi in this order can be frequently found as asexual stage and rarely found in sexual stage (Liu et al. 2024). However, molecular phylogeny confirmed *Davidiellomyces* as the sexual morph of *Cladosporiaceae*.

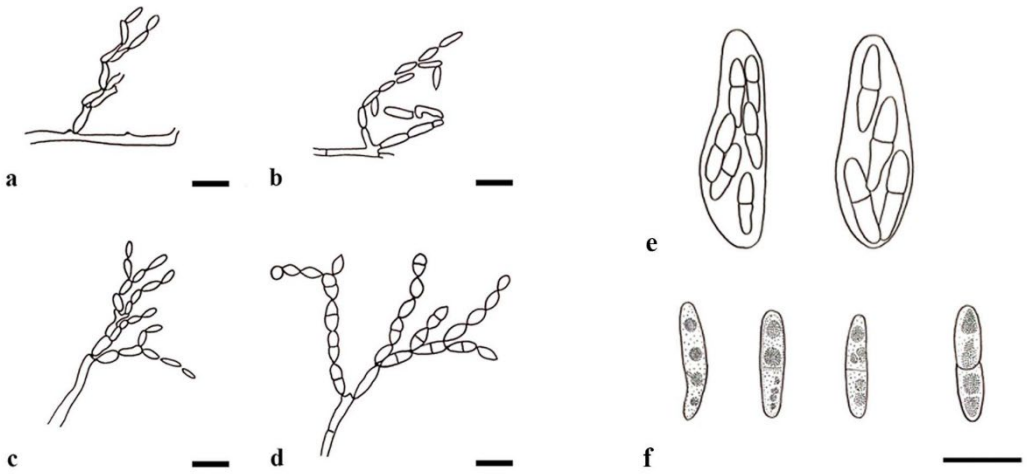


Figure 22 – Conidiophores and conidia morphology of *Cladosporiales*. a *Neocladosporium leucadendri.* b *Neocladosporium leucadendri.* c *Rachicladosporium luculiae.* d *Toxicocladosporium irritans*. e Asci of *Davidiellomyces australiensis*. f Ascospores of *Davidiellomyces australiensis*. (drawn from Crous et al. 2007b, Bezerra et al. 2017b, Crous et al. 2017b). Scale bars: a–d = 10 μm.

Sexual morph: *Ascomata* immersed to superficial, scattered or gregarious, brown to black, globose to subglobose, uniloculate, with or without ostioles. *Ostiole* numerous periphysoids. *Peridium* composed of several layers of brown *textura angularis* cells. *Hamathecium* hyaline, pseudoparaphyses with subcylindrical shape, septate. *Asci* 8-spored, bitunicate, obovoid to ellipsoid or subcylindrical, smooth, hyaline, sessile to subsessile, with or without apical ring. *Ascospores* fasciculate, obovoid, sometimes ellipsoid to fusiform, guttulate, hyaline to pale brown, smooth to slightly roughened, septate, with or without gelatinous sheath. Asexual morph: Hyphomycetous. *Colonies* effuse, velvety, greyish-brown to brown on host substrate. *Mycelium* immersed, branched, septate, pale brown, smooth to verruculose hyphae. *Conidiophores* macronematous, mononematous, solitary, growing terminally and laterally from hyphae, erect, straight to slightly curved, cylindrical, oblong to filiform, sometimes geniculate, unbranched or branched. *Conidiogenous cells* polyblastic, integrated, terminal, and intercalary growth, often markedly sympodially proliferating, filiform,

cylindrical to oblong, prominent, subdenticulate to denticulate. *Conidia* catenate, in tightly branched, acropetal chains, straight to slightly curved, smooth or verruculose, subhyaline to brown; terminal conidia globose to obovoid, rounded at the apex, intercalary conidia subglobose, aseptate, with distal hila, broadly ellipsoid-ovoid, denticulate (Fig. 22)

Families included in *Cladosporiales*

Cladosporiaceae Chalm. & R.G. Archibald

Evolution

The evolution of *Cladosporiales* has been studied using various molecular approaches. Phylogenetic analyses based on DNA sequence data have provided insights into the relationships and evolutionary patterns within this group. Through the integration of phylogenetic analyses, along with considerations of morphology and ecology, it has been determined that the *Capnodiales*, in the broader sense, are not monophyletic (Abdollahzadeh et al. 2020).

According to multiple studies (Schoch et al. 2006, 2009b, Crous et al. 2009d, Suetrong et al. 2009, Bensch et al. 2012, Hyde et al. 2013, Van Nieuwenhuijzen et al. 2016b, Videira et al. 2017), members of *Cladosporiaceae* have been identified as a distinct clade separate from *Capnodiaceae*, *Mycosphaerellaceae*, and related families including *Dissoconiaceae*, *Extremaceae*, *Neodevriesiaceae*, *Phaeothecoidiellaceae*, *Schizothyriaceae*, and *Teratosphaeriaceae*. Abdollahzadeh et al. (2020) also found that *Cladosporiaceae* clustered separately from *Mycosphaerellales* and *Capnodiales sensu stricto*. As a result, *Cladosporiaceae* has been elevated to the ordinal level and recognized as *Cladosporiales*. In terms of morphology, members of *Cladosporiales* exhibit notable distinctions from those of *Mycosphaerellales*, characterized by elongated, individual, flexible conidiophores that form chains of dry, pigmented conidia (Liu et al. 2024). However, the members of *Cladosporiales*, which originated from a common ancestor, were saprobes, certain species within the *Cladosporiales* later returned to a parasitic lifestyle (Abdollahzadeh et al. 2020).

In summary, molecular evidence from phylogenetic and genomic studies, combined with ecological observations, provides insights into the evolutionary history of *Cladosporiales*. These studies suggest that the order has diversified in response to environmental pressures and interactions with other organisms, leading to the emergence of diverse lifestyles and ecological roles.

Justification of order and problems

Cladosporiales species were initially identified in the *Capnodiales*, which is the order dominated by sooty moulds. Previous phylogenetic studies on *Capnodiales* all suffered from their lack of sampling of real sooty moulds. However, Abdollahzadeh et al. (2020) included a large number of samples in the study and made a revision on *Capnodiales*. Abdollahzadeh et al. (2020) used two protein-coding genes (TEF1-α and RPB2) with rDNA sequence data (LSU and ITS) to generate a more reliable phylogeny for these highly diverse fungi. The revealed *Capnodiales* as polyphyletic and established *Cladosporiales* as a separate order from *Capnodiales*. Currently, ITS, ACT and TEF1-α are the common gene regions which used in many studies to construct phylogenetic tree for this fungal group.

Significance

Ecological and economic roles

The members of *Cladosporiales* are significant in their various ecological and economic roles. *Cladosporiales* taxa are among the dominant decomposers in a forest ecosystem (Baldrian et al. 2012). They are responsible for breaking down leaf litter and contributing to nutrient cycling in the soil (Baldrian et al. 2012). *Cladosporium* species play a significant role in straw degradation, releasing nutrients back into the soil (Benito et al. 2015). The potential of *Cladosporium cladosporioides* was evaluated in degrading the pesticide hexachlorocyclohexane (HCH). Dua et al. (2012) demonstrated that this fungus could effectively degrade HCH, suggesting its application in bioremediation processes. *Cladosporium cladosporioides* is able to remove heavy metals from

contaminated soil (Gupta et al. 2019) demonstrating its potential for soil remediation (Gupta et al. 2019). *Cladosporiales* species have negative impacts on indoor air quality as they are common fungi in many places where moisture is present. Sharma et al. (2017) analyzed indoor air samples from different locations and found that *Cladosporium* was one of the most prevalent genera, indicating their significance as indoor allergens. The impact of *Cladosporium* species on respiratory health in children revealed a positive association between *Cladosporium* exposure and the development of asthma symptoms (Simoni et al. 2010).

The taxa in this order have both advantages and disadvantages in both ecological and economic aspects (Rep et al. 2005, Jönsson et al. 2008, Shahzad et al. 2017, Fouda et al. 2019). *Cladosporiales* species as fungal pathogens, they can cause economic losses. *Cladosporium fulvum*, is the causal agent of tomato leaf mold disease. This pathogen can cause substantial yield losses in tomato crops (Rep et al. 2005). The impact of *Cladosporium* on the health of European beech trees was investigated that certain *Cladosporium* species caused foliar damage and reduced tree growth, highlighting their role as plant pathogens in forest ecosystems (Jönsson et al. 2008). Although several pathogens in *Cladosporiales* have negative impacts in economy, the endophytic members of *Cladosporiales* have positive impacts on agricultural sector. A rice associated endophyte, *Cladosporium cladosporioides* enhanced the growth and drought tolerance of their host (Shahzad et al. 2017). Fouda et al. (2019) studied the endophytic fungi in tomato plants and identified *Cladosporium cladosporioides* suppressing the growth of the fungal pathogen *Botrytis cinerea*.

Chemical diversity

Cladosporiales encompasses a diverse group of fungi known for their remarkable chemical diversity. Members of this order produce a wide array of secondary metabolites, which play significant roles in ecological interactions, including defense against competitors, pathogens and predators. The presence of alkaloids, flavonoids, phenols, terpenoids and tannins has been detected in the endophytes, *Cladosporium cladosporioides* and *C. tenuissimum* (Jayaram et al. 2021). *Cladosporium* species have been found to synthesize diverse natural compounds, including melanins that contribute to their characteristic coloration, antifungal cladosporides (Hosoe et al. 2000, 2001), plant growth factors known as cotylenins (Sassa et al. 1971, 1975), calphostins which is a protein kinase C inhibitor (Kobayashi et al. 1989), and the multifunctional compound cladosporin. Cladosporin exhibits a broad range of activities, including antifungal, antibacterial, insecticidal, phytotoxic, and immunosuppressive properties (Scott et al. 1971, Anke et al. 1978, Grove & Pople 1981, Springer et al. 1981, Fujimoto et al. 1999, Imhoff 2016). Cladosporin also holds significant promise as a targeted herbicide for controlling monocot weeds in agriculture. It also demonstrates for the potential as a valuable starting point in the development of agrochemicals targeting specific plant pathogens, as well as pharmaceuticals with applications against drug-resistant bacteria and parasites (Wang et al. 2016d). The fungus *Cladosporium cladosporioides*, obtained from the Chilean sponge *Cliona* sp. has been documented as the source of the natural product N-Methyl-1H-indole-2-carboxamide (Manriquez et al. 2009, Rateb & Ebel 2011). *Cladosporium cladosporioides*, the commonly found species from various habitats, is the source of various secondary metabolites such as *N*-*β*-acetyltryptamine and *β*-carboline (Salvatore et al. 2021b). According to Peng et al. (2013), *Cladosporium* species obtained from mangroves and known for their production of indole alkaloids exhibited significant activity against the influenza virus A (H1N1) (Archana & Nagadesi 2022).

Other relevant data and future recommendations

Members of *Cladosporiales* are common mold in both indoor and outdoor environments and can be found in a wide range of substrates and habitats (Bensch et al. 2010, 2012, Sandoval-Denis et al. 2015, Temperini et al. 2018, Chung et al. 2019). Species of *Cladosporiales* are saprobic, but some have also been reported as endophytes, pathogens on other fungi and plants as well as human and animal pathogens (Heuchert et al. 2005, Sandoval-Denis et al. 2016b, de Hoog et al. 2017, Marin-Felix et al. 2017). Several fungal taxa with similar morphology have been attributed to *Cladosporiales*. Due to the imprecise taxonomic status of *Cladosporium*, the genus has been assigned

numerous superficially similar but unrelated hyphomycetes, which makes this genus highly heterogeneous. Moreover, the species in this order are also the sources of diverse chemical compounds. Therefore, the systematic study of species and the discovery of secondary metabolites in this order are essential for taxonomists and researchers.

***Cladoriellales* Crous, Persoonia 39: 417 (2017)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction and History

Cladoriellales was established by Crous et al. (2017a) for a single family *Cladoriellaceae* and a single genus *Cladoriella*. The genus was established for the species that occurred on *Eucalyptus* leaf litter in Australia and South Africa (Crous et al. 2006, 2017a, Cheewangkoon et al. 2009). The order presently comprises five species: *Cladoriella eucalypti* (type), *C. kinglakensis*, *C. paleospora*, *C. rubrigena* and *C. xanthorrhoeae* All the taxa have only been reported in their asexual morph (Crous et al. 2006, 2017a, Cheewangkoon et al. 2009). *Cladoriella* resembles *Devriesia* in general morphology but differs in the absence of chlamydospores and forms distinct red pigments in culture (Cheewangkoon et al. 2009, Crous et al. 2017a). In phylogenetic analyses the order formed a sister clade to *Asterinales* (Crous et al. 2017a).

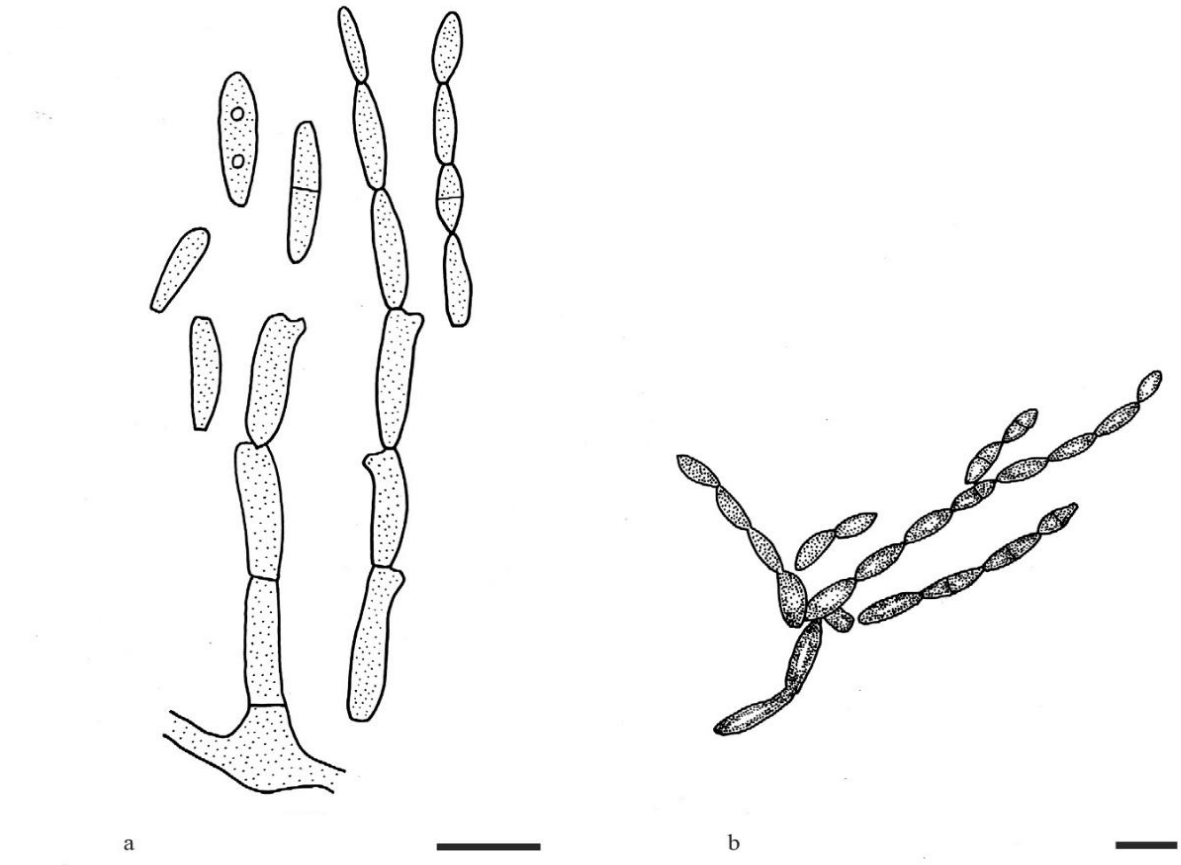


Figure 23 – Conidiophore and conidial morphology of *Cladoriellales*. a *Cladoriella eucalypti*. b *Cladoriella xanthorrhoeae* (drawn and redrawn from Crous et al. 2017a). Scale bar = 10 µm.

General description

The members of *Cladoriellales* are only reported in asexual morph (Crous et al. 2006, 2017a, Cheewangkoon et al. 2009) (Fig. 23).

Sexual morph: Unknown. Asexual morph: *External hyphae* coiling on the leaf surface, medium to dark brown, thick-walled, smooth to finely verruculose, branched, septate, swollen cells giving rise to conidiophores; hyphododia-like structures present, simple, intercalary. *Conidiophores* separate, erect, medium to dark brown, smooth to finely verruculose, thick-walled, subcylindrical, straight, septate. *Conidiogenous cells* terminal or intercalary, mono or polytretic, sympodial, with 1–2 conspicuous loci, thickened, darkened, refractive, with a minute central pore. *Conidia* frequently remaining attached in long acropetal chains, simple or branched, narrowly ellipsoidal to cylindrical or fusoid, septate, medium brown, thick-walled, finely verruculose, apical conidium with rounded apex, additional conidia with truncate, conspicuous hila; thickened, darkened, refractive, with a minute central pore (adapted from Crous et al. 2006, 2017a, Cheewangkoon et al. 2009).

Families included in *Cladoriellales*

Cladoriellaceae Crous

Evolution

The divergence time for *Cladoriellales* is estimated as 183 MYA (Hongsanan et al. 2020b).

Justification of order and problems

Cladoriellales formed a close phylogenetic relationship to *Parmulariales* (represented by *Parmularia styracis* VIC 42447) and *Thyrinulaceae* in the phylogenetic analyses conducted by Hongsanan et al. (2020a).

Significance

Ecological and economic roles

The taxa are reported as saprobes or pathogens on the leaf surfaces. The members mostly occur on *Eucalyptus*. *Cladoriella xanthorrhoeae* was exceptionally reported on dead leaves of *Xanthorrhoea* species (Crous et al. 2017a).

Chemical diversity

No chemical diversity is reported in *Cladoriellales*.

***Collemopsidiales* Pérez-Ort., Garrido-Ben. & Grube, Fungal Diversity 80: 296 (2016)**

Subphylum : *Pezizomycotina*
Class : *Collemopsidiomycetes*
Subclass : *Incertae sedis*

Introduction

Collemopsidiales includes over 78 species assigned to six genera in a single family *Xanthopyreniaceae* (Grube & Hafellner 1990, Mohr et al. 2004, Grube 2005, Pérez-Ortega et al. 2016, Khodosovtsev & Darmostuk 2017a, b, Diederich et al. 2018, Fernández-Brime et al. 2020). Wijayawardene et al. (2018) excluded the genera *Frigidopyrenia* and *Pyrenocollema* from *Xanthopyreniaceae* and placed them in *Pezizomycotina* genera *incertae sedis*. The order includes species with different habitat preferences and nutritional modes, such as algicolous, lichen-forming, lichenicolous fungi and so-called borderline lichen (Pérez-Ortega et al. 2016, Khodosovtsev & Darmostuk 2017a). The species are distributed across all continents and inhabit aquatic (marine and freshwater) as well as terrestrial habitats. The diversity of the order has been largely underestimated due to insufficient sampling and lack of molecular data.

History

Collemopsidiales was established by Pérez-Ortega et al. (2016) to accommodate the genera *Collemopsidium* and *Zwackhiomyces*. Later, Tedersoo et al. (2018) introduced the class *Collemopsidiomycetes* for *Collemopsidiales* within *Ascomycota*. However, Hongsanan et al. (2020a) did not accept the new class and instead suggested that *Collemopsidiomycetes* should be synonymized with *Dothideomycetes* (Pérez-Ortega et al. 2016).

Xanthopyreniaceae was introduced by Zahlbruckner (1926) with *Xanthopyrenia* as the type genus. Later, the generic type *Xanthopyrenia tichothecioides* (Arnold) Bachm. (= *Arthopyrenia tichothecioides*), was transferred to *Pyrenocollema* (Tucker & Harris 1980). Consequently, *Pyrenocollema* was long applied to species that were originally classified under *Arthopyrenia* or *Verrucaria*, characterized by their unique anastomosing paraphyses, two-celled ascospores, and cyanobacterial photobionts (Coppins et al. 1992, Harris 1995). Grube & Ryan (2002) refined the broad concept of *Pyrenocollema* by proposing that lichen-forming species previously included in this genus be transferred to *Collemopsidium*. However, *Pyrenocollema sensu stricto*, is restricted to the type species *Pyrenocollema tremelloides* which grows on leafy *Nostoc* species and is known only from the protologue. Obtaining fresh collections of this species and further typification are crucial for clarifying this taxonomic problem.

Pérez-Ortega et al. (2016) studied the phylogenetic relationships of marine *Xanthopyreniaceae* using six molecular markers and suggested that *Collemopsidium* is paraphyletic, encompassing species occurring in marine, terrestrial and freshwater habitats belonging to different lineages. The authors assumed that further sampling is critically needed especially from type materials and unexplored coastal regions (the North Pacific coasts, Australia, South Africa). Other genera affiliated with *Xanthopyreniaceae* are represented by lichenicolous (*Didymellopsis*, *Rhagadodidymellopsis*, *Zwackhiomacromyces* and *Zwackhiomyces*) or lichen-forming species (*Frigidopyrenia*). These genera have been intensively studied over the last decade, but most such research has been limited to morphological or anatomical data without phylogenetic analyses (Calatayud et al. 2007, Brackel 2008, Pérez-Ortega et al. 2011a, van den Boom & Etayo 2014, Khodosovtsev & Darmostuk 2017a, b, Fernández-Brime et al. 2020, Joshi et al. 2020, Darmostuk 2021, Joshi 2022, Poumarat et al. 2022). Only the type species of the lichenicolous genus *Zwackhiomyces* has been sequenced, which confirmed its placement within *Xanthopyreniaceae* (Pérez-Ortega et al. 2016). Other genera lack molecular data. Recently, Hyde et al. (2024b) accepted eight genera within *Collemopsidiales*.

General description

Members of the order share the common morphological features, such as perithecioid ascomata, branched and anastomosing net-like interascal filaments, fissitunicate asci with ocular chamber and 1-septate hyaline ascospores with gelatinous perispore. In recent years, the concept of the order has been expanded by describing a few new genera based on morphological features and habitat preferences.

Sexual morph: crustose, epilithic or endolithic, or lichenicolous forms. *Photobiont* cyanobacteria, filamentous or coccoid. *Ascomata* perithecioid (open perithecioid ascomata with apothecia-like appearance in some marine species), solitary, unilocular, with a distinct involucrellum or not. *Exciple* carbonized to hyaline, prosoplectenchymatous to pseudoplectenchymatous, branched and anastomosing, often irregularly thick, net-like physes, hymenial gel I-. *Asci* bitunicate, fissitunicate, with ocular chamber, ovoid to subcylindrical, usually stalked, I-. *Ascospores* hyaline (rarely brownish in mature specimens), oblong to ovoid-fusiform, 1-septate, gelatinous perispore usually present. Asexual morph: *Conidiomata* pycnidial. *Conidiogenous cells* ± cylindrical, conidiogenesis phialidic. *Conidia* bacilliform to ellipsoid (Fig. 24).

Families included in *Collemopsidiales*

Xanthopyreniaceae Zahlbr.

Evolution

Taxa of *Collemopsidiales* are poorly sampled. Therefore, the phylogenetic relationship with other higher taxa remains unclear. The Pérez-Ortega et al. (2016) study was based on multi-gene phylogenetic analyses, which suggested that species of *Collemopsidium* and *Zwackhiomyces* represent separate and unique evolutionary lineages but without statistical support. Subsequent phylogenetic research conducted by Liu et al. (2017b) demonstrated strong support for the sister relationships of *Collemopsidiales* with *Monoblastiales*. The divergence time for *Collemopsidiales* is estimated to be 230 MYA (Hongsanan et al. 2020a). However, these studies are based on limited sampling from a few species of two genera. The inclusion of sequence data from other genera is crucial for determining their taxonomic affiliation and establishing a robust phylogenetic framework for the order.

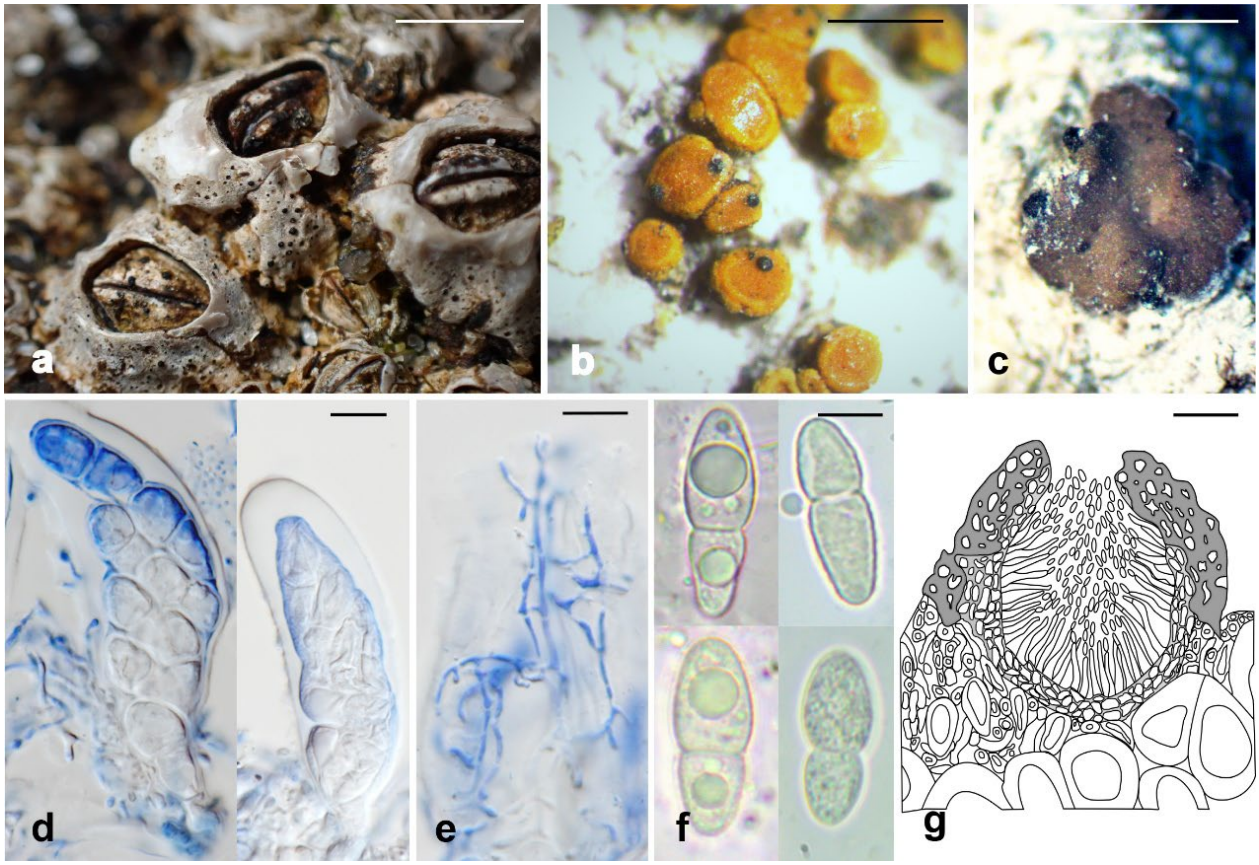


Figure 24 – Morphology of the *Collemopsidiales* species. a *Collemopsidium foveolatum* (photo by Pierre Corbrion). b *Zwackhiomyces coepulonus* on *Xanthocarpia crenulatella* (KHER 11076). c *Didymellopsis perigena* on *Endocarpon* sp. (herb. VD 973). d Asci of *Collemopsidium* sp. (KRAM). e Interascal filaments of *Collemopsidium* sp. (KRAM). f Ascospores morphology of *Zwackhiomyces* spp. g Conidiomata of *Collemopsidium pelvetiae* (redrawn from Kohlmeyer et al. 2004). Scale bars: a = 5 mm, b, c = 1 mm, d, e, g = 10 µm, f = 5 µm.

Justification of order and problems

Collemopsidiales represents an independent and possibly ancient lineage of *Ascomycota* that is adapted to aquatic (fresh-water and marine) or terrestrial environments, rather than dwelling on other lichens (Pérez-Ortega et al. 2016). The lichenicolous genus *Rhagadodidymellopsis* was described by Fernández-Brime et al. (2020) to accommodate a species that was reported on *Endocarpon*, that has superficial stromatic ascomata with a coarse and irregular surface. Another genus, *Zwackhiomacromyces*, was introduced by van den Boom & Etayo (2014); this genus is characterized by lageniform ascomata with large and granulosa papillae, as well as 3-septate ascospores. However, these genera lack molecular data and therefore their affiliation within the order

Collemopsidiales needs to be confirmed. *Collemopsidium* appears to be paraphyletic and exhibits high genetic variability among sampled specimens (Mohr et al. 2004, Pérez-Ortega et al. 2016). *Collemopsidium* species formed separate clades with marine and freshwater species, but molecular data for freshwater *C. iocarpum* (the generic type) is lacking, thus further study is needed to clarify the circumscription of the genus (Jones et al. 2019). Pérez-Ortega et al. (2016) considered that the number of marine species in *Collemopsidiales* has been largely underestimated.

Significance

Ecological and economic roles

Marine species of *Collemopsidium* may hold ecological significance as they actively contribute to bio-weathering in littoral rocky substrates and enhance the erosive action of waves (Hongsanan et al. 2020a). Some species are capable of colonizing and modifying mollusk shells, thereby facilitating mimicry in certain species (Espoz et al. 1995, Mohr et al. 2004). Recent research conducted by Nokes et al. (2022) utilized marine lichens, including *Collemopsidium halodytes*, as a bioindicator of water pollution.

Chemical diversity

Secondary metabolites have not been reported from *Collemopsidiales*.

Other relevant data and future recommendations

Species of *Collemopsidiales* require further extensive sampling and molecular investigation to clarify genus circumscription and to understand their phylogenetic relationships.

***Comminutisporales* Abdollahz. & Crous, Studies in Mycology 95: 390 (2020)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Dothideomycetidae*

Introduction

Comminutisporales was introduced to accommodate a single family, *Comminutisporaceae* by Abdollahzadeh et al. (2020). *Comminutisporaceae* presently includes only one genus, *Comminutispora* (Index Fungorum 2025). The type species, *Comminutispora agavacearum*, was described with an asexual morph which was originally reported as *Hyphospora agavacearum* (Ramaley 1996). *Comminutispora* was considered as a member of *Planistromellaceae* by Lumbsch & Huhndorf (2010). However, the evidence of phylogenetic analysis based on SSU and LSU genes revealed *Comminutispora* was closely related to *Capnodiales* (Hambleton et al. 2003, Crous et al. 2009c, Schoch et al. 2009b). Thus, the genus was placed in *Capnodiales* genera *incertae sedis*. Abdollahzadeh et al. (2020) resolved the taxonomic position of taxa in *Capnodiales sensu lato* and occupied *Comminutispora* in the new family, *Comminutisporaceae* and the new order *Comminutisporales*.

Comminutispora was found as a saprobe on dead leaves of *Dasylirion leiophyllum* (*Asparagaceae*) (Ramaley 1996). The sexual morph of *Comminutispora* is characterized by immersed ascostromata, abundant hamathecial tissues, periphysate ostiolar canals and muriformly septate ascospores (Ramaley 1996). Its asexual morph is characterized by hyaline hyphae, which become olivaceous, and hyaline and aseptate endoconidia (Ramaley 1996). *Comminutisporales* is different from *Capnodiales* based on both phylogeny and morphology as the former has immersed ascostromata, while the latter has superficial ascomata (Abdollahzadeh et al. 2020). *Comminutisporales* clearly differ from other endoconidial taxa in *Neophaeothecales* and *Phaeothecales* by phylogeny despite sharing similar characteristics (Zalar et al. 1999b, Abdollahzadeh et al. 2020).

History

Comminutispora was introduced by Ramaley (1996) with the type species, *C. agavacearum*. Morphologically, *Comminutispora* is similar to some taxa in the order *Dothideales* which lack pseudoparaphyses, such as *Mycosphaerella* and *Sydowia* (Ramaley 1996). However, this genus has totally immersed ascomata, which differs from *Mycosphaerella* in the absence of immersed to semi-immersed or erumpent ascomata (Ramaley 1996). This genus can be distinguished from *Sydowia* by its apparent polysporous asci (the presence of remained locule cells between and above asci), whereas the latter has true polysporous asci (Barr, 1987b, Ramaley 1996). Therefore, Ramaley (1996) treated *Comminutispora* in *Dothideales sensu* Lindau (1897c) due to their distinctive ascomata characters (*viz*. immersed unilocular ascostromata, with abundant interascal pseudoparenchyma, periphysate ostioles) and phragmosporous ascospores. The asexual morph of *Comminutispora agavacearum* was linked to *Hyphospora agavacearum* by the presence of melanized endoconidia in culture (Ramaley 1996). *Hyphospora* is morphologically similar to *Phaeotheca*, which has unicellular, meristematic or hyphae thalli (Sigler et al. 1981). However, they can be differentiated based on cultural and physiological characteristics as *Hyphospora* has initial hyaline hyphae becoming melanized at maturity (Zalar et al. 1999b). Phylogenetic analysis based on SSU gene supported the distinct placements of *Phaeotheca* and *Hyphospora* in *Dothideales* (Sterflinger 1999). Nomenclaturally, *Comminutispora* was protected over *Hyphospora* (Wijayawardene et al. 2014a, Rossman et al. 2015b).

The taxonomic placement of *Comminutispora* was uncertain based on molecular data of ITS and SSU genes (de Hoog 1999). Hambleton et al. (2003) showed that *Comminutispora agavacearum* clustered within the clade of *Capnodiales* based on phylogenetic analysis of SSU gene. *Comminutispora agavacearum* formed a weak statistical support branch distant from the main clade of *Capnodiales* (Crous et al. 2009c, Schoch et al. 2009b), thus this species was assigned in *incertae sedis* (Crous et al. 2009c). Lumbsch & Huhndorf (2010) listed *Comminutispora* in the family *Planistromellaceae*. However, Monkai et al. (2013) redescribed *Planistromellaceae* including *C. agavacearum* and showed that *Comminutispora* was unrelated to this family based on the phylogenetic of SSU and LSU genes and transferred it to *Capnodiales* genera *incertae sedis*. Abdollahzadeh et al. (2020) erected a new family *Comminutisporaceae* and a new order *Comminutisporales* as *C. agavacearum* formed a basal clade to *Capnodiales sensu stricto* based on the phylogenetic analysis of combined LSU, ITS, TEF1-α and RPB2 genes.

General description

The morphological description of sexual morph was provided based on the protologue (Ramaley 1996) and holotype observation (Monkai et al. 2013). Whereas, details of asexual morph characteristics were adapted from Ramaley (1996) and Zalar et al. (1999b).

Sexual morph: *Ascostromata* apothecial, or elongate hysterothecium, unilocular to multilocular, scattered to loosely, immersed, opening by a sunken longitudinal slit, periphysate ostioles, with numerous interascal pseudoparenchymous cells when mature. *Asci* 8-spored, bitunicate, fissitunicate, clavate or cylindrical, with a long pedicel, with a large ocular chamber. *Ascospores* obovoid, ellipsoid to fusoid, 0–3-septate when immature, transversely 1–5-septate and many longitudinal septate with ultimately forming tiny secondary ascospores when mature, roughened, with thin gelatinous coat. Asexual morph: *Hyphae* hyaline, becoming olivaceous. *Conidiogenous cells* mostly broader than vegetative cells or differentiated. *Endoconidia* unicellular, hyaline, elongation or long chains, variable shape, forming secondary endoconidia of dictyochlamydospores, with transverse and longitudinal septation, constricted at the septa, dark brown, smooth or slightly verrucose (Figs. 25, 26).

Families included in *Comminutisporales*

Comminutisporaceae Abdollahz. & Crous

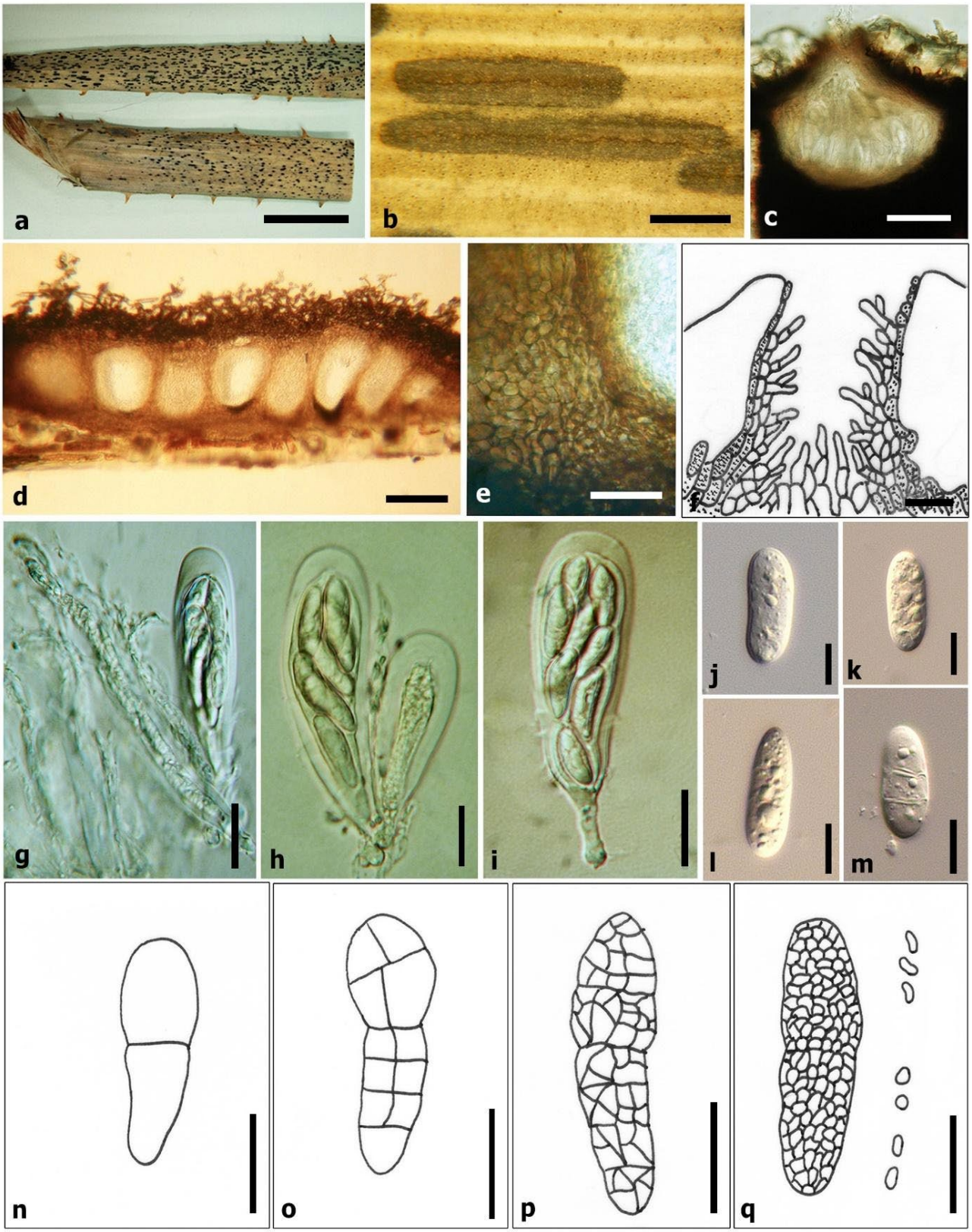


Figure 25 – The sexual morph of *Comminutisporales* (*Comminutispora agavacearum*). a, b Ascostromata on host surface. c, d Section of ascostromata. e Ascostroma wall. f Section of ostiole (redrawn from Ramaley 1996). g Asci and interascal cells. h, l Asci. j, k, l, m Immature ascospores. n Ascospore with the first septum (redrawn from Ramaley 1996). o, p Ascospores with transversely and longitudinal septa (redrawn from Ramaley 1996). q Mature ascospores and secondary ascospores (redrawn from Ramaley 1996). Scale bars: a, b, d = 100 µm, c, e, d, f = 10 µm, g–i = 20 µm, j–q = 10 µm.

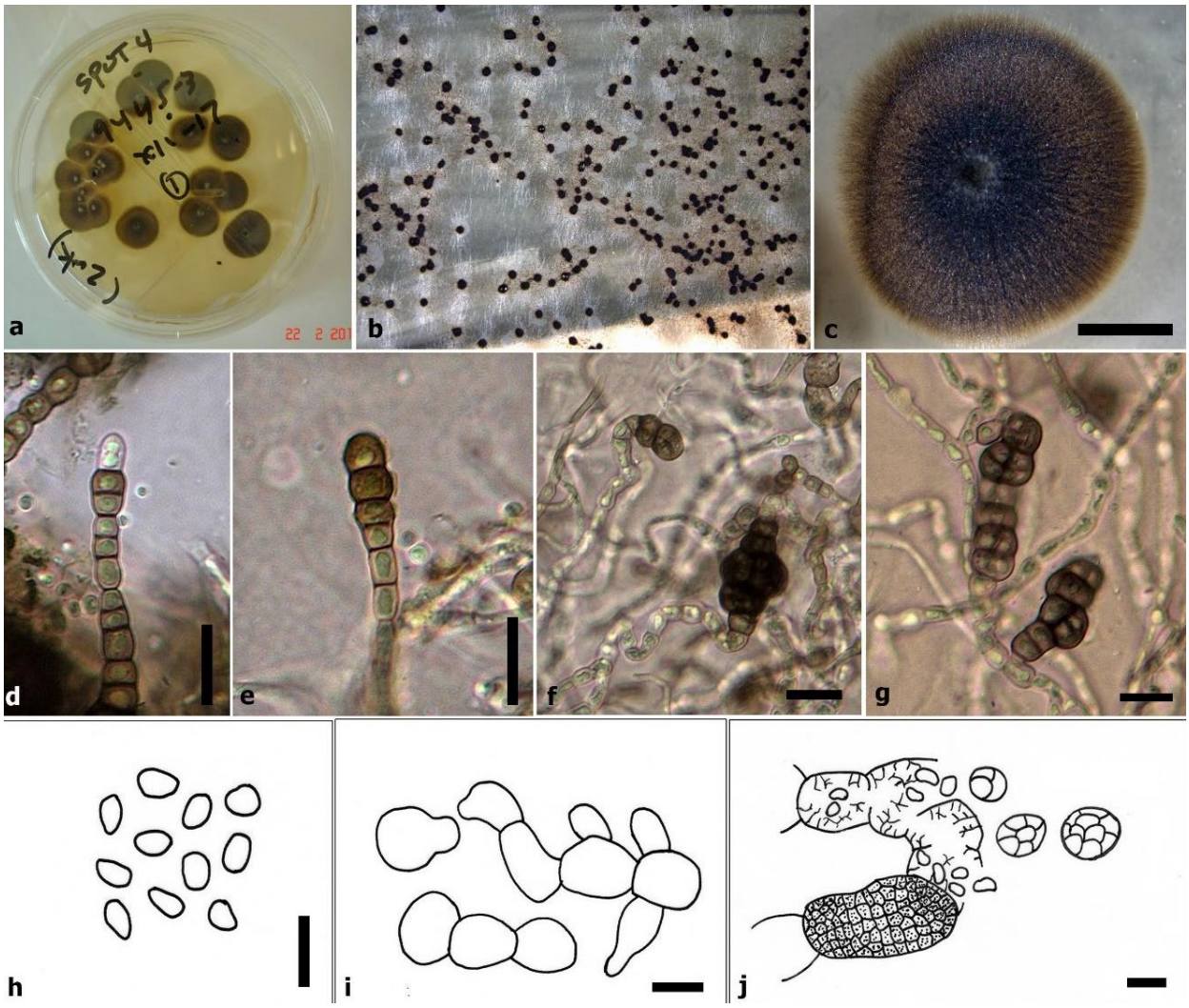


Figure 26 – The asexual morph of *Comminutisporales* (*Comminutispora agavacearum*). a, b, c Colonies on Malt agar at two weeks (23–25 ºC). d, e, f, g Dictyochlamydospores. h Endoconidia (redrawn from Ramaley 1996). i Germination of endoconidium and young colony formation (redrawn from Ramaley 1996). j Endoconidia developing secondary endoconidia (redrawn from Ramaley 1996). Scale bars: c = 500 µm, d–g = 20 µm, h–j = 5 µm.

Evolution

As saprobes *Comminutispora* represent the earliest diverging lineages of taxa in *Capnodiales* (Crous et al. 2009c). Based on the ancestral state reconstruction, the saprobic lifestyle is likely to be a primitive state in *Comminutisporales* (Abdollahzadeh et al. 2020).

Significance

Ecological and economic roles

Comminutispora is reported as a saprobe on *Dasylirion leiophyllum* (*Asparagaceae*) (Ramaley 1996). Zalar et al. (1999b) investigated the physiological profile of the type strain of *Comminutispora agavacearum* and revealed its ability for assimilation of D-glucosamin, arbutin and ribitol, but no growth with sucrose, which were different from *Phaeotheca fissurella* and *Neophaeotheca triangularis* (=*P. triangularis*). In addition, *C. agavacearum* was not able to grow in high salt addition (up to 20% of NaCl), where *N. triangularis* is halophilic as it occurred in dry and salinity conditions (De Hoog et al. 1997, Zalar et al. 1999a, b).

Chemical diversity

There are no reports for chemical production from *Comminutisporales*.

Justification of order and problems

Molecular analysis supported the placement of *Comminutisporales* in *Capnodiales sensu lato* with a close relationship to *Cladosporiales*, *Phaeothecales*, *Racodiales* and *Neophaeothecales* (Abdollahzadeh et al. 2020). Characteristics of *Comminutisporales* are unique comprising muriform ascospores in the sexual morph and melanized endoconidia in the asexual morph (Ramaley 1996). The muriform ascospore is also found in some taxa in *Capnodiales* (Crous et al. 2009c). Endoconidial taxa in *Phaeothecales* and *Neophaeothecales* have overlapping characters with *Comminutisporales*, however, those two orders were commonly explored in dry and extreme environments (De Hoog et al. 1997, Zalar et al. 1999a, b). The order, *Comminutisporales* is only known for the single genus, *Comminutispora*. Therefore, extensive sampling and more collection from the same or different hosts and habitats are needed to discover more taxa in this order to better understand the taxonomic position, lifestyles, and ecological distribution.

Other relevant data and future recommendations

It will be interesting to investigate the secondary metabolite production from strains of *Comminutispora agavacearum*.

***Coniosporiales* Crous, Spatafora, Haridas & I.V. Grig. Studies in Mycology 96: 151 (2020)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Coniosporiales was introduced by Haridas et al. (2020) to accommodate a newly established family *Coniosporiaceae* based on phylogenetic analysis. The order comprised a single genus *Coniosporium* with *Coniosporium olivaceum* as the type. The taxa form black spots or patches on plant leaves, bamboo surfaces, rotten wood, and rock surfaces. It has also been reported as a pathogen on human skin. On their natural substrates, the taxa form black, velvety colonies and are seen as thick-walled, heavily pigmented arthroconidia with subsequent meristematic development under the microscope. The genus was found to be polyphyletic (Li et al. 2008).

History

Coniosporium was introduced for a melanized, meristematic fungus *Coniosporium olivaceum* that was found on the wood of *Pinus maritima* (Link 1809). Ellis (1971, 1976b) refined this genus for the taxa with erumpent stromata, muriform, and pale to dark brown conidia arising in basipetal chains. Hughes (1953) transferred *Coniosporium peziza* to *Sirodesmium* based on the formation of basipetal chains of multicellular conidia from meristematic conidiophores. However, Hughes (1958) again reinstated *Coniosporium* as a distinct genus. Tubaki (1958) examined a culture of *Coniosporium olivaceum* that had been isolated from a trunk of *Zelkova serrata* and reported meristematic conidiophores that produced multicellular conidia in basipetal chains. Accordingly, *Coniosporium* was again placed in *Sirodesmium*. Tsuneda et al. (2011) reexamined the culture characteristics of *Coniosporium perforans* and *C. epidermidis* and found a similar morphology in multicellular bodies to other dematiaceous hyphomycetous genera such as *Capnobotryella* (Hambleton et al. 2003), *Endoconidioma* (Tsuneda et al. 2004), *Endosporium* (Tsuneda et al. 2008) and *Knufia*. Both species lacked meristematic conidiophores and basipetal production of muriform conidia. Their multicellular bodies are not conidia (they may be called chlamydospores) because they are produced in undifferentiated hyphal cells and most of them remain attached to hyphae (Li et al. 2008, Tsuneda et al. 2011). In addition, both species were found as phylogenetically distinct to the type. Thus, both species were transferred to *Knufia*. A phylogenetic analysis based on 18S rDNA sequencing data showed the close association of *Coniosporium* to *Chaetothyriales* which was entirely comprised of rock-associated species. Later, it was assumed that *Coniosporium* might comprise human associated taxa. For example, *Coniosporium perforans* shows dual ecology and the taxon was

reported from both rocks and humans (Li et al. 2008). In the multigene phylogenetic analysis conducted by Ruibal et al. (2009), *C. apollinis* and *C. uncinatum* were recovered in *Dothideomycetes*. However, their phylogenetic placement was not resolved due to limited taxon sampling. The genus was also recovered in *Chaetothyriales*, based on SSU phylogeny data (Sert & Sterflinger 2010), in which it was represented by *C. apollinis* and *C. sümbülii*.

Coniosporium was accepted under *Hysteriaceae* (Wijayawardene et al. 2018, Dayarathne et al. 2020) and was later accepted under *Dothideomycetes* genera *incertae sedis* (Wijayawardene et al. 2021b). *Coniosporium apollinis* was recovered within *Patellariaceae* (*Patellariales*) in the phylogenetic analysis conducted by Hongsanan et al. (2020a). Haridas et al. (2020) accepted this genus under the newly established order *Coniosporiales* which was consequently accepted by Wijayawardene et al. (2022a).

General description

The taxa are only reported in their asexual morph.

Sexual morph: Undetermined. Asexual morph: *Conidiomata* sporodochial, pulvinate, punctiform, olivaceous to black. Mycelium immersed. *Conidiophores* arising from a stroma, macronematous straight to flexuous, densely aggregated, unbranched, smooth, rugulose to verruculose. *Conidiogenous cells* integrated, terminal, subcylindrical, fragmenting. *Conidia* catenate, schizogenous, dry, ellipsoid, oblong, obovoid, pyriform to subspherical, pale to dark brown, muriform septate, smooth to verruculose (adapted from Haridas et al. 2020) (Fig. 27).

Families included in *Coniosporiales*

Coniosporiaceae Crous, Spatafora, Haridas & I.V. Grig.

Justification of order and problems

Many *Coniosporium* species (including the type) lack molecular data and were mostly described based on their characteristics in culture and further studies are required. The definition and taxonomic concept of *Coniosporium* has been controversial (Hughes 1951b, 1953, 1958, Moore 1958, Tubaki 1958, Ellis 1971a, b). *Coniosporium perforans* resembles *Monodictys* in having non-catenate, dictyosporous conidia but differs in its phylogeny. It has been assumed to represent an undescribed genus (Sterflinger et al. 1997, Haridas et al. 2020). *Coniosporium olivaceum* and *C. memorandum* are commonly reported species. However, molecular data are not available for these species.

Significance

Ecological and economic roles

The members of *Coniosporium* occur mostly on living and dead plant material, but have also been reported on rocks and humans. *Coniosporium aeroalgicola*, *C. apollinis*, *C. perforans* and *C. uncinatum* were reported from marble monuments, on which they caused esthetic damage. *Coniosporium perforans* can also cause mechanical destruction to rocks (Sterflinger et al. 1997). *Coniosporium aeroalgicola* was reported as a semi-lichenized species that occurs on corticolous and saxicolous algae, colonizing sandstone and calcareous rock (Turian 1977). *Coniosporium corticale* caused pneumonitis in human lungs (Emanuel et al. 1962). *Coniosporium mali* was reported as parasitic on crab apples and several varieties of common apples in British Columbia (Canada). The species affected the leaves, petioles, and fruits of apple trees, with symptoms similar to those produced by *Fusicladium dendriticum* (Dearness & Foster 1938). *Coniosporium* is also commonly reported in bamboo (Hyde et al. 2002).

Chemical diversity

No chemical diversity is reported in the members of *Coniosporiales*.

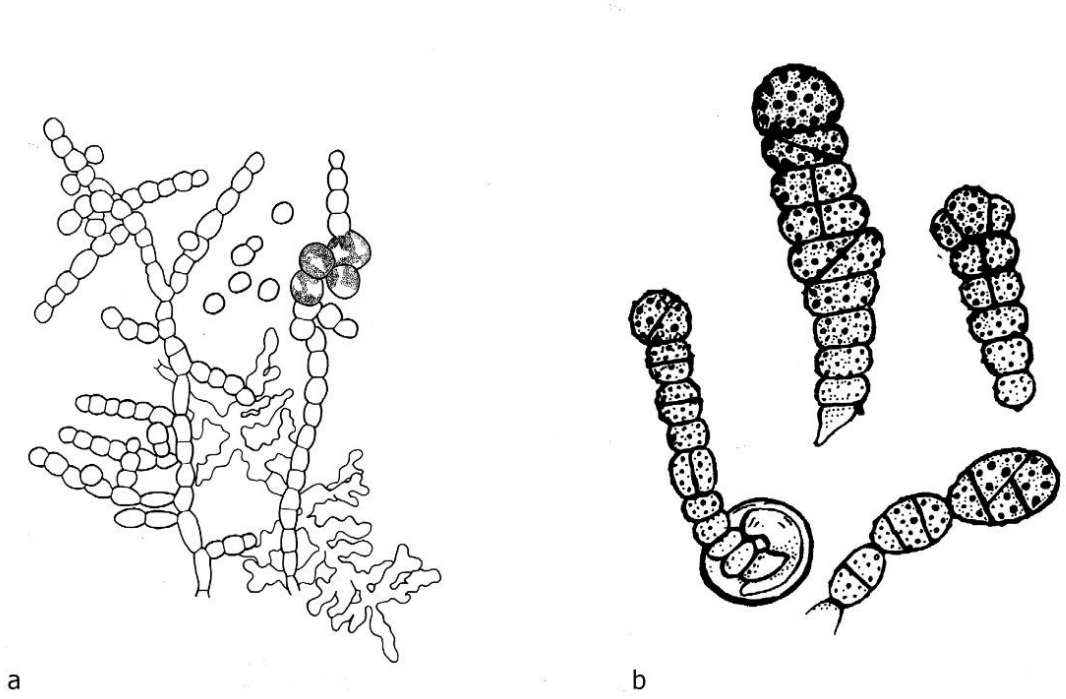


Figure 27 – Morphology of *Coniosporiales* (hyphae, Conidiophore, Conidia). a *Coniosporium epidermidis*. b *Coniosporium aeroalgicolum*. (drawn from Turian 1977). Scale bars: b × 800.

Dothideales **Lindau, Teil. I (Leipzig) 1(1): 373 (1897)**
= *Neocelosporiales* Crous, Persoonia 41: 307 (2018)

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Dothideomycetidae*

Introduction

Dothideales is an interesting and unique order in *Dothideomycetes* and is considered the basis of the class *Dothideomycetes*. Most of the members of this order are saprobic, while some pathogenic species are occasionally found. They mainly occur on a range of woody and herbaceous plants in terrestrial habitats and a few of them cause human diseases (Hyde et al. 2013, Thambugala et al. 2014, Chen et al. 2016c). *Dothideales* currently comprises four families, *viz*. *Dothideaceae*, *Neocelosporiaceae*, *Saccotheciaceae* and *Zalariaceae* which are supported by multigene phylogenetic analyses as well as phenotypic characters (Hongsanan et al. 2020b). *Dothideaceae* was introduced by Chevallier (1826) as '*Dothideae'*, and later Fuckel (1869) established this family with *Dothidea* as the type genus, which was characterized by locules embedded in ascostromata without definite perithecia. However, this family has a rather varied past as can be seen from the inclusion of genera by various authors (Luttrell 1973, von Arx & Müller 1975, Thambugala et al. 2014, Hongsanan et al. 2020b). Crous et al. (2018a) introduced *Neocelosporiaceae* to accommodate the genera *Neocelosporium* and *Muellerites*. Crous et al. (2018a) placed this family in the new order *Neocelosporiales* mainly based on a phylogeny that was not occupied with the recently introduced family *Zalariaceae*. Later, Hongsanan et al. (2020b) included *Neocelosporiaceae* as a family in *Dothideales* based on a comprehensive phylogenetic analysis. *Saccotheciaceae* was established by Bonorden (1864) to accommodate *Saccothecium* and is considered as a distinct family in *Dothideales* (Li et al. 2016a, Hongsanan et al. 2020b). Currently, seven genera *viz*. *Aureobasidium* Viala & G. Boyer, *Columnosphaeria*, *Kabatiella* (*Kabatella* is a synonym of *Aureobasidium*), *Pseudoseptoria* Speg. *Pseudosydowia*, *Saccothecium* and *Selenophoma* are accepted in the family. Humphries et al.

(2017) proposed *Zalariaceae* to accommodate a new genus *Zalaria* which resembles the asexual morphs of *Aureobasidium* and *Hormonema*. The members of this genus are yeast-like organisms and have been found in house dust. *Zalariaceae* is accepted as a distinct family in *Dothideales* based on morpho-molecular characterizations (Humphries et al. 2017).

History

Studies on *Loculoascomycetes* commenced when mycological research first started, and it was a difficult time for mycologists who attempted higher fungal classifications. The fungal classifications became rather subjective during that period as certain characters were chosen as important over others, without any real evidence for their importance (Thambugala et al. 2014). Lindau (1897c) introduced the order *Dothideales* to accommodate a single family *Dothideaceae*. The order was subjected to various treatments during the last 100 years. Many families were included or removed from this order depending on the perspectives of the authors and different taxonomic features (Luttrell 1973, von Arx and Müller 1975, Barr 1987a, Hawksworth et al. 1995, Thambugala et al. 2014).

Dothideales was revised by Theissen & Sydow (1915) and included four families; *Dothideaceae*, *Montagnellaceae*, *Phyllachoraceae* and *Polystomellaceae* which were comprising both unitunicate and bitunicate ascomycetes. Luttrell (1951b) treated *Capnodiaceae*, *Coryneliaceae*, *Dothideaceae*, *Dothioraceae*, and *Pseudosphaeriaceae* in *Dothideales*. Later, Luttrell (1955) synonymized the orders *Pseudosphaeriales*, *Capnodiales*, and *Dothiorales* under *Dothideales* and accepted only four families in *Dothideales*. Luttrell (1955, 1973) in a narrow sense treated the order only with bitunicate ascomycetes and loculi containing several asci and lacking paraphyses. Subsequently, Luttrell (1973) categorized eight families in *Dothideales*, while Von Arx & Müller (1975) placed 34 families and synonymized *Dothioraceae* under *Dothideaceae*. The order was treated with five families by Barr (1979a) who considered *Dothideaceae* and *Dothioraceae* as distinct families. Barr (1987b) categorized six families in *Dothideales* including a newly introduced *Kriegeriellaceae*. Hawksworth et al. (1995) synonymized *Asterinales*, *Capnodiales*, *Chaetothyriales*, *Dothiorales*, *Melanommatales*, *Myriangiales*, "*Perisporiales*", *Pleosporales* and *Pseudosphaeriales* under *Dothideales* and considered it to be the largest and most varied group of the *Ascomycota*. They included most ascolocular ascomycetes with bitunicate asci in *Dothideales* while assigning 58 families to the order.

Planistromellaceae was introduced in *Dothideales* by Barr (1996) including six genera. Later, Kirk et al. (2001) included *Dothideales* with other bitunicate orders, *Capnodiales* and *Myriangiales*, in the subclass *Dothideomycetidae* which was characterized by the absence of paraphyses, pseudoparaphyses and paraphysoids. Kirk et al. (2008a) treated *Dothideales* with four families *viz*. *Dothideaceae*, *Dothioraceae*, *Coccoideaceae* and *Planistromellaceae*. All the above treatments were based on morphological characteristics. However, taxonomy based on morphology is not always adequate in fungal systematics as it may be subjective or even wrong. Molecular based identifications and taxonomy have become controversial in most cases. Hence, after 2005 mycologists have begun to incorporate multi-gene phylogenetic analyses-based identification and classifications other than the morphology in fungal taxonomy including the order *Dothideales* (Schoch et al. 2006, 2009b, Ariyawansa et al. 2014, Li et al. 2016a, Thambugala et al. 2014, Hongsanan et al. 2020b).

The first two phylogenetic treatments to the order were done by Schoch et al. (2006, 2009b) and they showed *Dothideales* to be a well-supported order with nine other orders in the class *Dothideomycetes*. They also used their phylogenetic analyses to show that some other families in the subclass *Loculoascomycetes* (such as *Botryosphaeriaceae*) which was previously classified in *Dothideales* are distinct from *Dothideales*. Hyde et al. (2013) highlighted that *Dothioraceae* should be combined under *Dothideaceae* and the requirement of a new family for the other taxa in *Dothideales*. Later, Thambugala et al. (2014) synonymized *Dothioraceae* under *Dothideaceae* and introduced a new family *Aureobasidiaceae* to accommodate *Aureobasidium*, *Saccothecium* and five other genera. However, this family is a homonym of *Aureobasidiaceae* which had been previously introduced (Ciferri 1958). *Saccotheciaceae* was therefore proposed instead of *Aureobasidiaceae* as

Saccotheciaceae is the oldest available name for the family that contains *Aureobasidium* and *Saccothecium* (Liu et al. 2015a). Humphries et al. (2017) introduced a new family *Zalariaceae* in *Dothideales* to accommodate a hyphomycetous genus that contains aureobasidium-like and hormonema-like species. The most recent treatment to the order was done by Hongsanan et al. (2020b) and included four families, namely *Dothideaceae*, *Neocelosporiaceae*, *Saccotheciaceae* and *Zalariaceae*.

General description

Dothidealean taxa inhabit a wide range of plant hosts which are in *Anacardiaceae*, *Cactaceae*, *Cornaceae*, *Grossulariaceae*, *Pinaceae* and *Rosaceae*. In addition, human pathogenic and dust-associated taxa have also been reported (Thambugala et al. 2014, Crous & Groenewald 2017, Humphries et al. 2017, Crous et al. 2018a, Hongsanan et al. 2020b).

The taxa form immersed to erumpent, pulvinate to globose, black, multi-loculate ascostromata which show a range of morphological characteristics. Most of the ascostromata consist of two or more locules. Locules are usually globose to subglobose, broadly rounded, or papillate with a central ostiole. Hamathecium usually lacks pseudoparaphyses. But, *Stylodothi*s and *Uleodothis* comprise cellular pseudoparaphyses. However, molecular data are lacking to confirm their placement in *Dothideales* (Thambugala et al. 2014, Hongsanan et al. 2020b). Asci can be saccate to clavate with eight or more spores, and ascospores are obovate to ellipsoidal to fusoid transversely septate, or muriform, hyaline to brown, constricted at the primary septum, sometimes wall smooth to verrucose, at times with a thin mucoid sheath. The morphology of ascospores in *Dothideales* greatly varies and 1–several-septate, or muriform, hyaline to pigmented ascospores can be observed. In addition, ascospore color, size, septation and ornamentations were used in species delineation of *Dothideaceae* (Thambugala et al. 2014, Crous & Groenewald 2017). The asexual morph is reported in several genera of *Dothideales* which produce coelomycetous or hyphomycetous asexual morphs. *Zalariaceae* was recently described in *Dothideales* for aureobasidium-like species isolated from house dust (Humphries et al. 2017). *Aureobasidium* is the prominent asexual morph of *Saccotheciaceae*, while *Neocelosporiaceae* mainly comprises coelomycetous asexual genera; *Neocelosporium*, and *Celosporium* (Crous et al. 2018a).

Sexual morph: *Ascostromata* immersed to erumpent or superficial, solitary to scattered, pulvinate or crustose, dark brown to black, globose to subglobose, uniloculate or multiloculate, locules up to 15, papillate with central ostiole or apically opening by a lysigenous pore or by dehiscence, multi-layered ascostromata comprising pale to dark brown cells of *textura angularis*. *Peridium* of locules multi-layered, lightly pigmented to dark brown, thick-walled cells of *textura angularis* becoming flattened towards the inner layers. *Hamathecium* usually lacking pseudoparaphyses, or cellular pseudoparaphyses in some genera (e.g., *Stylodothis* and *Uleodothis*). *Asci* eight to multi-spored, bitunicate, fissitunicate, saccate to clavate, short-pedicellate, apically rounded with an ocular chamber. *Ascospores* uni to multi-seriate, obovate to ellipsoidal to fusoid, often inequilateral or slightly curved with broad to narrow rounded ends, partially overlapping, muriform, small, hyaline to brown, transversely septate, constricted at the primary septum, sometimes wall smooth to verrucose, at times with a thin mucoid sheath. Asexual morph: Coelomycetous or hyphomycetous. *Hyphae* lightly pigmented to brown, verruculose, constricted at septa, giving rise to a hormonema-like synasexual morph. *Conidiomata* pycnidial, stromatic, immersed to erumpent, epidermal to subepidermal, solitary or aggregated in a stroma, globose to subglobose to flask-shaped, sometimes irregular, dark brown to black, uniloculate to multi-loculate, sometimes convoluted with or without central ostioles. *Conidiomatal wall* multi-layered, hyaline to lightly pigmented and dark brown cells of *textura angularis*. *Conidiophores* present, or reduced to conidiogenous cells, branched, septate, at the base hyaline to pale brown when present. *Conidiogenous* cells enteroblastic, phialidic, integrated to discrete, cylindrical or ampulliform to doliiform, determinate, hyaline to brown, smooth-walled, lining the inner cavity. *Conidia* cylindrical or subcylindrical to ovoid or oblong, hyaline, aseptate to one-septate, guttulate, smooth, granular, or not, mostly straight, rarely slightly curved (adapted from Thambugala et al. 2014, Crous &

Groenewald 2017, Humphries et al. 2017, Hongsanan et al. 2020b) from Thambugala et al. 2014, Crous & Groenewald 2017, Humphries et al. 2017, Hongsanan et al. 2020b) (Fig. 28).

Families included in *Dothideales*

Dothideaceae Chevall.
Neocelosporiaceae Crous
Saccotheciaceae Bonord.
Zalariaceae Visagie, Z. Humphries & Seifert

Dothideales genera *incertae sedis*
Asteromellopsis H.E. Hess & E. Müll.
Atramixtia Tsuneda, M.L. Davey & Currah
Botryochora Torrend
Coccodomyces Sastoque, Cano-Lira & Stchigel
Hormonema Lagerb. & Melin
Pringsheimia Schulzer
Pseudohormonema Crous
Rhizosphaera L. Mangin & Har.
Scleroconidioma Tsuneda, Currah & Thormann

Evolution

Liu & Hall (2004) showed that *Pleosporales* and *Melanommatales* (ascostroma with pseudoparaphyses) are closely related to *Dothideale*s (ascostroma without pseudo-paraphyses). Later, Schoch et al. (2006) proposed the two subclasses, *Pleosporomycetidae* and *Dothideomycetidae* to accommodate the pseudoparaphysate *Pleosporales* (order *Pleosporales*) and the aparaphysate *Dothideales* (orders *Dothideales*, *Capnodiales* and *Myriangiales*). These findings were also supported by the phylogenetic analysis done by Haridas et al. (2020) using whole-genome data. The divergence time for *Dothideales* is estimated at 177 MYA (stem age) (Hongsanan et al. 2020b).

Justification of order and problems

Since the sequence data for some genera and most species in *Dothideaceae* and *Saccotheciaceae* are not available, they require re-collection to carry out further culture and molecular sequence data assay to confirm their status and the correct taxonomic placements (Thambugala et al. 2014, Hongsanan et al. 2020b). *Asteromellopsis*, *Botryochora*, *Coniozyma*, *Hormonema*, *Pringsheimia*, *Rhizosphaera* and *Scleroconidioma* are in *Dothideales* genera *incertae sedis*. In addition, *Columnosphaeria*, *Endodothiora*, *Kabatina*, *Kabatiella*, *Pseudoseptoria*, *Selenophoma*, and *Uleodothis* also lack sequence data of the type species (Hongsanan et al. 2020b). Therefore, linking the type species of these genera to their DNA sequence data is crucial.

Phenotypic variability within *Aureobasidium* and *Kabatiella* strains presented limitations in the morphological identification of *Aureobasidium* species (van Nieuwenhuijzen et al. 2016a). In the phylogenies generated from the recent studies, *Aureobasidium*, *Kabatiella*, *Selenophoma* species, and *Columnosphaeria fagi* (CBS 171.93) distributed in *Saccotheciaceae* without forming distinct clades (Humphries et al. 2017, Hongsanan et al. 2020b). Thus, a broad sampling of *Kabatiella, Columnosphaeria* and *Selenophoma* species with their types is required to resolve the taxonomic boundaries of these genera. Furthermore, due to the black yeast asexual morphology, *Zalaria* is difficult to distinguish from *Aureobasidium* and *Hormonema*. Therefore, molecular data also play a major role in species identification.

Significance

Ecological and economic roles

Members of *Dothideales* can be biotrophic, saprobic or necrotrophic on twigs, branches, leaves and other plant parts including fruits (Thambugala et al. 2014, van Nieuwenhuijzen et al. 2016a, Crous & Groenewald 2017, Hongsanan et al. 2020b). *Aureobasidium* is an important pathogen

of *Proteaceae* (Crous et al. 2011c). In addition, *Aureobasidium* species have been found as human pathogens causing a range of human diseases including fungemia (Mittal et al. 2018), septicemia (Hawkes et al. 2005, Huang et al. 2008), and chronic fungal meningitis (Kutleša et al. 2012). Furthermore, *Aureobasidium* strains are useful in agricultural and industrial applications. Their antagonistic activities against a range of postharvest pathogens make them suitable biocontrol agents for postharvest preservation of fruits and vegetables (Prasongsuk et al. 2018, Thambugala et al. 2020). *Kabatina* species plays a major role as a parasite on branches of *Abies*, *Juniperus*, *Mahonia*, *Populus* and *Thuja* species and is associated with needle dieback and tip blight in conifer hosts (Tisserat & Pair 1997, Thambugala et al. 2014, Hongsanan et al. 2020b). *Phaeocryptopus* species are also parasitic on conifer needles, especially on Douglas-fir needles (Temel et al. 2003, Winton et al. 2003, Hongsanan et al. 2020b).

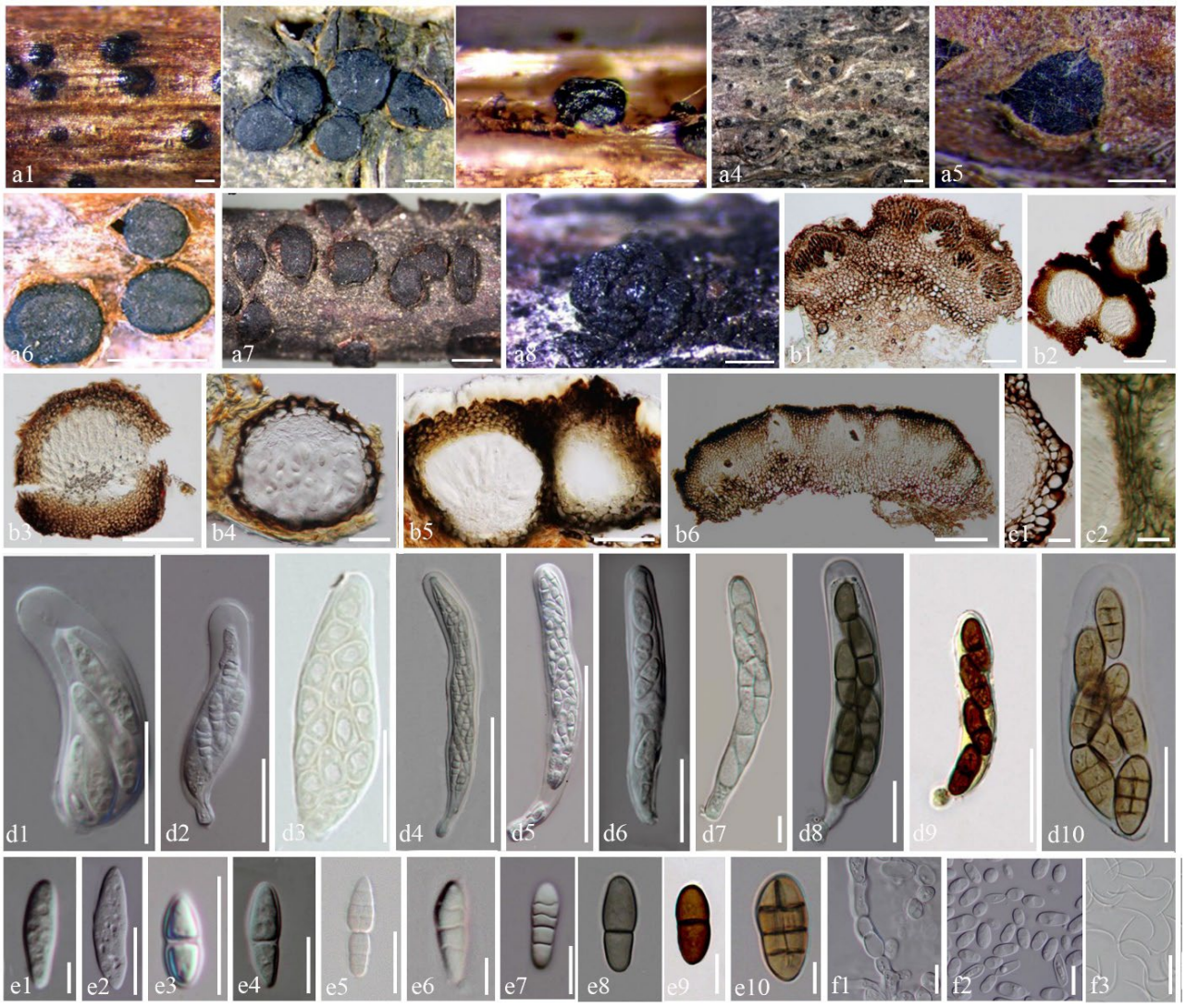


Figure 28 – Characteristic features of the sexual and asexual morphs of *Dothideales*. a1–a8 Appearance of ascostromata on host (a1 *Saccothecium sepincola*, a2, a3 *Dothidea insculpta*, a4 *Sydowia gregaria*, a5 *Dictyodothis berberidis,* a6 *Dothidea sambuci*, a7 *Plowrightia ribesia* a8 *Plowrightia abietis*). b1–b6 Vertical cross section through ascostroma (b1 *Stylodothis puccinioides*, b2 *Delphinella strobiligena*, b3 *Sydowia gregaria*, b4 *Columnosphaeria fagi*, b5 *Saccothecium sepincola*, b6 *Dictyodothis berberidis*). c1 & c2 Peridium (c1 *Dothidea insculpta*, c2 *Plowrightia ribesia*), Asci (d1 *Columnosphaeria fagi*, d2 *Saccothecium sepincola*, d3 *Phaeocryptopus* nudus, d4 *Sydowia gregaria*, d5 *Delphinella strobiligena*, d6 *Dothidea insculpta*, d7 *Plowrightia ribesia*, d8 *Dothidea sambuci*, d9 *Stylodothis puccinioides*, d10 *Dictyodothis berberidis*). e1–e10 Ascospores (e1 *Columnosphaeria fagi*, e2 *Columnosphaeria sarothamni*, e3 *Delphinella strobiligena*, e4

Dothidea insculpta, e5 *Dothiora pyrenophora*, e6 *Sydowia gregaria*, e7 *Saccothecium sepincola*, e8 *Dothidea sambuci*, e9 *Stylodothis puccinioides*, e10 *Dictyodothis berberidis*), f1 Conidiophores and conidiogenesis (*Aureobasidium pullulans*). f2, f3 Conidia (f2 *Aureobasidium pullulans*, f3 *Dothiora pyrenophora*) (pictures are adapted from Thambugala et al. 2014). Scale bars: a2, a4, a5–a7 = 1000 µm, a8, b6 = 500 µm, a3 = 200 µm, a1, b1–b3= 100 µm, b5, d4, d5 = 50 µm, b4, d2 = 25 µm, c1, c2, d1, d3, d6, d8–d10, e5, e9, f3 = 20 µm, d7, e3, e4, e7, e8, f1, f2 = 10 µm, e1, e6, e10 = 5 µm.

Chemical diversity

Aureobasidium species are associated with a wide range of metabolite production (Abdel-Lateff et al. 2009, Prasongsuk et al. 2018). *Aureobasidium pullulans* appears to be a potent source of single-cell protein. Furthermore, many strains of *A. pullulans* comprise a wide range of industrially important enzymes and these strains also produce poly (β-L-malic acid), heavy oil liamocins, siderophore, and aubasidan-like β-glucan which can be used in many biotechnological applications (Prasongsuk et al. 2018). Shigemori et al. (1998) discovered two new diketopiperazines with a D-*cis*-4-hydroxyproline residue, orcinotriol, and a new 1,3-dihydroxyphenol derivative from cultured broth of *Aureobasidium pullulans* strains isolated from an Okinawan marine sponge. Later, Abdel-Lateff et al. (2009) isolated two antifouling compounds, aureobasidin, a new ester with an unusual 4,6-dihydroxydecanoic acid residue, and (3R,5S)-3,5-dihydroxydecanoic acid were also isolated from the marine-derived *Aureobasidium* sp.

Other relevant data and future recommendations

Both coelomycetous and hyphomycetous species have been reported as the asexual morphs of *Dothideales* even in the same genus. For instance, *Dothiora* is shown to produce dothichiza- and hormonema-like synasexual morphs in culture (Crous & Groenewald 2017). Many dothidealean fungi are yet to be described and the generic and species delineation of several taxa remains uncertain. Thus, detailed investigations on allied taxa are required for future conservation as well as better taxonomic resolution. Moreover, only nrDNA sequence data are available in the GenBank for most species, and species delimitation using these sequence data is not enough for a better understanding of the order. Therefore, multi-locus phylogenetic analyses including protein-coding genes for all the species in *Dothideales* is recommended (Thambugala et al. 2014).

***Dyfrolomycetales* K.L. Pang, K.D. Hyde & E.B.G. Jones, Fungal Diversity 63: 7 (2013)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Dyfrolomycetales thrive in marine environments and exhibit distinct morphological characteristics. The order was introduced by Hyde et al. (2013) to accommodate *Dyfrolomycetaceae*. This taxonomic classification was established to accommodate the newly identified genus *Dyfrolomyces*, a mangrove fungus discovered in Malaysia. *Dyfrolomyces* is characterized by forming a clypeus on substrates, immersed perithecial ascomata, bitunicate/fissitunicate asci, and multi-septate ascospores with or without a sheath. These distinctive characteristics contribute to delineating *Dyfrolomyces* within the fungal taxonomy introduced by Pang et al. (2013).

History

Pang et al. (2013) established *Dyfrolomycetaceae* to encompass *Dyfrolomyces*, a mangrove fungus discovered in Malaysia. The fungus first exhibited morphological similarities to *Saccardoella*, a marine species, while the phylogenetic analysis revealed it was close to *Saccardoella rhizophorae* within *Dothideomycetes*. *Dyfrolomyces* and *Saccardoella* were identified as well-supported clades alongside *Acrospermum* in *Acrospermaceae*. Notably, neither species aligned with *Saccardoella*, a genus characterized by unitunicate asci. Consequently, *Dyfrolomyces* was established to accommodate the novel fungus, identified as *Dyfrolomyces tiomanensis* while the three marine

Saccardoella species (*S. mangrovei*, *S. marinospora*, and *S. rhizophorae*) were reclassified and transferred to *Dyfrolomyces* (Pang et al. 2013). Later, *Dyfrolomycetaceae* was synonymized under *Pleurotremataceae*, based on taxonomic adjustment supported by the re-examination of the isotype of *Pleurotrema polysemum* (Maharachchikumbura et al. 2016). The recent fungal taxonomy by Wijayawardene et al. (2022a) placed *Dyfrolomyces*, *Melomastia*, and *Pleurotrema* in the family *Pleurotremataceae*. Later, Li et al. (2022c) merged all *Dyfrolomyces* species into *Melomastia* based on morphological characteristics and phylogenetic analysis. This analysis separated *Melomastia* into two major clades with strong bootstrap support. However, Kularathnage et al. (2023) conducted a phylogenetic analysis of *Melomastia* species and identified three subclades, each representing distinct morphotypes. As a result, the researchers proposed dividing *Melomastia* into two subclades: *Melomastia sensu stricto* (Clade A), which closely resembles the type species *M. mastoidea* (Kang et al. 1999), and *Melomastia sensu lato* (Clade B). They noted the lack of clear morphological characteristics to reliably distinguish species within *Melomastia*, which led to the re-evaluation of the identification of the genus *Dyfrolomyces* (Clade C). The researchers provided key morphological differences among species in subclades A, B, and C to facilitate a clearer understanding of fungi in this group. This subdivision aimed to acknowledge the morphological variation observed within *Melomastia* and the challenges in establishing clear distinctions between these closely related genera. So far, many species have been added to this order (Pang et al. 2013, Hyde et al. 2017b, 2018b, Norphanphoun et al. 2017, Zhang et al. 2017b, Dayarathne et al. 2020, Hongsanan et al. 2020b, Mapook et al. 2020a, Phukhamsakda et al. 2020, Li et al. 2022c, Kularathnage et al. 2023).

General description

The members of *Dyfrolomycetales* can be identified by their perithicoid, coriaceous, and immersed ascomata, which have a clypeate structure, ostiole, and papillate attributes. The asci of these fungi are bitunicate, fissitunicate, and cylindrical, displaying a short pedicel and a distinctive ocular chamber with a ring-like subapical apparatus. Other defining features include hyphae-like pseudoparaphyses surrounded by a gelatinous matrix, along with uniseriate, broadly fusiform, symmetrical, hyaline, multiseptate ascospores that have wide septa and smooth walls. Importantly, these fungi differ from *Monoblastiales* in that they have nonlichenized ascomata, hyphae-like pseudoparaphyses, and hyaline, multiseptate ascospores. Additionally, they can be distinguished from *Kirschsteiniotheliaceae* by the absence of brown, 1-septate ascospores and an asexual state observed in *Dendryophiopsis* (Hyde et al. 2013).

Sexual morph: *Ascomata* solitary or gregarious, immersed or erumpent to superficial when mature, globose or pyriform, dark brown to black; in vertical section obpyriform, with a central periphysate ostiolar canal. *Peridium* comprising several layers of brown to dark brown, compressed cells. *Paraphyses* filamentous, flexuose, numerous. *Asci* 8-spored, cylindrical, thick-walled, non fissitunicate or fissitunicate, pedicellate, apically rounded, with a J- or J+, subapical ring. *Ascospores* uniseriate, fusiform to oblong with rounded ends or spindle-shaped with acute ends, hyaline, 2–11-septate, strongly constricted at the septa, with a lipid globule in each cell, with or without gelatinous sheath. Asexual morph: Undetermined (adapted from Hongsanan et al. 2020b) (Fig. 29).

Families included in *Dyfrolomycetales*

Pleurotremataceae Walt. Watson

Evolution

The evolution of *Dyfrolomycetales* has been investigated using various molecular methods. DNA sequence data-based phylogenetic analyses have offered insights into the relationships and evolutionary patterns within this group. By integrating phylogenetic analyses with considerations of morphology and ecology, it has been determined that *Dyfrolomycetales* is not monophyletic (Li et al. 2022c, Kularathnage et al. 2023). The estimated divergence time for *Dyfrolomycetales* is 171 MYA (Hongsanan et al. 2020b), and it is sister to the order *Acrospermales*.

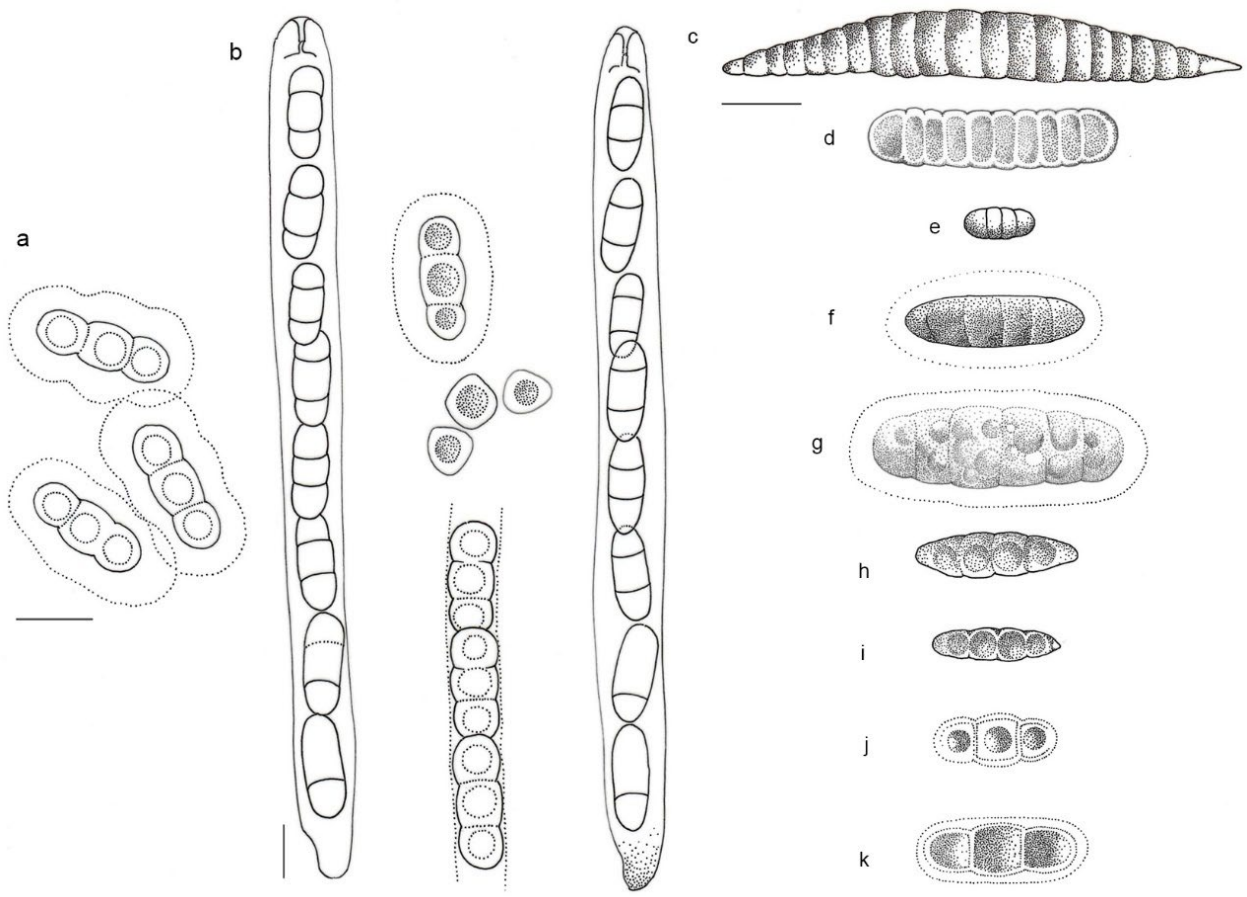


Figure 29 – Morphology of *Dyfrolomycetales*. a, b. *Melomastia mastoidea* asci and Ascospores. c–k Ascospores: c *Dyfrolomyces tiomanensis*. d *Melomastia phetchaburiensis*. e *M. polysemum*. f *M. rhizophorae*. g *M. thailandica*. h *M. thamplaensis*. i *M. maolanensis*. j *M. antarctica*. k *M. chilensis*. (redrawn from Spegazzini (1887), Petrak (1921), Barr (1994), Kang et al. (1999), Pang et al. (2013), Hyde et al. (2016b, 2017b), Maharachchikumbura et al. (2016), Zhang et al. (2017b)). Scale bar: a–k = 10 μm.

Justification of order and problems

Revising the family *Pleurotremataceae* is difficult due to the need for molecular data for the well-known genera *Melomastia* and *Pleurotrema* type species. Some researchers have proposed merging *Dyfrolomyces* and *Pleurotrema* under *Melomastia* because of their similar phenotypic traits. However, a detailed analysis using phylogenetic data and morphological features suggests that these groups should be treated as separate genera. While certain species within these genera show some different morphological features, such as septate ascospores, further research is expected to identify additional taxa and clarify their distinctions (Li et al. 2022c, Kularathnage et al. 2023). In particular, studies focusing on *Pleurotrema polysemum* are crucial for understanding the taxonomic relationships within *Pleurotremaceae*. The genus *Pleurotrema* is currently considered synonymous with *Lithothelium*, and is placed in the *Pyrenulaceae* and *Pyrenulales* according to Index Fungorum. This suggests that the exact classification of this genus is uncertain. Further research, including additional sequence data and new specimens, is needed to clarify the relationships within *Pleurotremataceae* and to explore the connections between sexual and asexual reproduction in these fungi.

Significance

Ecological and economic roles

The fungi in this taxonomic order have been observed to live as saprobes on woody branches, twigs, and culms in terrestrial, freshwater, and mangrove environments (Hyde & Lee 1998). These

fungi have a wide geographical distribution, including regions in Africa, Brunei, China, Colombia, Germany, India, Italy, Japan, Malaysia, Poland, Thailand, and the United States of America (California) (Pang et al. 2013, Hyde et al. 2017b, 2018b, Norphanphoun et al. 2017, Zhang et al. 2017b, Dayarathne et al. 2020, Hongsanan et al. 2020b, Mapook et al. 2020a, Phukhamsakda et al. 2020, Li et al. 2022c, Kularathnage et al. 2023). Although a few species are known as saprobes on mangrove wood (*Avicennia marina*, *Kandelia*, *Rhizophora* sp.), the rest are reported from various woody hosts (e.g., *Clematis* sp., *Chromolaena odorata*, *Olea europaea*, and *Vitis vinifera*).

Chemical diversity

There is currently no report available on the chemical diversity of the species within *Dyfrolomycetales*.

Other relevant data and future recommendations

Dyfrolomycetales species are found in diverse environments, including marine, freshwater, and terrestrial habitats. These fungi exhibit distinct morphological characteristics, such as bitunicate/fissitunicate asci and multiseptate ascospores, which are crucial for their identification and classification. However, the chemical diversity within *Dyfrolomycetales* is not well understood, representing a significant gap in our knowledge, especially regarding their potential ecological roles and applications in biotechnology or medicine. To address these gaps, several future research directions are recommended. Continued molecular and phylogenetic analyses are essential to clarify the relationships between *Dyfrolomyces*, *Melomastia*, and *Pleurotrema*. These studies should focus on obtaining more genetic data from a broader range of species to better resolve their taxonomic boundaries. Detailed morphological studies, particularly on newly discovered species, should be conducted to identify subtle differences that may not be apparent in current classifications. This includes thorough documentation of reproductive structures and spore characteristics. Additionally, exploring the chemical diversity of *Dyfrolomycetales* species could uncover novel compounds with potential pharmaceutical or industrial applications. Studies on their adaptations to different environments, particularly extreme habitats like mangroves, may also reveal valuable stress tolerance mechanisms. As new data emerges, it may also be necessary to revisit and revise the taxonomic classifications within *Dyfrolomycetales*. Particular attention should be given to genera that show overlapping morphological, ensuring that classifications reflect both genetic and phenotypic evidence. Addressing these research gaps will provide a more comprehensive understanding of *Dyfrolomycetales*, contributing to both fundamental mycological knowledge and potential practical applications.

Endophytiales **G.G. Barreto, Souza-Motta, G.A. Silva, J.Z. Groenew., Crous & J.D.P. Bezerra, Fungal Systematics and Evolution 14: 81 (2024)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction and History

Endophytiales was recently introduced by Barreto et al. (2024) to accommodate a single family *Endophytiaceae*, with the genus *Endophytium.* The genus comprises two species namely, *Endophytium albocacti* with the type species *Endophytium cacti*. The order formed a close phylogenetic association with *Gobabebomyces* and *Lembosiniella* and they together formed a basal clade to *Myriangiales* in the multigene phylogenetic analyses (ITS, LSU, SSU and RPB2). A detailed morphological comparison with morphologically and phylogenetically closely related taxa is provided by Barreto et al. (2024).

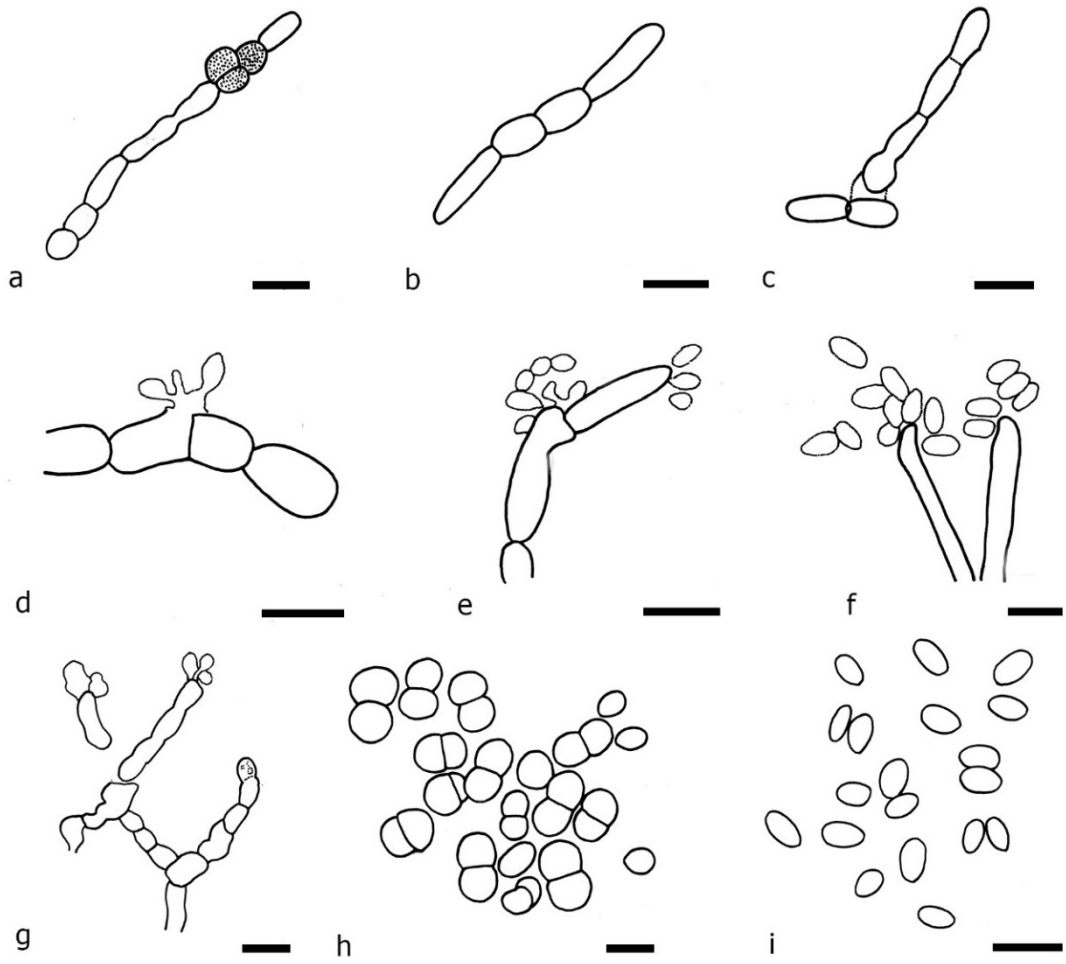


Figure 30 – Asexual morph of *Endophytiales.* a–d Conidiogenous cells and conidia (a–f *Endophytium albocacti*, g *Endophytium cacti*). h Details of cells dividing into globose to subglobose cells (*Endophytium cacti*). i Conidia (*Endophytium cacti*) (Barreto et al. 2024). Scale bars: a–i = 10 μm.

General description

The taxa are only reported from the hypomycetous asexual morph (Barreto et al. 2024). Sexual morph: Not observed. Asexual morph: See Barreto et al. (2024) for detailed description (Fig. 30).

Families included in *Endophytiales*

Endophytiaceae G.G. Barreto, Souza-Motta, G.A. Silva, J.Z. Groenew., Crous & J.D.P. Bezerra

Justification of order and problems

In this study, we provided a brief overview of this order, which was recently established to accommodate a monotypic family, with updated information available in Barreto et al. (2024).

Significance

Ecological and economic roles

The taxa are reported as endophytic fungi from Brazil and are reported in asexual morph (Barreto et al. 2024).

Chemical diversity

No relevant studies are available regarding the chemical diversity of the members of *Endophytiales.*

***Endosporiales* G.G. Barreto, Souza-Motta, G.A. Silva, J.Z. Groenew., Crous & J.D.P. Bezerra, Fungal Systematics and Evolution 14: 83 (2024)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Endosporiales was introduced to accommodate *Endosporiaceae* with the single genus *Endosporium* (Barreto et al. 2024).

History

Endosporium was introduced to accommodate the type species *Endosporium populi-tremuloides* with *E. aviarium* and the genus was reported as the first black meristematic fungus producing endoconidia within *Myriangiales* (Tsuneda et al. 2008). The genus showed similar morphology to dematiaceous hyphomycetous genus *Phaeotheca* but showed distinct morphology in conidiomatal and endoconidial features. Further, the genus recovered within *Myriangiales* in the phylogenetic analysis conducted based on SSU, LSU and ITS sequences data (Tsuneda et al. 2008). However, *Endosporium* was not clustered within *Myriangiales* in the multigene phylogenetic analyses (ITS, LSU, RPB2 and SSU) conducted by Hongsanan et al. (2020b) but formed a basal clade to *Myriangiales* in the LSU sequence data. Thus, the author accepted *Endosporium* under *incertae sedis*. The genus formed a close phylogenetic clade to *Lembosiniella* and a newly established genus *Gobabebomyces* in the phylogenetic analyses conducted by Crous et al. (2020a) and they together formed a sister clade to *Myriangiales*. The author highlighted the close phylogenetic association of *Gobabebomyces* to *Endosporium populi-tremuloides* based on LSU sequence data. Consequently, a new family *Endosporiaceae* was introduced to accommodate *Endosporium* based on morphological reinvestigation of *Endosporium populi-tremuloides* along with molecular analysis (Pem et al. 2019b). The genus formed a basal clade to *Myriangiales* and close to *Dothideales* and the family was accepted under *incertae sedis* without designating its ordinal placement (Pem et al. 2019b). However, the genera *Lembosiniella* and *Gobabebomyces* were not accounted in their phylogenetic analyses. Wijayawardene et al. (2022a) and Pem et al. (2024) accepted *Endosporium* and *Gobabebomyces* under *Endosporiaceae* in *Dothideomycetes* families *incertae sedis* and *Lembosiniella* under *Dothideomycetes* genus *incertae sedis*. The multigene phylogenetic analyses (ITS, LSU, SSU and RPB2) conducted by Barreto et al. (2024) showed, that *Endosporium* formed a distinct clade basal to *Myriangiales*. Further, the genera *Gobabebomyces* and *Lembosiniella* formed a sister clade to *Endophytiales* but the clade was not supported. Due to the unstable relationship found according to the gene marker, *Gobabebomyces* and *Lembosiniella* were treated under *incertae sedis* at the family and order level and *Endosporiales* was established to accommodate *Endosporium* (Barreto et al. 2024).

General description

The taxa are characterized by subhyaline and dumbbell-shaped cells forming ellipsoidal to globose hyaline endoconidia and hyaline or light brown, cylindrical to ellipsoidal blastic conidia (Pem et al. 2019b) (Fig. 31).

Sexual morph: Not observed. Asexual morph: See Barreto et al. (2024) for updated morphological description.



Figure 31 – Asexual morph of *Endosporiales* (*Endosporium populi-tremuloides*). a Squash mount of mycelium. b, c Hyphae giving rise to cellular clumps. d, e Blastic conidia. Scale bars: a–g = 10 μm.

Genera included in *Endosporiales*

Endosporiaceae D. Pem, Doilom & K.D. Hyde

Justification of order and problems

The order was solely reported on the asexual morph. Thus, more collection of *Endosporium* with their closely related genera *Gobabebomyces* and *Lembosiniella* are important for better taxonomic understanding with closely related taxa.

Significance

Ecological and economic roles

The taxa were reported on the bud of *Populus tremuloides*, skin of *Bombycilla garrulus* twigs of *Populus balsamifera* and found in Canada (Tsuneda et al. 2008).

Chemical diversity

No relevant studies are available for the chemical diversity of *Endosporiales.*

***Eremithallales* Lücking & Lumbsch, Symbiosis 46(3): 163 (2008)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Eremithallales was introduced to accommodate a single family *Eremithallaceae* and a single species *Eremithallus costaricensis* which was collected from tree bark in Costa Rica (Lücking et al. 2008). The species showed unique features in its vegetative organization and arrangement of algae. The algae were identified as *Trentepohlia sensu lato* and were found within individual periderm cells of the bark and connected by hyaline fungal hypha beneath the base of the apothecia. The true thallus, medulla and (pseudo-)cortex are absent and only found in the upper cortex of the bark periderm. The fungus was identified as neither a tree parasite (on the basis of the absence of penetrating structures to the living tissue (phloem)) nor an endophloedic species in the presence of algal cells which are located in deep periderm within the individual cells without damaging cells.

Eremithallales presently comprises *Encephalographa* and *Melaspilea* (Ertz et al. 2015, Hongsanan et al. 2020b, Wijayawardene et al. 2020, 2022a). *Melaspilea* is considered to be a heterogenous group which includes saprotrophic, lichenized and lichenicolous species. Several other species are barely lichenized or non-lichenized on bark (Ertz et al. 2015). The taxa were traditionally characterized with arthonioid (round to irregular-shaped) to opegraphoid (ellipsoid to lirellate) ascomata and 1-septate spores with thin walls (Ryan & Nimis 2004).

History

Eremithallales was initially placed in *Lichinomycetes* based on morphological and molecular analyses. Ertz et al. (2015) synonymized *Eremithallaceae* under *Melaspileaceae* and *Eremithallus costaricensis* under *Melaspilea* based on multi-gene phylogenetic analyses and morphology. *Eremithallus* shares similar morphology with *Melaspilea sensu stricto* in ascomatal characteristics and the presence of trentepohlioid photobionts. *Melaspileaceae* was initially established by Watson (1929) to accommodate *Melaspilea*, *Micrographa* (= *Lembosia*) and *Pycnographa* (= *Parmularia*). *Melaspileaceae* presently comprises two genera including *Encephalographa* and *Melaspilea*. The family was placed in *Graphidales* (Poelt 1974a), *Patellariaceae* (von Arx & Müller 1975) or *Buelliaceae* (Eriksson 1981). The placement of *Melaspilea* was doubtful because it comprised a heterogonous assemblage of poorly known species. It was tentatively placed in *Arthoniales* (Lumbsch & Huhndorf 2010). Ertz et al. (2015) initially provided sequence data for the type *M. arthonioides* and consequently reclassified the family *Melaspileaceae*.

Encephalographa was introduced by Massalongo (1854) to accommodate two species, namely, *E. elisae* and *E. rubiformis* which formed clustered, lirelliform ascomata, two-celled brownish ascospores with a thin perispore (Tretiach & Modenesi 1999). *Encephalographa* differs from *Melaspilea* by its dichotomously branched, laterally anastomosed, lirelliform ascomata with a longitudinal sulcus (Ertz et al. 2015). *Encephalographa* was typified with *Encephalographa elisae* and was identified as a lichenicolous (Renobales & Aguirre 1990) and lichenized fungus on limestone (Tretiach & Modenesi 1999). Renobales & Aguirre (1990) placed this genus within *Hysteriaceae* without molecular data. Boehm et al. (2009b) initially sequenced the type species that was reported from Mauro Tretiach and formed a sister clade relationship to *Pleosporomycetidae* and *Dothideomycetidae*. The phylogenetic analysis conducted by Ertz et al. (2015) demonstrated the inclusion of the genus within *Melaspileaceae*. The placement within *Lichinomycetes* was not supported further by the absence of cyanobacterial or rarely trebouxioid photobionts (Ertz et al. 2015). Perez-Ortega & Etayo (2010) established a new lichenicolous genus for *Labrocarpon canariense* that shared similar morphology to *Melaspilea* but was distinguished by having periphyses and was accepted under *Melaspileaceae*. Ertz et al. (2015) transferred this genus to *Asterinales* based on phylogenetic analyses. However, periphyses also can be present in members of *Eremithallales* and *Asterinales* that are often only visible in well-developed ascomata rather young ascomata or specimens with poor condition (Ertz et al. 2015).

General description

Melaspilea form lirelliform apothecioid ascomata, an exciple composed of several cell layers and brown 1-septate ascospores whereas *Encephalographa* forms clustered, lirelliform ascomata, two-celled brownish ascospores with a thin perispore (Fig. 32).

Sexual morph: *Thallus* crustose. *Photobiont* Trentepohlioid. *Ascomata* apothecial, lirelliform, immersed to superficial, densely aggregated in compact clusters, with a disk reduced to a narrow slit, slightly convex disk and a slightly elevated margin, often surrounded by marginal lobes from the substrate. *Exciple* reddish-brown, dark brown to black, K+ olivaceous brown. *Hymenium* non-amyloid. *Paraphyses* dense net of branched and anastomosed. *Periphyses* anastomosed, arising from the inner exciple. *Asci* elongate clavate, clavate to subcylindrical, thick walled sometimes apically thickened, 8-spored asci, distinct ocular chamber, I– and K/I. *Ascospores* ellipsoid, 1-septate, smooth to finely ornamented, hyaline to brownish ascospores that are constricted near the septum, thin

perispore and or K/I+ blue gelatinous sheath. Asexual morph: Undetermined (adapted from Hongsanan et al. 2020b).

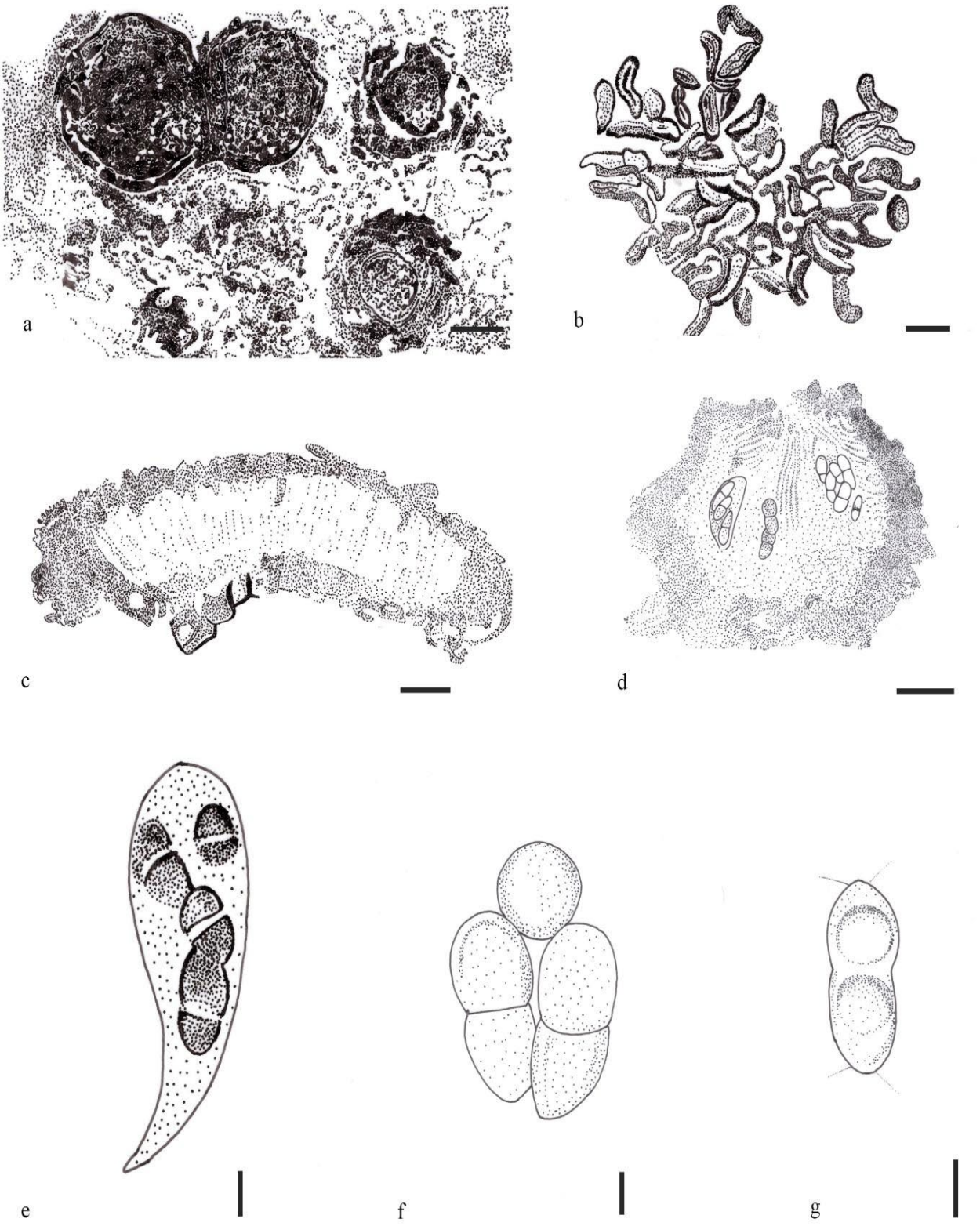


Figure 32 – Morphology of *Eremithallales.* a Ascomata of *Melaspilea enteroleuca*. b Ascomata of *Encephalographa elisae*. c Vertical section through *Melaspilea urceolata*. d *Melaspilea diplasiospora*. e Asci of *M. arthonioides*. f Ascospores of *Melaspilea proximella*. g Ascospores of

Melaspileopsis cf. *diplasiospora* (redrawn from Ertz et al. 2015). Scale bars: a = 100 µm, b = 500 µm, c, d = 50 µm, e = 10 µm, f, g = 5 µm.

Families included in *Eremithallales*

Melaspileaceae W. Watson (= *Eremithallaceae* Lücking & Lumbsch)

Evolution

The co-evolution of *Melaspileaceae* will be particularly interesting due to the varying life styles reported in individual species. However, the evolution of *Eremithallales* remains understudied, with Hongsanan et al. (2020a) estimating the divergence time of this order to be around 238 MYA.

Justification of order and problems

Lücking et al. (2008) placed *Eremithallales* within *Lichinomycetes* based on analyses of mtSSU, LSU and RPB1 sequences. However, Ertz et al. (2015) transferred this order to *Dothideomycetes* based only on the LSU gene region. However, considering the extensive taxon sampling and morphological similarities between *Eremithallus costaricensis* with *Melaspilea*, placement within *Dothideomycetes* can be acceptable. Ertz et al. (2015) also studied material from Thailand that was identified as non-lichenized *Melaspilea* with simple or more often branched and star-like lirelliform ascomata, strongly elevated margin, dark brown, K+ olivaceous brown exciple, epihymenium medium to dark brown, branched and anastomosed paraphyses, clavate apically thickened, with a distinct ocular chamber and ellipsoid, 1-septate, smooth, hyaline to brownish ascospores. Nonetheless, the species differs significantly from the extant members of *Melaspileaceae*. It is currently treated as unidentified due to the lack of data available for the type material of *Melaspilea sensu lato*.

Significance

Ecological and economic roles

The taxa are reported as lichenized, lichenicolous, and non-lichenized saprotrophic species (Ertz et al. 2015). *Melaspilea bagliettoana* was found on rough bark surfaces of living, old aspen trees (*Populus tremula*) (Jordal et al. 2022). However, the lifestyle of this species is doubtful. Coppins (2002) and Sanderson et al. (2009) treated the species as a lichen. Woods & Coppins (2012) described it as probably non-lichenized, but Nimis (2016a) described it as doubtfully lichenized.

Chemical diversity

No chemical studies are reported in *Eremithallales*.

***Eremomycetales* Crous, Spatafora, Haridas & I.V. Grig. Studies in Mycology 96: 151 (2020)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Eremomycetales was introduced by Haridas et al. (2020) and placed in *Dothideomycetes*. *Eremomycetaceae* is the only family in *Eremomycetales* and comprises two genera: *Rhexothecium* and *Eremomyces* as the type genus (Lumbsch & Huhndorf 2010). *Eremomycetaceae* was introduced by Malloch & Cain (1971b) to accommodate species having solitary ascomata and hyaline ascospores without septate. The morphology of *Eremomycetaceae* is most similar to *Pseudeurotiaceae* (Malloch & Sigler 1988), but differs in ascomatal initials (coiled ascomata in *Pseudeurotiaceae* whereas pseudoparenchymatous ascomata in *Eremomycetaceae*). The members of *Eremomycetaceae* are distributed worldwide as saprobic on animal dung or soil and are commonly found in Egypt, Kenya, North America and the Netherlands (Hongsanan et al. 2020b). *Eremomyces* has fabiform and hyaline ascospores which are similar to *Trichosporiella* (*Helotiales*), but *Trichosporiella* differs by having subglobose to globose, black conidiomata and scopulariopsis-like hyaline conidia (Hongsanan et al.

2020b). *Rhexothecium* has broadly oblate and pale yellow to brown ascospores and morphology resembles *Trichosporiella* (*Helotiales*) in having solitary to catenulate, lateral, and hyaline, basic truncate conidia (Hongsanan et al. 2020b).

History

Malloch & Sigler (1988), transferred *Pithoascus langeronii* to the genus *Eremomyces* (*E. langeronii*). Later, molecular data showed that *Eremomyces langeronii* belongs to *Pezizales* (Kang et al. 2010) and it was synonymized as *Arthrographis arxii*. The morphology of *Eremomyces* resembles some tropical parasites (*Cleistosphaera* and *Pilgeriella*) (Malloch & Cain 1971b). *Eremomyces* is distinct from all other genera and always clustered within *Eremomycetaceae* (Hongsanan et al. 2020b). Presently, *Eremomycetaceae* consists of three genera; *Arthrographis*, *Eremomyces* and *Rhexothecium* (Hyde et al. 2024b).

General description

Members of the *Eremomycetaceae* have similar morphological features to *Pseudeurotiaceae* as both families have dark ascomata without ostiolate, hyaline ascospores, and are unicellular (Lumbsch & Huhndorf 2010). *Pseudeurotiaceae* however, differs by having pale-brown or olive-brown ascospores and an asexual morph with poorly differentiated conidiophores sympodially and subspherical to ovoidal conidia (Malloch & Sigler 1988) (Figs. 33, 34).

Sexual morph: *Ascomata* spherical to ellipsoid, superficial on hyphae, or submerged in the agar, dark brown to black, solitary, scattered, without ostioles, but tending to split open before maturity, glabrous to setose. *Peridium* thin-walled, composed of large brown cells of *textura angularis*, pseudoparenchymatous. *Hamathecium* lacking pseudoparaphyses. *Asci* 8-spored, bitunicate, obovoid to clavate, irregularly disposed, pedicellate, evanescent, thin-walled. *Ascospores* multi-seriate, fabiform to broadly oblate, hyaline to pale brown, aseptate, lacking germ pores, smooth-walled to slightly verrucose (adapted from Malloch & Cain 1971b, Hyde et al. 2013). Asexual morph: Coelomycetous or hyphomycetous. *Pycnidia* globose to subglobose, papillate, thin-walled. *Conidiophores* filiform, hyaline to brown, septate. *Conidia* ellipsoidal, hyaline, aseptate, guttulate, thin-walled (adapted from Hongsanan et al. 2020b). *Arthroconidia* (present in *Arthrographis*) unicellular, cylindrical, cuboid or doliiform, straight, hyaline to subhyaline. *Chlamydospores* terminal or intercalary, solitary, unicellular, globose, or subglobose. Trichosporiella-like anamorph reported in *Rhexothecium globosum* (adapted from Pem et al. 2024).

Families included in *Eremomycetales*

Eremomycetaceae Malloch & Cain

Evolution

The divergence time for *Eremomycetales* is estimated as 262 MYA (stem age) (Hongsanan et al. 2020b).

Justification of order and problems

Arthrographis was traditionally considered a member of *Eremomycetaceae* (Malloch & Sigler 1988). Giraldo et al. (2014a) also demonstrated that the genera *Arthrographis sensu stricto*, *Rhexothecium* and *Eremomyces* encompass the family *Eremomycetaceae*. Later, *Arthrographis* was included in a new family *Arthrographaceae* by Liu et al. (2017b). Wijayawardene et al. (2018, 2020) included *Arthrographis* in *Eremomycetaceae*. However, *Arthrographaceae* has not been mentioned in the literature or Index Fungorum so whether the family is valid or not is unclear (Hongsanan et al. 2020b). *Arthrographis* produces similar conidia as *Eremomyces* by having hyaline to subhyaline conidia but differs by having unicellular arthroconidia and chlamydospores which are absent in *Eremomyces* (Hongsanan et al. 2020b). Therefore, Hongsanan et al. (2020b), used a combined dataset and included *Arthrographis* in *Eremomycetales*, genera *incertae sedis* until further studies are carried out. Hernández-Restrepo et al. (2020) recently introduced several new *Arthrographis* species and the genus was recovered within *Eremomycetaceae* in the phylogenetic analyses and consequently the

genera *Arthrographis, Eremomyces* and *Rhexothecium* were accepted under this family (Hyde et al. 2024b).

Significance

Ecological and economic roles

Arthrographis species are implicated as opportunistic human pathogens (Cannon & Kirk 2007, Pem et al. 2024). *Eremomyces bilateralis* was found on animal dung (especially rodents) in Canada (Ontario), Kenya, Tanzania and the USA (California) (Hongsanan et al. 2020b). *Rhexothecium globosum* was found in desert soil in Egypt (Hyde et al. 2013).

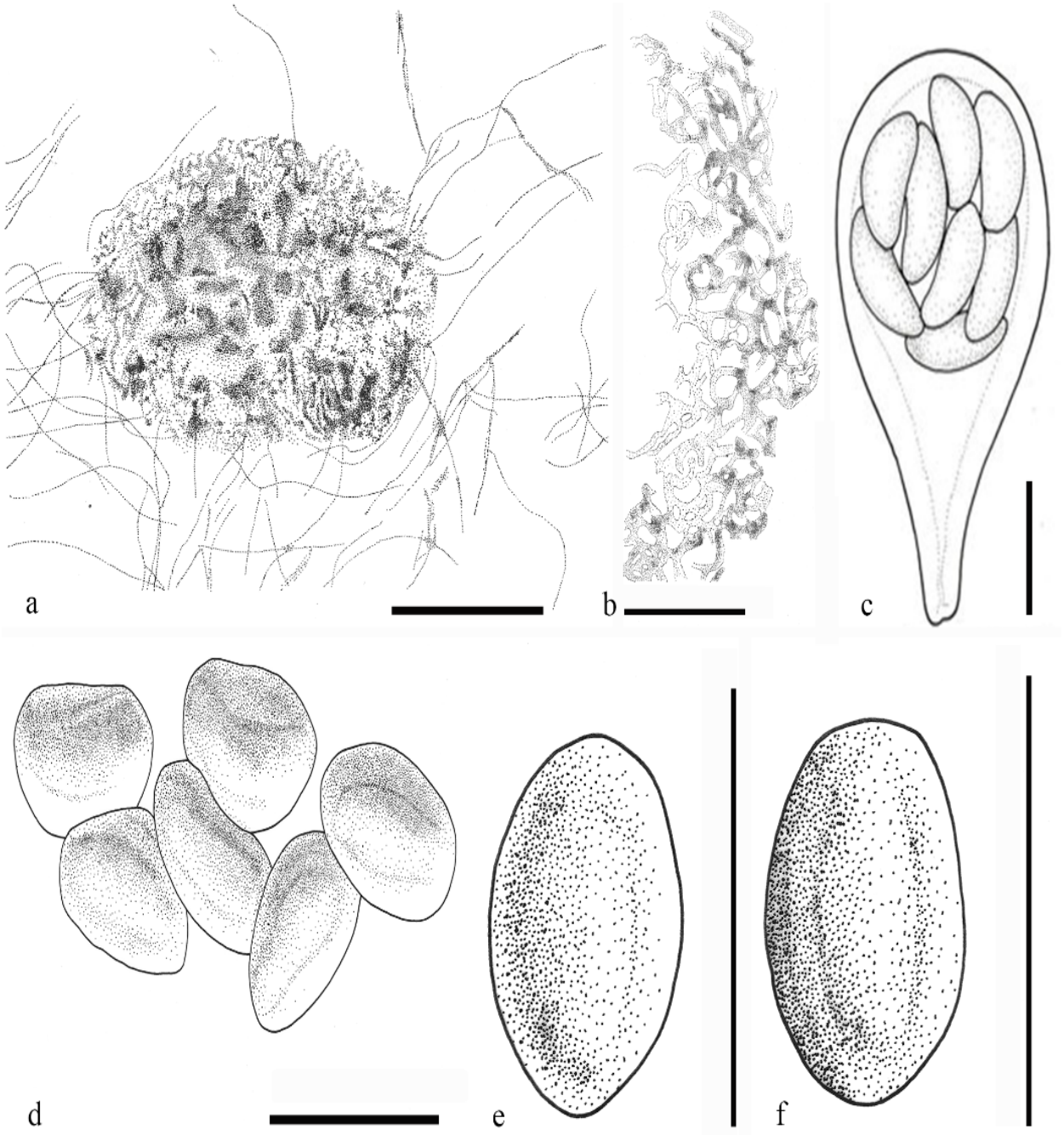


Figure 33 – Morphology of *Eremomyces bilateralis* (TRTC 045344, holotype). a Ascomata on hyphae. b Peridium. c Ascus. d–f Ascospores (redrawn from Hyde et al. 2013, Hongsanan et al. 2020b). Scale bars: a = 50 µm, b = 25 µm, c–f = 5 µm.

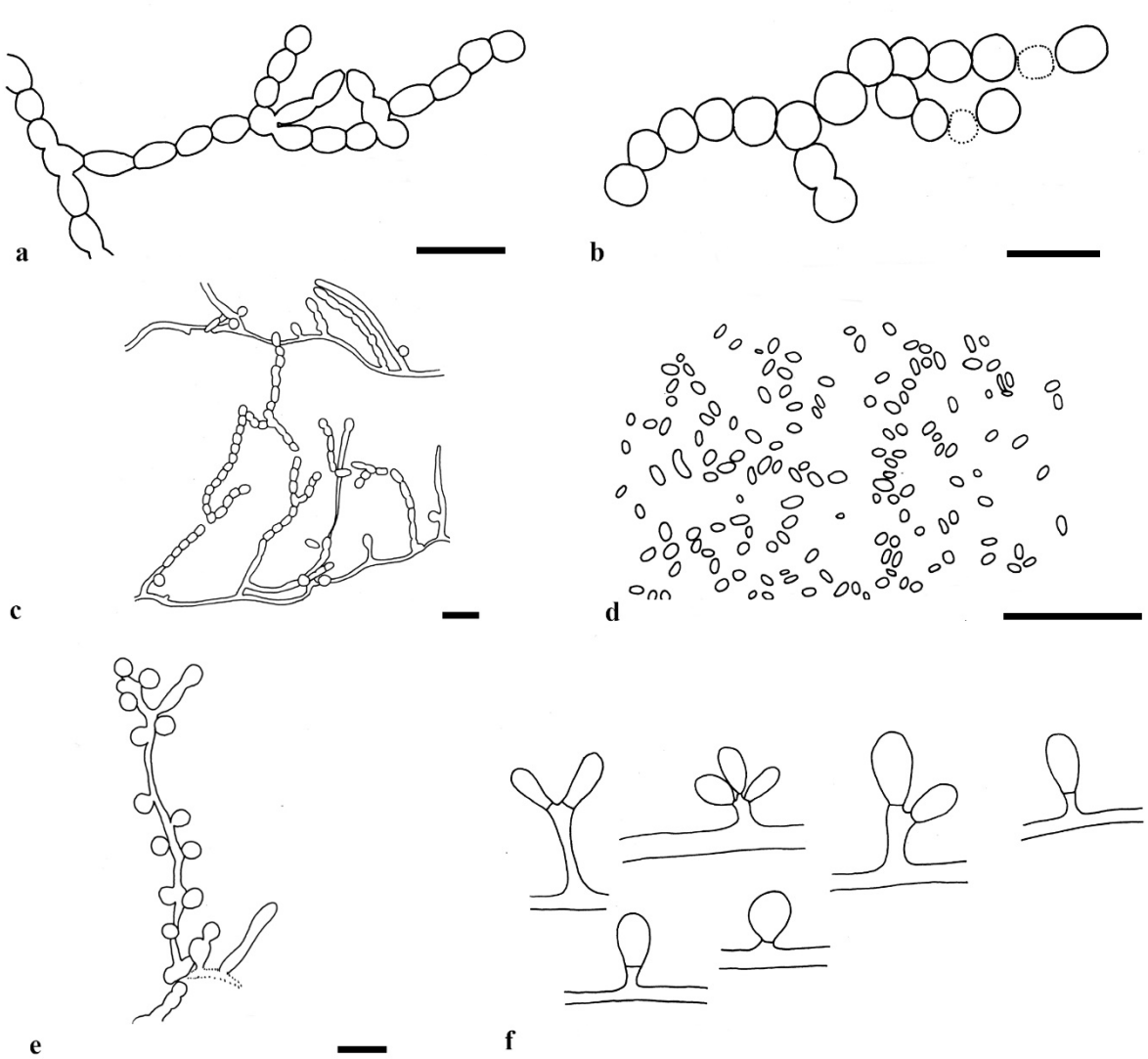


Figure 34 – Asexual morph of *Eremomycetales.* a Conidiogenous hyphae fragmenting schizolytically producing ellipsoidal, doliiform, slightly fusiform and globose arthroconidia. b Globose arthroconidia (a, b *Arthrographis globosa*). c Poorly branched conidiophores and arthroconidia. e Trichosporiella-like synasexual morph (c, e *Arthrographis grakistii*). d Conidia (*Eremomyces bilateralis*). f Trichosporiella-like anamorph (*Rhexothecium globosum*) (drawn from Giraldo et al. 2014a, Hernández-Restrepo et al. 2020, redrawn from Malloch & Sigler 1988). Scale bars = 10 μm.

Chemical diversity

Aamri et al. (2020) recently reported the Lipases (triacylglycerol acyl hydrolases EC 3.1.1.3) enzymes from *Arthrographis curvata* which have high biotechnological and industrial potential. Okeke & Obi (1992) reported cellulolytic and xylanolytic enzymes from *Arthrographis.* However, more studies in the future are needed to find chemical compounds in this order.

Other relevant data and future recommendations

Only a few species of *Eremomycetales* (*Eremomyces* and *Rhexothecium*) have been reported and although cultures and sequences of those species are available, they lack herbarium specimens (Wijayawardene et al. 2017a). Therefore, fresh collections of these genera need to be obtained for further studies so that they can be epitypified and isolates and molecular data can be analyzed to obtain a natural classification.

Gloniales **Jayasiri & K.D. Hyde, Mycosphere 9(4): 809 (2018)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Pleosporomycetidae*

Introduction

Gloniales was introduced by Jayasiri et al. (2018a) with *Gloniaceae* as the type based on the evidence from phylogeny and morphology. The order comprises one family, *Gloniaceae*, and three genera, *Cenococcum*, *Glonium* and *Purpurepithecium*, comprising a total of 73 species according to Species Fungorum (2024). Taxa in *Gloniales* are saprobes on bark, wood, pine cones, and ectomycorrhiza found in soil. Ectomycorrhizal *Cenococcum* species, are globally distributed and associated with a wide variety of host trees. They can be found in more than 200 tree species from 40 genera of both angiosperms and gymnosperms, such as *Betulaceae*, *Fagaceae*, and *Pinaceae* (Li et al. 2023). Phylogenetically, *Gloniales* forms a distinct sister clade to the *Mytilinidiales* clade based on phylogenetic analysis of combined LSU, SSU, RPB2 and TEF1 sequence data (Jayasiri et al. 2018a). Morphologically, *Gloniales* has modified hysterothecia, which are progressive dichotomous branched or scattered to gregarious. In contrast, *Mytilinidiales* is characterized by delicate and persistent carbonaceous ascomata that vary in shape from globoid to obovoid to strongly laterally compressed erect structures resembling bivalve shells standing on edge, with their lateral walls more or less connivant and extending vertically.

History

Corda (1842a) proposed *Gloniaceae* (currently belonging to *Gloniales*) as a subfamily within the family *Hysteriaceae*, encompassing both *Glonium* and *Hysterographium*. The sub-familial rank was amended and restricted to family rank by Boehm et al. (2009b) based on the monophyletic genus *Glonium*. However, the insufficient molecular sequence data of taxa in *Gloniaceae* hindered the establishment of their ordinal status. Therefore, Boehm et al. (2009c) classified *Gloniaceae* within the *Pleosporomycetidae* family *incertae sedis*. Boehm et al. (2009b) later added *Cenococcum* to *Gloniaceae*, and more recently, Jayasiri et al. (2017) added *Purpurepithecium* to this family. Based on the morphology and phylogenetic analysis of combined LSU, SSU, RPB2 and TEF1, Jayasiri et al. (2018a) placed *Gloniaceae* in a new order *Gloniales*. The order presently accommodates three genera (*Cenococcum, Glonium* and *Purpurepithecium*) (Hyde et al. 2024b).

General description

It is noted that *Cenococcum* species exist as sterile mycelia and lack sexual and asexual spores. Therefore, the current general description of *Gloniales* is based on the morphological characteristics exhibited by species in *Glonium* and *Purpurepithecium*. *Gloniales* has modified hysterothecia, progressively dichotomously branched or scattered to gregarious on bark and wood. Hysterothecia sometimes seat upon a conspicuous brown felt-like subiculum presenting as subiculum a dense mat of thick, dark hyphal strands, which anchors the ascoma to the substrate; sometimes lacking subicula, and ascoma borne in a loose stroma, rarely naked on the substrate (Hyde et al. 2013). Pseudoparaphyses are persistent narrow cellular in a gel matrix. Asci are clavate to cylindrical and fissitunicate, and ascospores are hyaline to lightly pigmented to dark brown, with a single conspicuous septum to muriform.

Sexual morph: *Hysterothecia* dark, progressively dichotomously branched or scattered to gregarious, erumpent to superficial, sometimes overlapping, with a prominent longitudinal slit. *Peridium* wide, thick, carbonaceous, and brittle when dry. *Hamathecium* pseudoparaphyses, cellular, septate, persistent, wide, hyaline, branched with darkened apices, in a gel matrix. *Asci* 8-spored, fissitunicate, clavate to cylindrical. *Ascospores* overlapping biseriate, hyaline, lightly pigmented to dark brown, 2-celled to muriform. Asexual morph: psiloglonium stygium-like which is observed in culture (adapted from Boehm et al. 2009b, Jayasiri et al. 2017) (Fig. 35).

Families included in *Gloniales*

Gloniaceae (Corda) E. Boehm, C.L. Schoch & Spatafora

Evolution

The estimated divergence time for *Gloniales* is 109 MYA (stem age) (Hongsanan et al. 2020b).

Justification of order and problems

The justification for the placement of *Gloniales* is based on the morphology and DNA sequence data of *Glonium stellatum*, *G. circumserpens*, *Cenococcum geophilum*, *Purpurepithecium murisporum*, and *P. minus*. Regarding the phylogenetic analysis of combined LSU, SSU, RPB2 and TEF1 sequence data, *Purpurepithecium* grouped in *Gloniales* and formed a distinct sister clade to the *Mytilinidiales* (Jayasiri et al. 2018a). However, Jayasiri et al. (2018a) demonstrated that phylogenetic analysis based on individual RPB2 placed *Purpurepithecium* as a distinct clade from members in *Gloniales*. As a result, further investigation with more fresh collections and sequence data of LSU, SSU, RPB2 and TEF1 is required to clarify this discrepancy.

Significance

Ecological and economic roles

The genus *Cenococcum*, a member of *Gloniales*, which represents an ectomycorrhizal fungus among *Dothideomycetes* in *Ascomycota*, holds ecological significance in the forest ecosystem. *Cenococcum geophilum* exhibits high tolerance to various abiotic stresses, including drought, salinity, heavy metals, and high temperatures (Matsuda et al. 2017, Shi et al. 2022, Li et al. 2023b). This fungus facilitates host plants to absorb nutrients and water, promotes the growth of plants, and enhances resistance against environmental stresses such as drought and salinity (Jany et al. 2003, Wen et al. 2022). For example, Zhang et al. (2024a) demonstrated that *C. geophilum* effectively mitigated Cadmium (Cd) toxicity in *Pinus massoniana* by enhancing the uptake and assimilation of inorganic nitrogen in plants while impeding the translocation of Cd from roots to shoots. Zhang et al. (2024c) showed that the inoculation of *C. geophilum* strains enhanced the drought resistance of *P. massoniana* seedlings during the initial stages of drought stress, by influencing the water content, photosynthesis, accumulation of osmotic adjustment substances, and antioxidant enzyme activities in both shoots and roots of seedlings. With global warming *C. geophilum* could become a significant contributor to the root mycota.

Chemical diversity

Cenococcum geophilum produces extracellular enzymes that can hydrolyze soil substrates to obtain essential nutrients for both itself and its host plant. *Cenococcum geophilum* has been shown to hydrolyze Carbon-14 labeled substrate common in plant litters, including hemicellulose and cellulose (Durall et al. 1994). The ECM fungus *Cenococcum geophilum* has also been demonstrated to produce high levels of laccase, glucoronidase, xylodase and phosphatase enzymes (Courty et al. 2005). It also can produce monoterpenes that are repressed in the presence of plant roots (Ditengou et al. 2015).

Other relevant data and future recommendations

Gloniales includes over 70 species, yet only six of them have available DNA sequence data (Hongsanan et al. 2020b). It is necessary to reexamine the existing type specimens of species described in *Cenococcum*, *Glonium* and *Purpurepithecium* (*Gloniales*) to verify their identity. Fresh collections are required to facilitate epitypification and provide additional insight for taxonomic and molecular phylogenetic studies in *Gloniales*.

The coelomycetous fungus *Cleistonium*, collected from bark of *Eugenia speciosa* in Brazil is characterized by aseptate and hyaline ellipsoidal conidia. It was previously included in *Gloniaceae* by Hyde et al. (2013) and Wijayawardene et al. (2012b, 2014a). However, due to the unavailability of its cultures and sequences, it is currently accepted as an *Ascomycota* genus *incertae sedis* according to Wijayawardene et al. (2017a, 2018, 2022a). Further studies are required to confirm the

classification of this fungus. Additionally, the morphology of *Cenococcum* species is currently described only as mycelia, making taxonomic study further challenging.

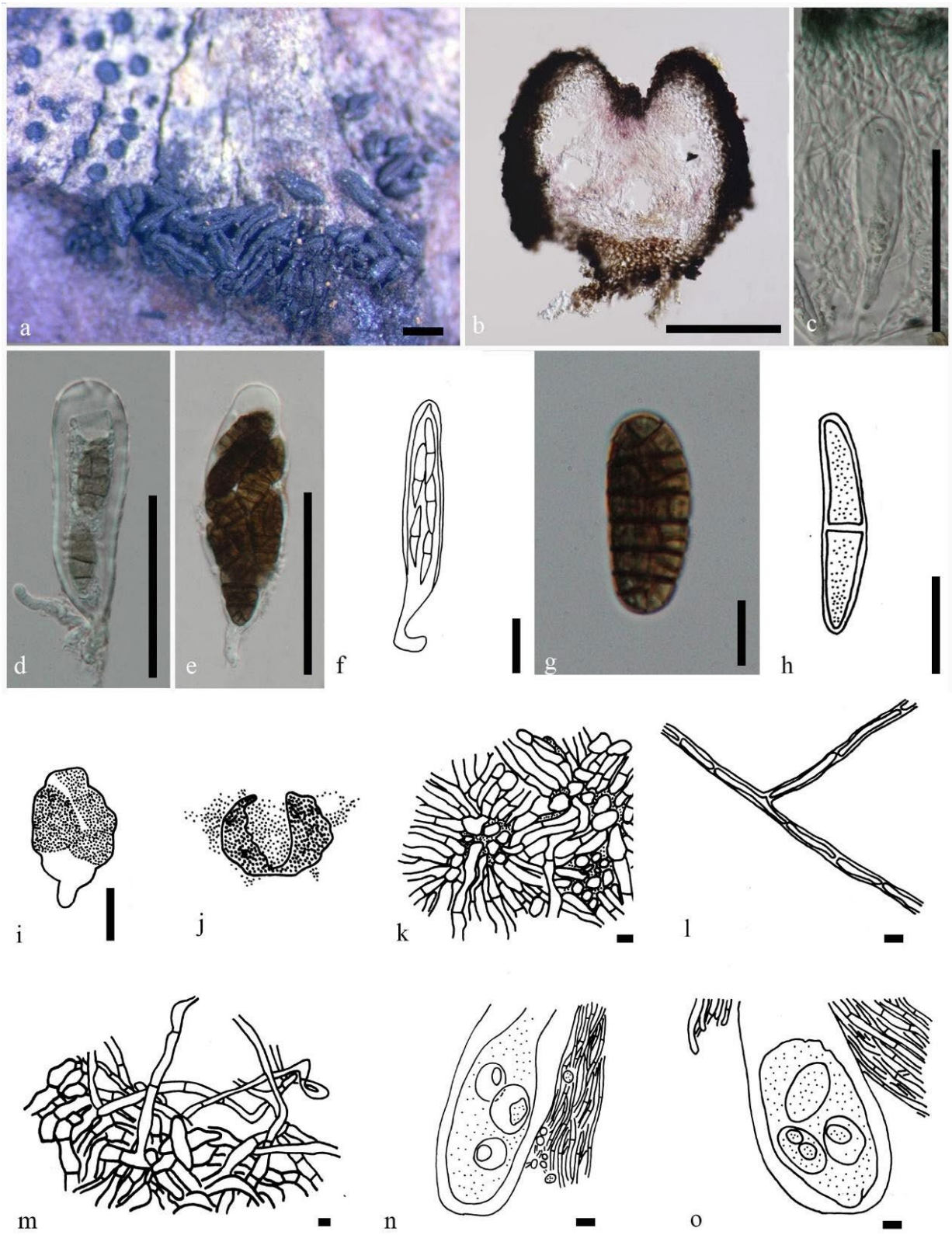


Figure 35 – Morphology of *Gloniales*. a View of hysterothecia on host surface (*Purpurepithecium murisporum*). b Section through hysterothecium (*P. murisporum*). c Ascus and Paraphyses (*P. murisporum*). d, e, f Ascus (d, e, f *P. murisporum*). g, h Ascospores (g *P. murisporum*, h *P. murisporum*). i *P. murisporum*. j General view morphological aspects of the cleistothecium. k Outer layer of the cleistothecium with emanating hyphae. l Ramified hyphae. m Margin of the

cleistothecium with emanating hyphae. n, o Ascus with ascospores (j–o *Cenococcum geophilum* (63X)) (drawn from Hyde et al. 2013, Jayasiri et al. 2019, redrawn from Fernández-Toirán & Águeda 2007). Scale bars: a = 200 μm, b–e = 100 μm, f, i = 20 μm, g, h, k–o = 10 μm.

Holmiellales **Maharachch. & Wanas. Fungal Diversity 106: 240 (2021)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Holmiellales was introduced by Maharachchikumbura et al. (2021b) based on the evidence from phylogeny and morphology to accommodate *Holmiellaceae* which presently includes *Holmiella*. *Holmiellales* represents a distinct lineage within *Dothideomycetes* and is related to *Homortomycetaceae* and *Catinellales* based on phylogenetic analyses of combined SSU, 5.8S, LSU, RPB2 and TEF1-α sequences (Maharachchikumbura et al. 2021b). To date, *Holmiellales* comprises four *Holmiella* species, namely *H. junipericola*, *H. macrospora*, *H. sabina* (the type species), and *H. juniperi-semiglobosae*.

History

The history of the type species of *Holmiella* (*H. sabina*) in *Holmiellales* had been discussed as detailed in Pirozynski & Reid (1966). It was previously identified as *Triblidium sabinum* De Not. [as '*Tryblidium*'] by De Notaris (1867) collected on *Juniperus sabina* in Aosta, Italy. In addition, the species of *Holmiella* have morphological similarities to *Eutryblidiella* (Pirozynski & Reid 1966, Kutorga & Hawksworth 1997). However, it has been demonstrated that *Holmiella* is not phylogenetically related to these taxa (Ekanayaka et al. 2017a). Species of *Holmiellales* were previously placed in the *Patellariaceae*, *Patellariales* (Eriksson & Hawksworth 1993b, Kutorga & Hawksworth 1997, Lumbsch & Huhndorf 2010, Yacharoen et al. 2015, Pem et al. 2018). Based on the evidence from morphology and phylogeny of combined SSU, 5.8S, LSU, RPB2 and TEF1-α sequences, Maharachchikumbura et al. (2021b) proposed that the species of *Holmiella* do not belong to *Patellariales*, thereby refuting earlier suggestions of its placement in *Patellariaceae* (Yacharoen et al. 2015, Pem et al. 2018) and introduced *Holmiella* in *Holmiellales*.

General description

Taxa of *Holmiellales* have apothecial ascomata that are initially enclosed within host parenchyma, subsequently rupturing to ultimately exposure through a wide and irregular hymenium. Ascomata are typically circular or elliptical, although elongated forms are occasionally observed. They begin as completely enclosed structures that later open via an irregular splitting of the upper surface layer into lobes, revealing a black disc within. Once opened, they do not reclose even upon drying. The ascomata are entirely intracortical and lack a stromatic origin. An epithelial layer is formed by the apices of paraphyses that are embedded in a black, amorphous matrix. This substance is brown in 100% lactic acid and green blue in 3% KOH, with the reaction being reversible. The J- paraphyses are red in 3% KOH and subhyaline in 100% lactic acid. However, this reaction is irreversible, and the presence of KOH does not affect paraphyses that have been previously immersed in 100% lactic acid (Kutorga & Hawksworth 1997). Additionally, these structures are not enclosed within a gelatinous sheath. The asci are bitunicate, J- and broadly clavate. Ascospores are opaque, dark brown to black and equally bicellular with a thin, poroid area at each end of each spore. Tissue of the medullary excipulum is hyphal. The corniculariella-like is reported as an asexual morph which is characterized by pycnidial, superficial or immersed conidiomata in cultures, branched, hyaline, septate conidiophores, integrated conidiogenous cells, and straight to curved, hyaline conidia. Chlamydospores are observed as detailed below (Maharachchikumbura et al. 2021b) (Figs. 36, 37).
Sexual morph: *Ascomata* apothecial, solitary or gregarious, immersed to superficial, globose to subglobose, uni- to multi-locular, black. *Exciple* pseudoparenchymatous. *Hamathecium* composed of

filamentous, anastomosing pseudoparaphyses, forming a dark brown epithecium above the asci. *Asci* 8-spored, bitunicate, clavate to cylindro-clavate, short or long-pedicellate, apically rounded with an ocular chamber. *Ascospores* 2–3-seriate overlapping, septate, clavate to ellipsoidal or ovoid, hyaline to brown, with or without a mucoid sheath. Asexual morph: cornicullariella-like. *Conidiomata* pycnidial, superficial or immersed in cultures. *Conidiophores* branched, hyaline, septate. *Conidiogenous cells* integrated, hyaline. *Conidia* straight to curved, unicellular, hyaline. *Chlamydospores* unicellular, globose to subglobose or ellipsoidal, hyaline to pale brown, thick-walled, outer cell wall often ruptures before the new cell is formed, arising directly on terminal hyphae or laterally, often remain attached in terminal hyphae (adapted from Pem et al. 2018, 2024 Maharachchikumbura et al. 2021b).

Families included in *Holmiellales*

Holmiellaceae Maharachch. & Wanas.

Evolution

Holmiellales has a stem age of 97 million years and shares a common ancestor with the *Homortomycetales*, which dates back to 120 MYA (Maharachchikumbura et al. 2021b). While *Patellariales* existed, it underwent evolution between the crown age of 31 MYA and the stem age of 276 MYA (Hongsanan et al. 2020a).

Justification of order and problems

The justification of *Holmiellales* is based on *Holmiella sabina* (G.M. 2015-04-29.3 and G.M. 2015-04-29.2), *H. junipericola* (MFLUCC 18-0503), *H. junipericola* (SQUCC 15186), and *H. juniperi-semiglobosae* (MFLUCC 17-1955). Phylogenetic analyses of combined genes in Maharachchikumbura et al. (2021b) indicated that the order is closely related to the *Homortomycetales*, *Catinellales*, and *Botryosphaeriales*. The apothecial ascomata in *Holmiellales* are clearly distinct from these three orders and unlike most other *Dothideomycetes*. Although the justification of *Holmiellales* is not problematic, further investigations with an expanded taxon sampling will provide additional insights into the classification of *Holmiellales* and it phylogenetically closely related taxa in *Botryosphaeriales*, *Catinellales*, and *Homortomycetales*.

Significance

Ecological and economic roles

Species in *Holmiellales* have been thus far isolated as saprobic on dead trunks and branches of *Juniperus macropoda*, *J. sabina*, *J. semiglobosa*, *J. seravschanica*, and *Calocedrus decurrens* (as *Libocedrus decurrens*) (*Cupressaceae*) in terrestrial habitats. They have been reported in Austria, California, Italy, Oman, and Uzbekistan (Petrini et al. 1979, Kutorga & Hawksworth 1997, Pem et al. 2018). The saprobic taxa could help in decomposition of organic matter in the ecosystem. However, their ecological and economic roles remain unexplored.

Chemical diversity

The chemical diversity of *Holmiella* in *Holmiellales* has yet to be investigated.

Other relevant data and future recommendations

Species of *Holmiellales* are mostly reported as saprobic, and the type species *Holmiella sabina* inhabits as an endophyte or saprobe within needles and wood of *Juniperus* species (Holm & Holm 1977, Kutorga & Hawksworth 1997). Further collection of *Holmiella* from asymptomatic living and dead trunks and branches of *Juniperus* spp. including the other hosts in *Cupressaceae* could provide the understanding of their relationship and species diversity. The ecological and economic roles, as well as the chemical diversity of species in *Holmiellales*, remain unexplored and require further investigation.

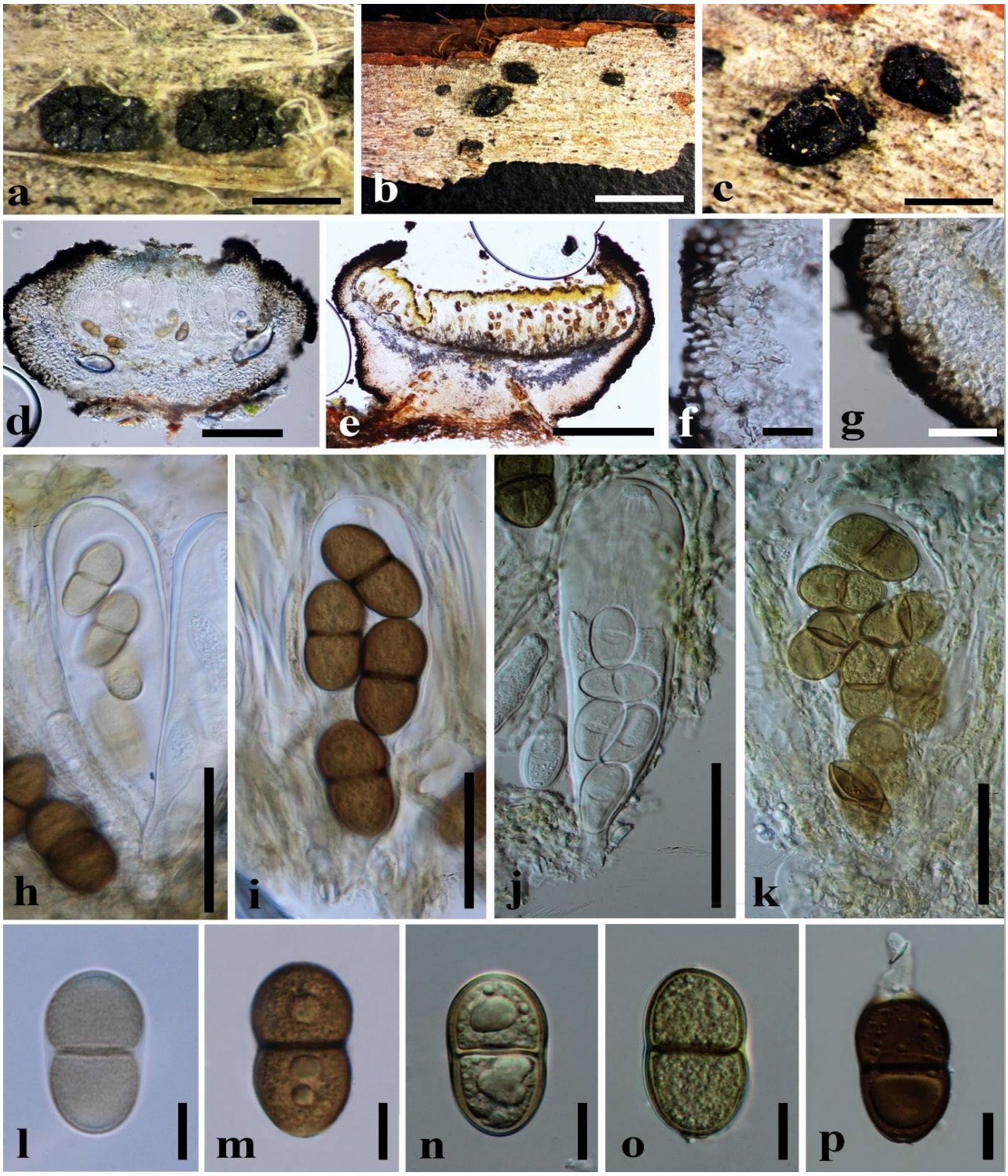


Figure 36 – Sexual morph of taxa in *Holmiellales*. a–c Ascomata on host surface. d, e Section through ascomata. f, g Peridium. h–k Asci. l–o Ascospores. p Ascospore with germ tube (b, c, e, f, h, i, l, m *Holmiella junipericola* (TASM 6136, holotype). a, d, g, j, k, n–p *Holmiella juniperi-semiglobosae* (TASM 6135, holotype)). Scale bars: a = 500 µm, b = 1000 µm, c = 800 µm, d, e = 100 µm, f = 20 µm, g–k = 50 µm, l–p = 10 µm.

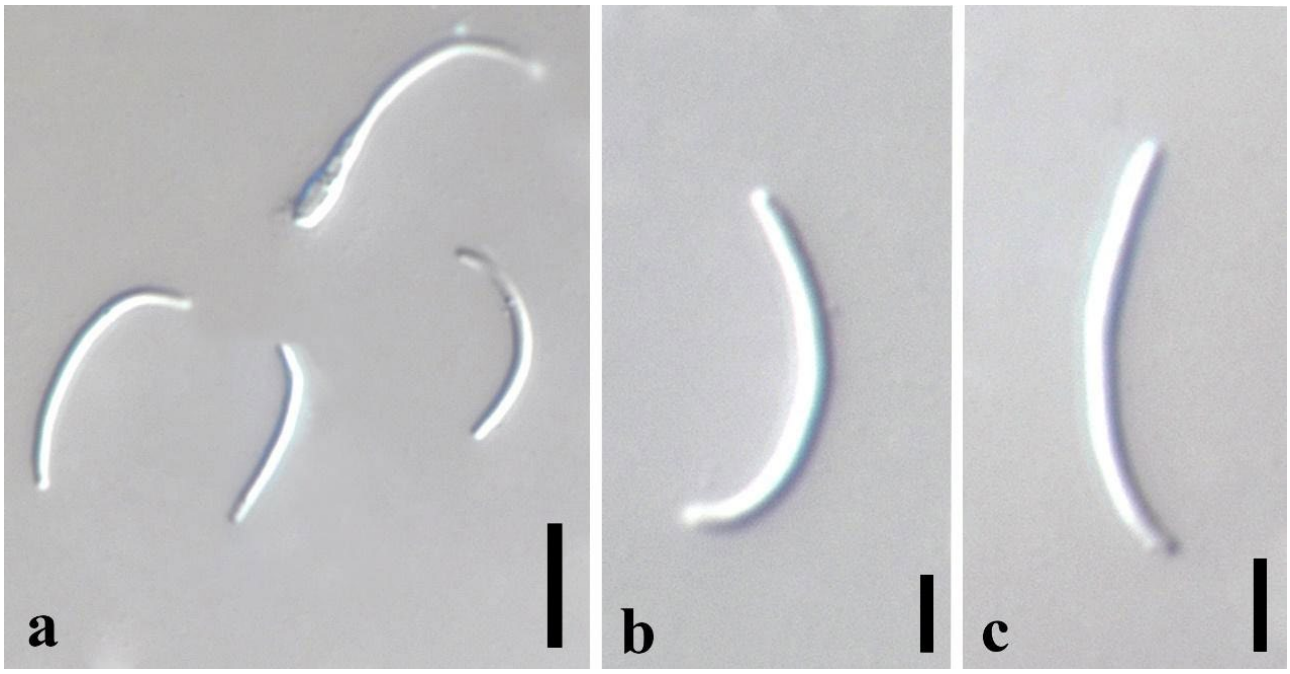


Figure 37 – Asexual morph of taxa in *Holmiellales*. a–c Conidia. Scale bars: a = 10 µm, b, c = 5 µm.

Homortomycetales **Maharachch. & Wanas. Fungal Diversity 106: 241 (2021)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Homortomycetales was introduced by Maharachchikumbura et al. (2021b) based on phylogenetic analyses of SSU, 5.8S, LSU, RPB2 and TEF1-α sequence data. This order comprised a monotypic family (*Homortomycetaceae*) and a genus (*Homortomyces*). The family *Homortomycetaceae* was introduced by Thambugala et al. (2017a) as an *incertae sedis* family in *Dothideomycetes*. *Homortomycetaceae* shares similar features in both sexual and asexual morphs with *Botryosphaeriales* by having stromatic conidiomata with pigmented and thick-walled, diplodia-like conidia, and asci with a thick endotunicate and a well-developed apical chamber but *Botryosphaeriales* can be differed by uniloculate and thin-walled ascomata, 3-septate, pigmented ascospores and distoseptate conidia (Crous et al. 2012a, Phillips et al. 2013b, Thambugala et al. 2017a).

History

Homortomyces was introduced as a new coelomycetous genus by Crous et al. (2012a) in *Dothideomycetes incertae sedis*. In morphology, *Homortomyces* closely resembles *Stilbospora* (*Diaporthales incertae sedis*), but *Stilbospora* can be distinguished by the shape of conidiomata and distinct phylogenetic analysis (Crous et al. 2012a). Wijayawardene et al. (2014b) introduced a second species of *Homortomyces* (*H. tamaricis*) and their phylogenetic analysis showed *Homortomyces* clade grouped with *Tubeufiaceae* but they keep *Homortomyces* in *Dothideomycetes* genera *incertae sedis* pending further studies. According to LSU sequence analysis of Thambugala et al. (2017a), the closest relative to *Homortomycetaceae* is *Botryosphaeriales* but they tentatively referred to *Homortomycetaceae* in *Dothideomycetes incertae sedis*. Later, Maharachchikumbura et al. (2021b) used multigene analysis and resolved the placement of *Homortomycetaceae* and introduced *Homortomycetales* as a new order.

General description

The taxa are saprobic on dead twigs or branches or foliicolous associated with leaf spots in terrestrial habitats.

Sexual morph: *Ascomata* immersed to erumpent, scattered, with ostiolate. *Ostiole* central, apapillate to papillate, filled with hyaline to brown cells. *Peridium* comprising *angularis cells*. *Hamathecium* composed of cellular pseudoparaphyses, septate. *Asci* 2–8-spored, bitunicate, fissitunicate, clavate to cylindrical clavate. *Ascospores* uni- to bi-seriate, fusiform, septate. Asexual morph: Coelomycetous. *Conidiomata* pycnidial, immersed or erumpent, uni- to multi-loculate, ostiolate. *Conidiomatal wall* comprising cells of *textura angularis*. *Hamathecium* hyaline, flexuous, sparingly septate, paraphyses. *Conidiophores* reduced to conidiogenous cells or with one supporting cell. *Conidiogenous cell* hyaline, percurrent, proliferate, with a supporting cell. *Conidia* ellipsoid to subcylindrical, 3(− 4)-euseptate (Figs 38, 39).

Families included in *Homortomycetales*

Homortomycetaceae Thambugala, A.J.L. Phillips & K.D. Hyde



Figure 38 – Sexual morph of *Homortomyces tamaricis* (MFLU 14–0595). a Appearance of ascomata on host surface. b Section through ascoma. c Peridium. d–f Ascospores. g, h Asci. i Pseudoparaphyses. Scale bars: a = 2000 µm, b = 100 µm, c = 50 µm, d g, h = 20 µm, e, f, i = 10 µm.

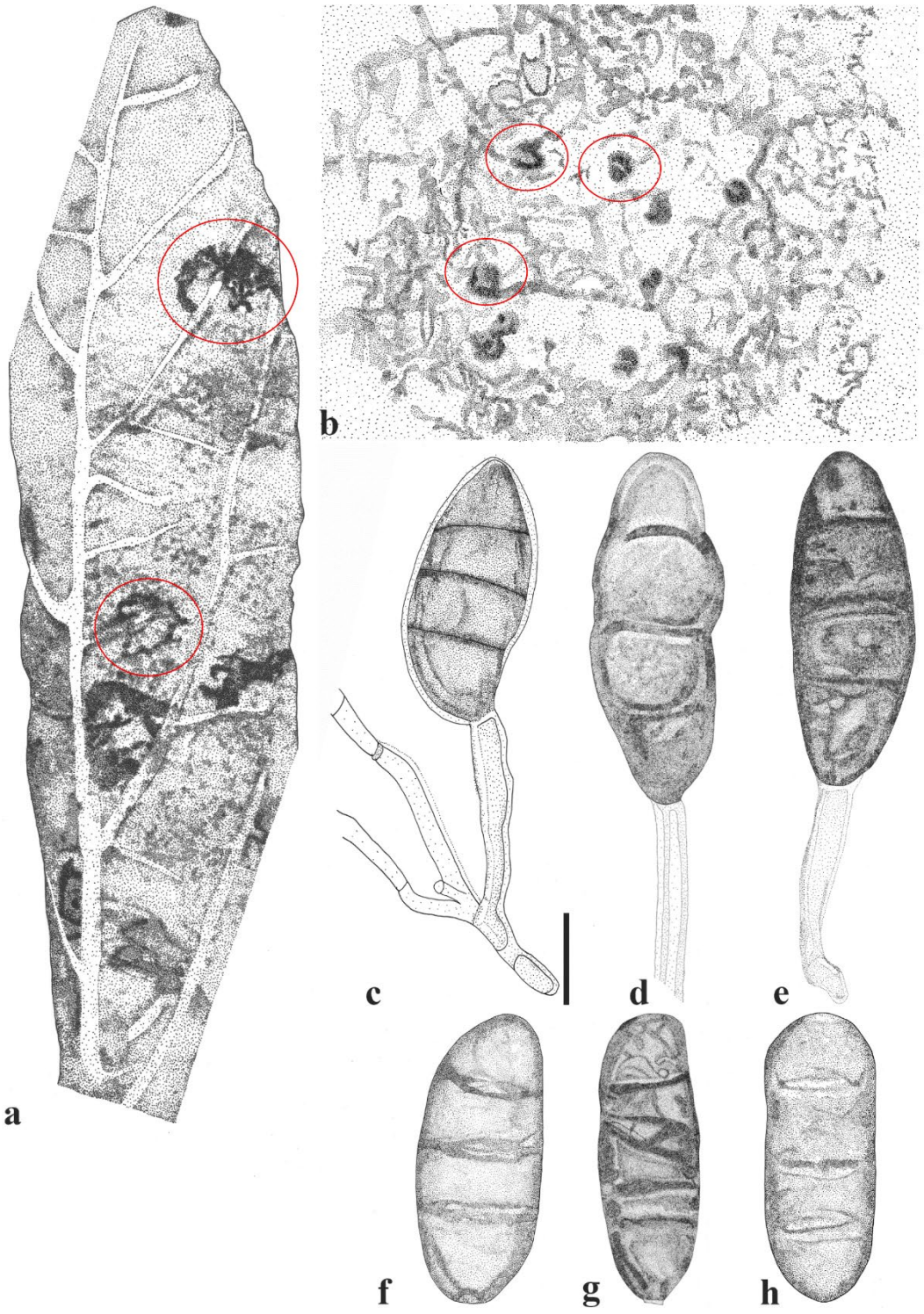


Figure 39 – Asexual morph of *Homortomyces combreti* (CPC 19800). a, b Prominent leaf spots on host plant with black pycnidia (red cycle indicates symptoms on the host). c–e Conidiogenous cells giving rise to conidia. f–h Conidia (redrawn from Crous et al. (2012a). Scale bars: c–h = 10 µm.

Evolution

Maharachchikumbura et al. (2021b) reported the divergence time of *Homortomycetales* as 120 MYA (stem age at 97 MYA).

Justification of order and problems

Based on phylogenetic analyses of combined genes in Hongsanan et al. (2020a) and Maharachchikumbura et al. (2021b), *Botryosphaeriales*, *Catinellales*, *Holmiellales* and

Homortomycetales are closely related. Therefore, Maharachchikumbura et al. (2021b) suggested more collections of fungi within these orders and more molecular data which can be analyzed to obtain a natural classification.

Significance

Ecological and economic roles

The members of *Homortomycetales* can be associated with leaf spots or saprobic in terrestrial habitats (Maharachchikumbura et al. 2021b). The type species of *Homortomyces* (*H. combreti*) has been associated with a destructive leaf and shoot disease of *Combretum erythrophyllum* from South Africa (Crous et al. 2012a). This species, primarily infects young leaves and shoots, and later infections are reported in branches and main stems, which results in obvious stem cankers (Crous et al. 2012a).

Chemical diversity

No relevant studies are available for the chemistry of *Homortomycetales* and need more studies in the future to find chemical compounds in this order.

Other relevant data and future recommendations

Homortomycetales was introduced in 2021 with only two species. Information on their ecological roles, and secondary metabolites are lacking. *Homortomyces combreti* has been reported as pathogen-associated on *Combretum erythrophyllum* but they did not confirm whether is a pathogen or not but they mentioned this species most likely the causal agent of this disease (Crous et al. 2012a). Further studies are needed to confirm its pathogenicity as well as host-specificity.

***Hysteriales* Lindau, Nat. Pflanzenfam. Teil. I (Leipzig) 1(1): 265 (1897)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Pleosporomycetidae*

Introduction

In general, different terminologies are used for this group of fungi based on their ascomatal morphology i.e. “hysteriaceous”, “hysteriform” and “hysterothecioid” ascomycetes (Boehm et al. 2009b, c). Hysteriaceous ascomycetes incorporate those fungi having lirelliform ascomata, generally called hysterothecia (Clements & Shear 1931). They are found worldwide as saprobes and occur on twigs or bark of various woody and herbaceous plants in terrestrial and aquatic environments (Boehm et al. 2009b, c, Hyde et al. 2013, 2016b, Liu et al. 2015a, Li et al. 2016a, Doilom et al. 2017). Some members of *Rhytidhysteron* are weak pathogens and some are rarely found as human pathogens (Thambugala et al. 2016, Soto-Medina & Lücking 2017, De Silva et al. 2020, Wanasinghe et al. 2021, Ren et al. 2022).

Currently, hysteriform ascomycetes are known from four orders, namely *Hysteriales*, *Mytilinidiales*, *Pleosporales*, and *Stigmatodiscales* (Boehm et al. 2009b, c, Voglmayr et al. 2017b). *Hysteriales* and *Mytilinidiales* exclusively only contain hysterothecioid taxa. *Hysteriaceae* is the only family in order *Hysteriales*. Nine genera belong to this family based on morphological and phylogenetic studies *viz*. *Gloniopsis*, *Graphyllium*, *Hysterium*, *Hysterobrevium*, *Hysterodifractum*, *Oedohysterium*, *Ostreichnion*, *Psiloglonium* and *Rhytidhysteron* (Boehm et al. 2009b, c, de Almeida et al. 2014, Jayasiri et al. 2018a). However, five other genera, *Actidiographium*, *Gloniella*, *Hysterocarina*, *Hysteroglonium* and *Hysteropycnis* also belong to *Hysteriaceae* based on morphological similarities (Boehm et al. 2009b). Presently, 13 genera have been accepted under *Hysteriaceae* (Hyde et al. 2024b).

History

There have been numerous studies on hysteriform *Dothideomycetes* and many epithets in this group have been introduced, mostly in the 20th century. During this time various researchers tried to

identify these fungi by ascomatal macroscopic features, and host occurrence (Boehm et al. 2009b, c). Zogg (1962) emphasized the color, number of septa and size of ascospores as the main criteria for separating species and genera. At the ordinal level, *Hysteriaceae* have been classified in *Pseudosphaeriales* (Gäumann 1949), *Dothiorales* (Müller & von Arx 1950), *Dothideales* (Von Arx & Müller 1975), *Pleosporales* (Barr 1987b) or in its own order, *Hysteriales* (Luttrell 1955, Kirk et al. 2001, 2008a). Hysteriaceous fungi producing conchate or dolabrate, thin-walled, laterally compressed ascomata with an evaginated slit, were segregated from *Hysteriaceae* and placed in *Mytilinidiaceae*, under *Melanommatales* (Barr 1990a), because of their trabeculate pseudoparaphyses. This character, which occurs in most hysteriform taxa, was later shown to have evolved in many groups of *Dothideomycetes* (Liew et al. 2000). The family *Mytilinidiaceae* has also been placed in *Pleosporales* (Kirk et al. 2008a) or *Mytilinidiales* (Boehm et al. 2009c, Lumbsch & Huhndorf 2010). Boehm et al. (2009c) were the first to study the group at the molecular level and produce a phylogenetic outline. Phylogenetic studies based on molecular data have shown that hysteriaceous fungi do not form a monophyletic group (Boehm et al. 2009b, c, Mugambi & Huhndorf 2009).

The traditional circumspection of *Hysteriaceae* was based on character states related to hysterothecium and spore morphology (e.g., septation and pigmentation), character states previously considered synapomorphic (Zogg 1962). However, recent molecular data underscore the potential for morphology to be difficult to interpret, and even unhelpful in phylogenetic inference and reconstruction for this group of fungi (Schoch et al. 2006, Boehm et al. 2009c, Mugambi & Huhndorf 2009, Jayasiri et al. 2018a). Thus, several examples of convergent evolution were presented in Boehm et al. (2009b), which related not only to the ascoma, but to spore morphology as well. As a result, three genera were removed from the family (*Glonium*, *Hysterographium* and *Farlowiella*), based on convergence associated with the ascoma. Additionally, within the family, several genera have their members spanning different clades. This necessitated the description of two new genera (*Oedohysterium* and *Hysterobrevium*), as well as three new species, one in *Hysterium* and two in *Gloniopsis*, in addition to several new combinations involving *Psiloglonium*, *Oedohysterium*, *Hysterobrevium* and *Gloniopsis* (Boehm et al. 2009b). These taxonomic changes had de-emphasized both spore septation and spore pigmentation as reliable character states for deducing phylogenetic relationships within the family.

Hysteriaceae include thin-walled mytilinidioid forms previously in the *Mytilinidiaceae* (e.g., *Ostreichnion*), as well as patellarioid forms previously in the *Patellariaceae* (e.g., *Rhytidhysteron*). The inclusion of *Ostreichnion* within *Hysteriaceae* was unexpected. Unlike most members of the family, the peridium in *Ostreichnion* is sclerenchymatoid and thin-walled, defining a fragile mytilinidioid ascoma, and with a hamathecium typified by trabeculate pseudoparaphyses (Barr 1975, 1990a). Including the genus *Ostreichnion* in *Hysteriaceae* implies that, either morphological features within the genus need to be re-evaluated, or that the family *Hysteriaceae* must also encompass mytilinidioid forms. Difficult to understand perhaps is the inclusion of the genus *Rhytidhysteron* within *Hysteriaceae*. Although included within the *Patellariaceae* (Kutorga & Hawksworth 1997), phylogenetic data presented in Boehm et al. (2009b), clearly indicate that this genus lies quite distant from other members of the *Patellariaceae*.

Some authors have included several additional genera within *Hysteriaceae*. For instance, the genera *Hysteropatella*, *Hysteroglonium*, and *Pseudoscypha* were included in *Hysteriaceae* by Eriksson (2006). The genera *Hemigrapha*, *Graphyllium*, and *Encephalographa* were included in the family by Kirk et al. (2001). In Boehm et al. (2009b), two species belonging to *Hysteropatella*, *Hp. clavispora* (CBS 247.34) and *Hp. elliptica* (CBS 935.97), did not cluster with any of the hysteriaceous taxa surveyed. Instead, they formed a distant clade within the *Pleosporomycetidae*, postulated to represent the emergence of the *Patellariales*.

General description

Sexual morph: *Ascomata* hysterothecia, dense, persistent, thick-walled, carbonaceous, distinctly navicular in outline, bearing a pronounced longitudinal slit running the length of the long

axis, immersed to erumpent or entirely superficial, solitary or gregarious, ellipsoid to greatly elongated, sometimes branched, triradiate, or borne on a subiculum. *Peridium* thick, globose to obovoid, three-layered, composed of small pseudoparenchymatous cells, the outer layer heavily encrusted with pigment and often longitudinally striated on the surface, the middle layer lighter in pigmentation and the inner layer distinctly thin-walled, pallid, and compressed. *Hamathecium* comprises persistent cellular, or trabeculate, hypha-like, hyaline, septate, pseudoparaphyses, often borne in a gelatinous matrix, with tips darkened or branched at maturity above the asci. *Asci* 8-spored, bitunicate, fissitunicate, borne in a basal layer, typically clavate to cylindric at maturity, with a distinct ocular chamber. *Ascospores* overlapping 1–2-seriate, obovoid, clavate, ellipsoid or fusoid, hyaline to light- or dark- brown, 1–several-septate, or muriform; often showing bipolar asymmetry, smooth-walled, foveolate or verruculose, at times surrounded by a gel coating; contents granular, often with oil inclusions, especially when young. Asexual morph: Primarily coelomycetes morph present (adapted from Boehm et al. 2009b, Jayasiri et al. 2018a) (Figs. 40, 41, 42, 43).

Families included in *Hysteriales*

Hysteriaceae Chevall.

Hysteriales genera *Incertae sedis*
Graphyllium Clem.

Evolution

The *Hysteriaceae* underwent rapid speciation in response to the angiosperm radiation of the mid- to late-Cretaceous, 65–100 MYA (Boehm et al. 2009b). Although, this must have occurred prior to the complete loss of continental contiguity, which occurred during the same time. The reason for this is remarkable degree of intraspecific stability, in both morphology and sequence data, among geographically disparate accessions (Boehm et al. 2009b). For example, little morphological or sequence variation was detected in *Hysterium angustatum*, from North America (CBS 123334), Kenya (GKM 243A), New Zealand (SMH 5211.0), and South Africa (CMW 20409). Similarly, little variation was detected in *Psiloglonium clavisporum*, from Kenya (GKM L172A, GKM 344A) and North America (e.g., CBS 123338), or in *Oedohysterium sinense*, from South Africa (CBS 123345) and North America (EB 0339). The break-up of Pangea during the Triassic 200 MYA, and the formation of the nascent central Atlantic Ocean, separating Gondwana from Laurasia, during the Jurassic, 150 MYA, must have effectively disrupted once contiguous populations (Boehm et al. 2009b).

Although most flowering plant families were established by the end of the Cretaceous, 65–70 MYA, it is now believed that they diversified into their present lineages (e.g., eudicots, Magnoliids and monocots) much earlier, around 140 MYA (Davies et al. 2004, Moore et al. 2007). This may have allowed for remnants of once contiguous populations to colonise early angiosperm lineages, prior to the complete dissolution of continental integrity during the mid- to late-Cretaceous. Lücking et al. (2009) recalibrated published molecular clock trees, using internally unconstrained, uniform calibration points, and suggested an origin for the fungi between 760 MYA to 1.0 BYA, with the origin of the *Ascomycota* set at 500-650 MYA. Whatever the timing, hysteriaceous fungi incurred little appreciable intraspecific morphological or genetic (e.g., LSU, SSU, TEF1-α and RPB2) change over significant periods of geologic time, on different continents. Thus, except for *Hysterobrevium mori*, and perhaps, *Gloniopsis subrugosa*, most members of the *Hysteriaceae* appear to be stable species**.** Recent studies confirmed that the crown age of *Pleosporales* is 206 MYA, and *Hysteriales* diverged from *Pleosporales* approximately 236 MYA during the Triassic period (Phukhamsakda et al. 2016, Liu et al. 2017b, Hongsanan et al. 2020b, Bhunjun et al. 2021).



Figure 40 – Appearance of hysterothecia of *Hysteriales*. a *Rhytidhysteron* sp. b *Psiloglonium macrosporum*. c *Hysterobrevium rosae*. d *Hysterographium fraxi*.

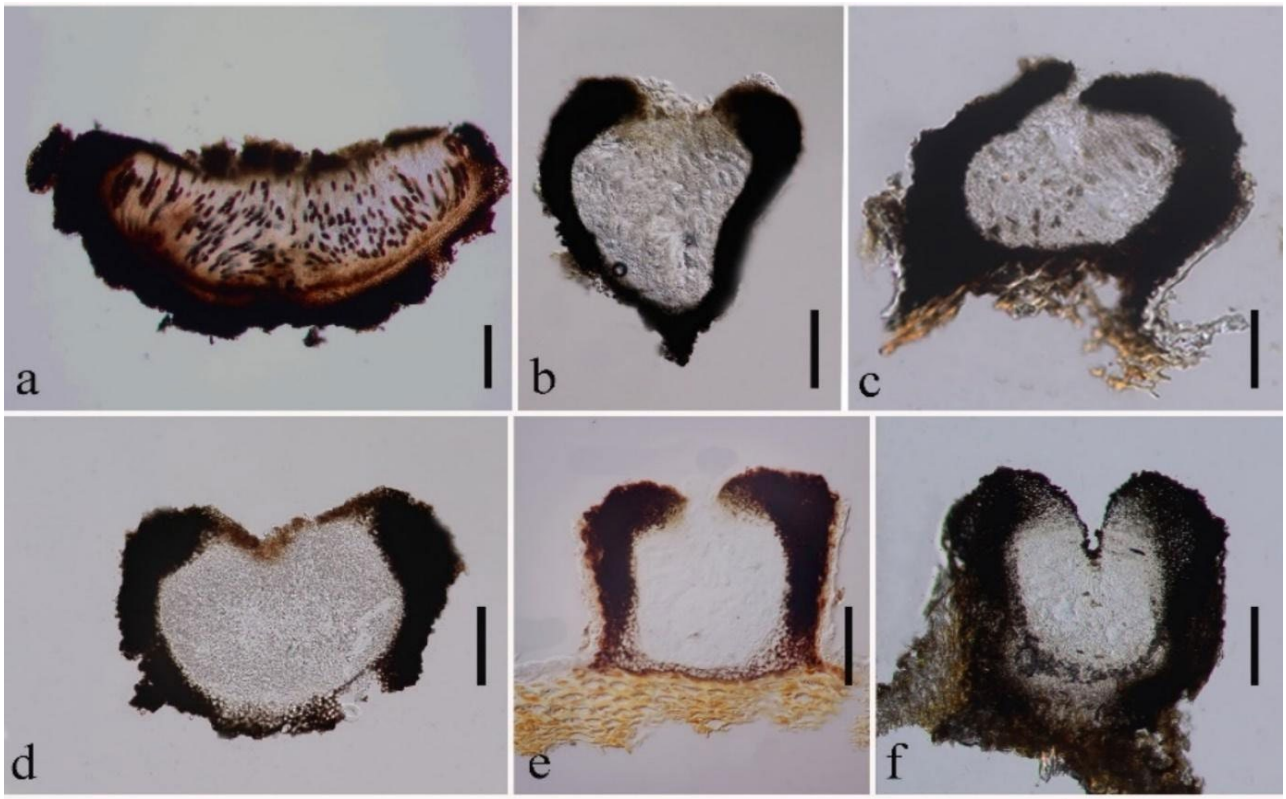


Figure 41 – Morphology of hysterothecium of *Hysteriales*. a *Rhytidhysteron* sp. b *Hysterobrevium hakeae*. c *Hysterium angustatum*. d *Psiloglonium macrosporum*. e *Hysterobrevium rosae*. f *Hysterographium fraxi*. Scale bars: a = 100 µm, b–f = 50 µm.

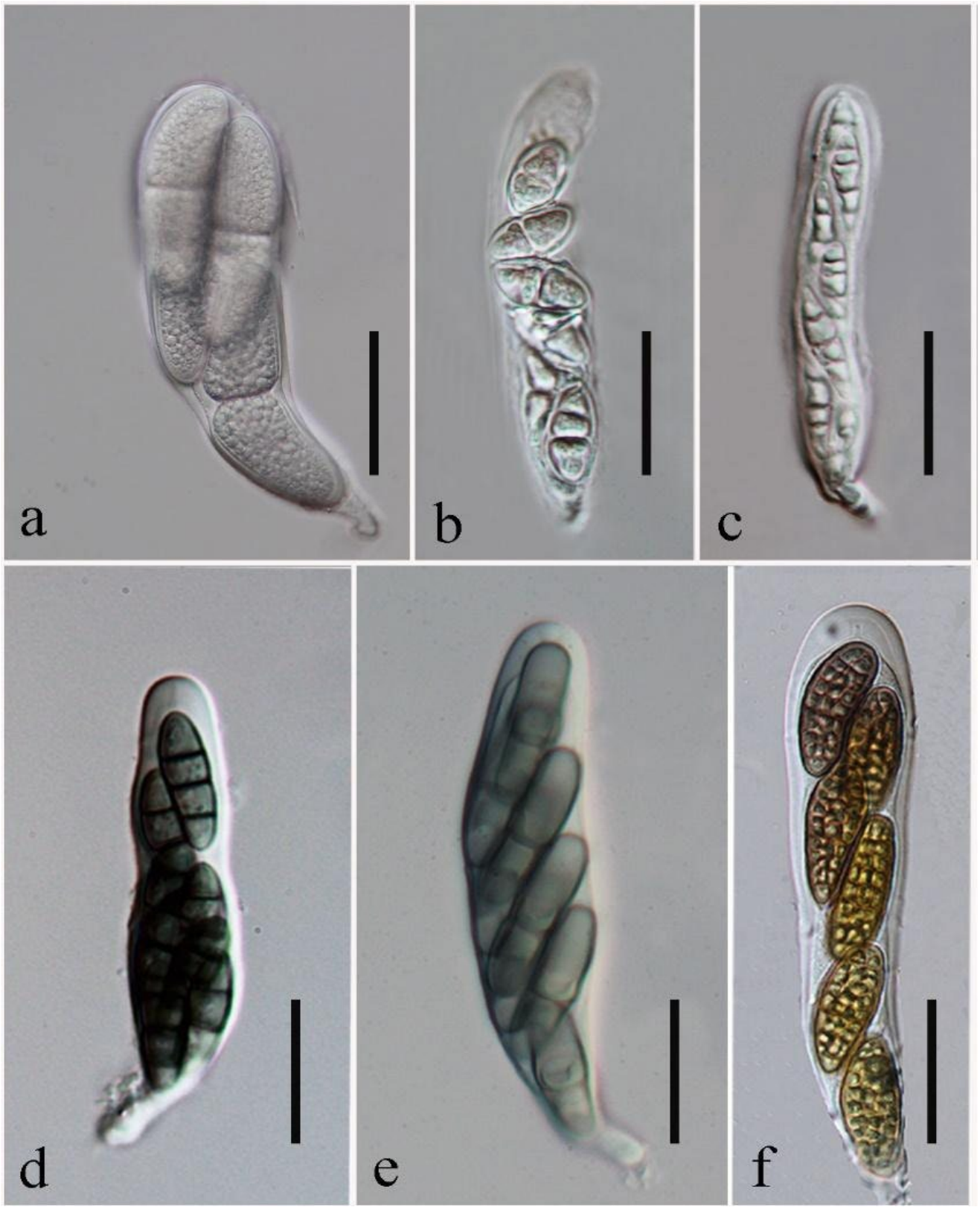


Figure 42 – Asci and ascospores morphology of *Hysteriales*. a *Psiloglonium macrosporum*. b *Hysterobrevium hakeae.* c *Hysterobrevium rosae*. d *Hysterium angustatum*. e *Hysterium doimaeensis*. f *Hysterographium fraxi*. Scale bars: a = 50 µm, b–f = 30 µm.

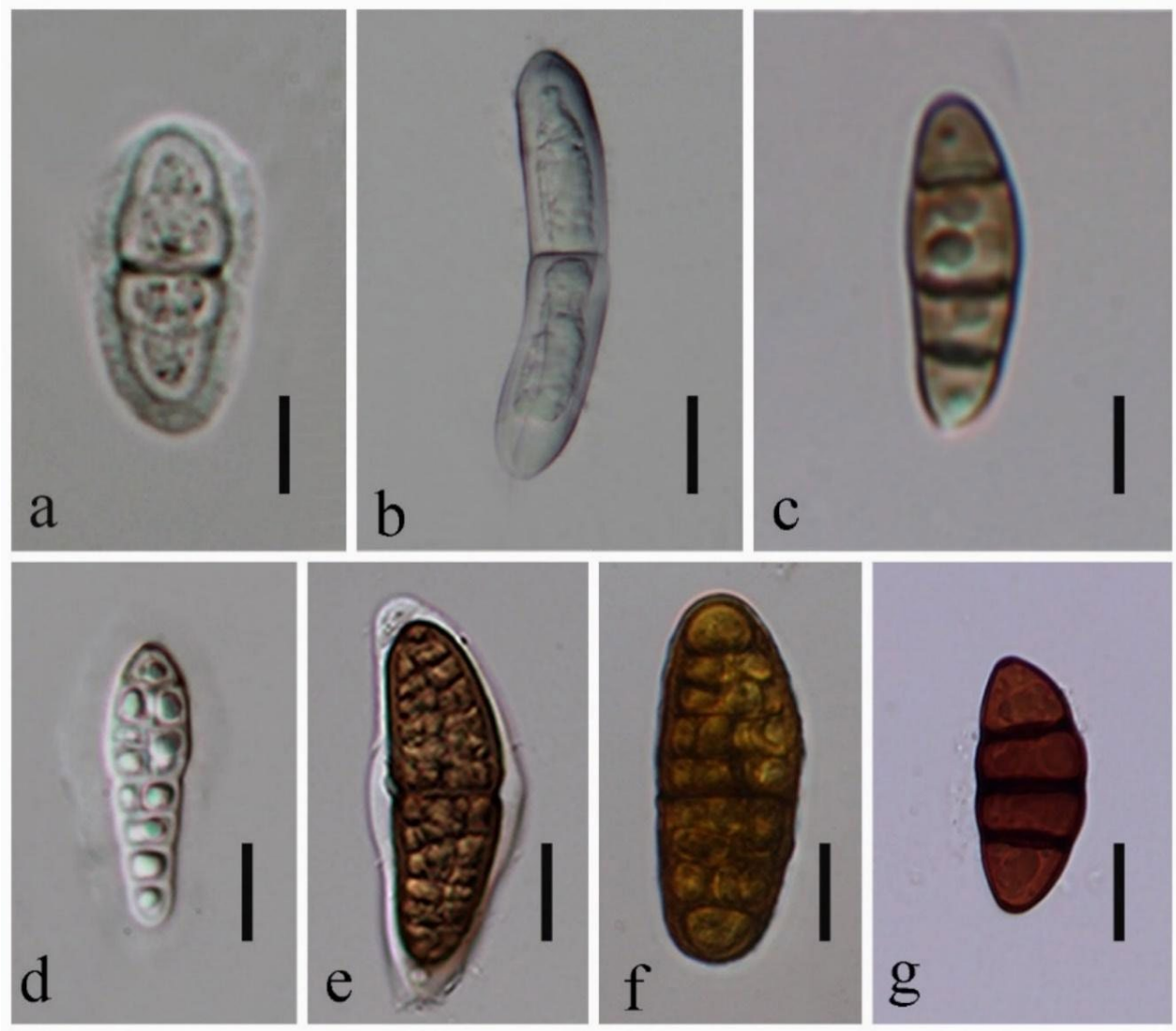


Figure 43 – Ascospores morphology of *Hysteriales*. a *Hysterobrevium hakeae*. b *Hysterium doimaeensis*. c *Hysterium angustatum*. d *Hysterobrevium rosae*. e *Psiloglonium macrosporum*. f *Hysterographium fraxi*. g *Rhytidhysteron* sp. Scale bars: a–g = 10 µm.

Justification of order and problems

Currently, hysteriform ascomycetes are known from four orders of ascomata, namely *Hysteriales*, *Mytilinidiales Pleosporales, and Stigmatodiscales* (Boehm et al. 2009b, c, Voglmayr et al. 2017b). *Hysteriales* and *Mytilinidiales* exclusively only contain hysterothecioid taxa. Phylogenetic placements of some hysterothecioid taxa are doubtful (Boehm et al. 2009b). Morphologically, they show similarities. However, phylogenetically they are significantly not closely related (Schoch et al. 2006, Boehm et al. 2009b). In the evolutionary process some mytilinidiaceous taxa invade hysteriaceous fungi and sit with them (Boehm et al. 2009b). The genus *Ostreichnion* comprised *O. curtisii* (CBS 198.34) and *O. sassafras* (CBS 322.34) introduced by Lohman (1933). *Ostreichnion nova-caesariense* is quite similar to *O. sassafras*, but no molecular data are available for comparison. However, the phylogenetic analysis shown that *O. curtisii* is distinct from the generic type, *O. sassafras*. These three species are morphologically similar, having mytilinidioid ascomata within *Hysteriaceae*, but differ with *O. sassafras* in having ascospores with up to 27 septa, and four spored asci. Therefore, the family *Hysteriaceae* must also encompass some mytilinidioid forms (Boehm et al. 2009c) as observed in the genera *Hysterium* and *Ostreichnion* (Boehm et al. 2009b, Jayasiri et al. 2018a).

Significance

Ecological and economic roles

Hysteriaceous taxa are an ancient and ecologically successful group of organisms, as shown by their wide geographic distribution on a multitude of gymnosperm and angiosperm host species. Whereas the *Mytilinidiaceae* are found almost exclusively on conifers, the *Hysteriaceae* occur primarily on angiosperms (Zogg 1962). Hysteriaceous taxa are distributed worldwide and live on or in various substrates like wood, the surface of bark, rocks (associated with lichens), and in some types of soil (Amano 1983, Checa et al. 2007, Messuti & Lorenzo 1997, 2003, Teng 1933, Vasilyeva 1999a, b, 2000, Zogg 1962). The saprobic fungi play an important role in plant litter decomposition in forest ecosystems through nutrient recycling and humus formation (Swift et al. 1979, Kuehn et al. 1999).

They colonize rotting wood or dead organic matter present in the soil and break down the lignocellulose matrix in the litter that other organisms are unable to assimilate (Kjoller & Struwe 1982, Cooke & Rayner 1984). Mytilinidiaceous taxa, however, are common in temperate regions and found in associated wood, bark, resin, plant parts of gymnosperms (cones, scales, needles, seeds, roots). Only rarely have some genera, like *Ostreichnion* been discovered from parts of angiosperms (Barr 1975, 1990b). Members of *Rhytidhysteron* play are weak pathogens on woody plants, and some are rarely found as human pathogens (Thambugala et al. 2016, Soto-Medina & Lücking 2017, De Silva et al. 2020, Wanasinghe et al. 2021).

Chemical diversity

The chemical diversity of *Hysteriales* needs further studies.

Other relevant data and future recommendations

Study of the pigmentation of hysterothecia in *Rhytidhysteron* and its application may need further studies.

Jahnulales K.L. Pang, Abdel-Wahab, El-Shar., E.B.G. Jones & Sivichai, Mycological Research 106(9): 1033 (2002)

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Jahnulales is a monophyletic order of predominantly freshwater ascomycetes primarily inhabiting rotting or submerged wood and palm fronds (Pang et al. 2002, Dong et al. 2020, Calabon et al. 2022).

History

Building upon the foundational work of Inderbitzin et al. (2001), who described *Aliquandostipite* and *Aliquandostipitaceae*, Pang et al. (2002) established *Jahnulales* as a distinct lineage closely related to *Dothideales*, *Patellariales*, and *Pleosporales*. The order is typified by *Jahnula* with *J. aquatica* (= *Amphisphaeria aquatica*) as the type species (Kirschstein 1936). Initially circumscribed based on *Aliquandostipite*, *Jahnula*, and *Patescospora*, the order was later expanded to include the marine genus *Manglicola* (Suetrong et al. 2009, 2011). Moreover, the discovery of anamorphic states, *Brachiosphaera* and *Xylomyces*, associated with *Jahnulales* taxa (Campbell et al. 2007, Prihatini et al. 2008, Sivichai & Boonyuen 2010) has contributed to a more comprehensive understanding of the order. Phylogenetic studies have consistently supported the division of *Jahnulales* into two major clades, represented by the families *Aliquandostipitaceae* and *Manglicolaceae* (Suetrong et al. 2009). Subsequent research, including morphological and molecular studies, has expanded the taxonomic breadth of *Jahnulales*, leading to the recognition of new genera and families. Dong et al. (2020) provided the most recent overview of freshwater *Jahnulales*,

introducing the genera *Neojahnula* and *Pseudojahnula*. Hongsanan et al. (2020a) provided the updated taxonomic account of two *Jahnulales* families, *Aliquandostipitaceae* and *Manglicolaceae*.

General description

Sexual morph: *Ascomata* solitary, scattered or in groups, immersed to erumpent or superficial, if superficial often attached to substrate by hyphal stalks, with repent or pendant thick brown hyphal strands, immersed in the substrate with a hypostroma, globose to subglobose, obtuse clavate to fusiform, coriaceous to subcarbonaceous, ostiolate, papillate, pedicellate, epapillate, periphysate. *Peridium* variable, 3–7 cell layers thick, inner layers hyaline, outer layers comprising very large, light brown to brown, thin-walled, cells of *textura globulosa* to *textura angularis*. *Hamathecium* numerous, simple, hyaline, septate, cellular pseudoparaphyses or trabeculate pseudoparaphyses. *Asci* 8-spored, bitunicate, fissitunicate, clavate to cylindrical, thick-walled, pedicel absent or very short, with or without an ocular chamber. *Ascospores* uni- to multiseriate, ellipsoid to fusiform, 1-septate, guttulate, with or without various types of appendages and/or sheaths. Asexual morph: Hyphomycetous. *Conidiophores* reduced or un-branched or sparingly branched, hyaline. *Conidiogenous cells* monoblastic, thallic or sympodial or percurrent, monilioid, hyaline or brown. *Conidia* phragmosporous or staurosporous, with globose central cell, with 4-several, radiating septate arms, hyaline or brown, single or branched or unbranched chains (Seifert et al. 2011) or tetraradiate with 4–8 appendages (adapted from Seifert et al. 2011, Suetrong et al. 2011, Hongsanan et al. 2020a) (Fig. 44).

Families included in *Jahnulales*

Aliquandostipitaceae Inderbitzin
Manglicolaceae Suetrong & E.B.G. Jones

Evolution

The evolutionary history of the *Jahnulales* dates back approximately 204 MYA (Hongsanan et al. 2020a). The taxonomic boundaries and composition of the order have undergone refinement since its inception. While *Jahnula* was initially considered monophyletic, subsequent studies revealed its paraphyletic nature within *Aliquandostipitaceae* (Schoch et al. 2006, Campbell et al. 2007, Schoch et al. 2009b, Shearer et al. 2009, Suetrong et al. 2009, 2011, Dong et al. 2020). *Jahnulales* shared the same clade with orders *Acrospermales*, *Dyfrolomycetales*, *Eremomycetales*, *Muyocopronales*, *Stigmatodiscales*, and *Strigulales* (Hyde et al. 2013, Wijayawardene et al. 2022a)

Significance

Ecological and economic roles

Manglicolaceae and *Aliquandostipitaceae* encompass species that are saprobes on woody material, playing a crucial role in the decomposition of dead woody structures, thereby contributing to nutrient recycling within aquatic ecosystems (Suetrong et al. 2011, Dong et al. 2020). *Manglicola* species are only known from mangroves where they occur on wood in brackish water (Hyde & Lee 1998). *Aliquandostipitaceae* species on the other hand occur in freshwater and are more likely to be found in habitats that are not polluted. They have been found in relatively undisturbed streams on wood in Hong Kong (Tsui et al. 2000), Malaysia (Ho et al. 2001), and lakes in Yunnan Province, China (Cai et al. 2002, Luo et al. 2004).

Chemical diversity

Jahnulales has demonstrated broad-spectrum antimicrobial properties. Li et al. (2021b) reported that *Brachiosphaera* sp. inhibits the growth of Gram-positive bacteria (*Staphylococcus aureus*, *Listeria monocytogenes*), Gram-negative bacteria (*Escherichia coli*, *Shigella* sp.), and the pathogenic fungus *Botrytis cinerea*. Similarly, *Neojahnula australiensis* exhibited antimicrobial activity against Gram-positive bacteria (*S. aureus*, *L. monocytogenes*, *Bacillus subtilis*) and Gram-negative bacteria (*Shigella* sp., *Salmonella* sp.).

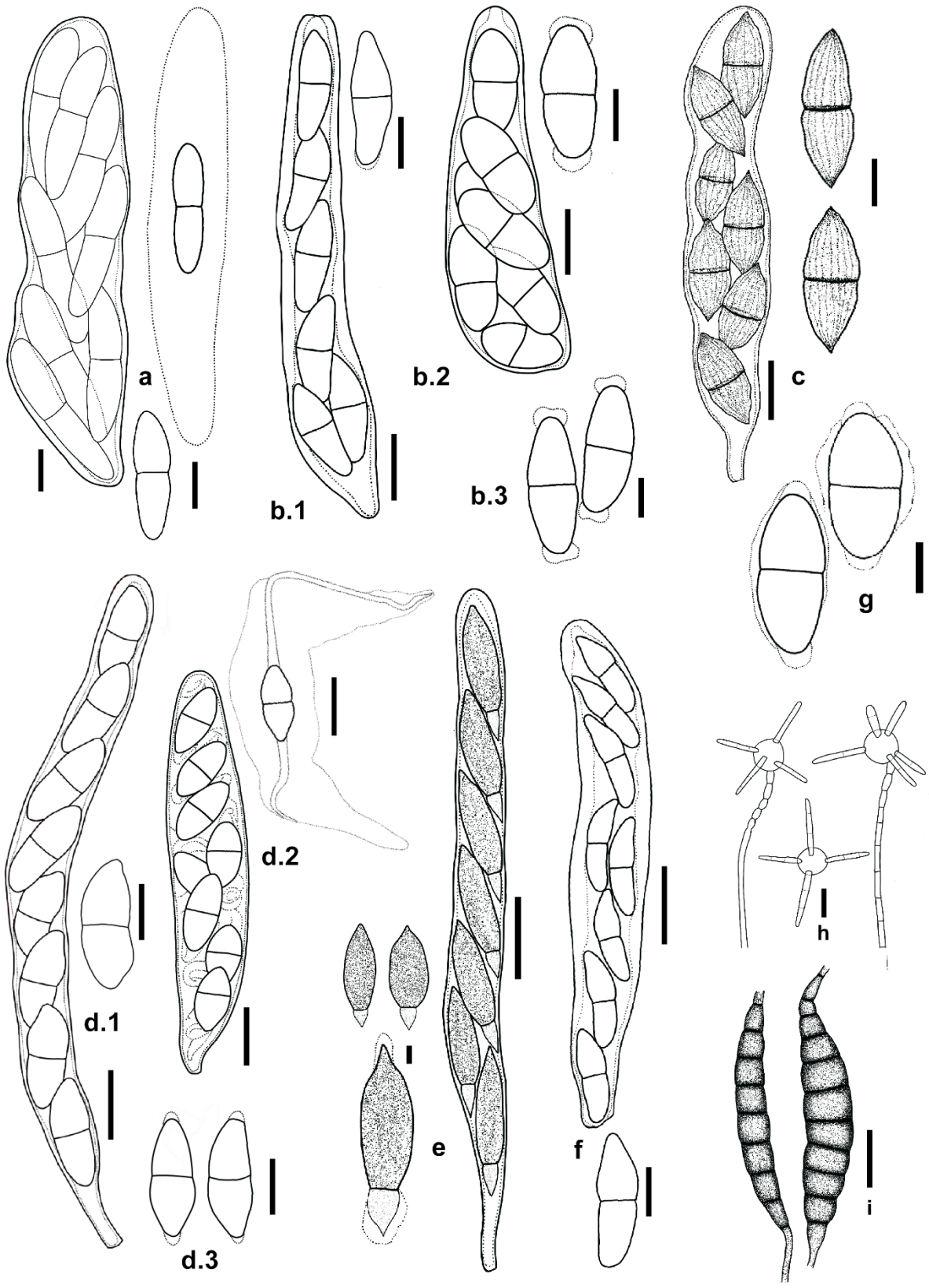


Figure 44 – Sexual (a–g) and asexual (h, i) morphs of *Jahnulales*. a Asci and ascospores of *Aliquandostipite khaoyaiensis*. b Asci and ascospores of *Ascagilis.* b.1 *A. thailandensis*. b.2 *A. submersa*). c *Megalohypha aqua-dulces*. d *Jahnula* d.1 *J. aquatica*. d.2 *J. appendiculata*. e *M. guatemalensis.* f *Neojahnula australiensis.* Ascospores of b.3 *Ascagilis bipolaris*. d.3 *Jahnula bipileata*. g *Pseudojahnula potamophila*. h Mature conidia on conidiophores of *Brachiosphaera tropicalis*. i Chlamydospores of *Xylomyces chlamydosporus*. (drawn from Dong et al. 2020). Scale bars: a–g = 20 µm, h, i = 50 µm.

Xylomyces chlamydosporus has also shown antimicrobial potential. Hosoe et al. (2010) isolated compounds radicinin and 3-epi-radicinin from *X. chlamydosporus* (strain H58-1) that demonstrated antifungal activity against *Fusarium verticillioides*. Wang et al. (2008) demonstrated the antimicrobial potential of *X. chlamydosporus* YMF 1.00956 against a range of pathogenic bacteria, including *Bacillus cereus*, *Brevibacillus laterosporus*, *Escherichia coli*, and *Staphylococcus aureus*.

Kirschsteiniotheliales **Hern.-Restr. R.F. Castañeda, Gené & Crous, Studies in Mycology 86: 72 (2017)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Kirschsteiniotheliales was introduced by Gené et al. (2017) in *Dothideomycetes*. *Kirschsteiniotheliales* comprised of only one family, *Kirschsteiniotheliaceae*, which includes *Kirschsteiniothelia* as type genus and two *incertae sedis* genera *viz*. *Brachysporiella* and *Taeniolella* (Wijayawardene et al. 2022a, Hyde et al. 2024b). Species in *Kirschsteiniotheliaceae* can be found as saprobes from terrestrial and aquatic environments (Boonmee et al. 2012, Hyde et al. 2013, 2023, Su et al. 2016a, Bao et al. 2018, Guegan et al. 2021, Sun et al. 2021a, Silva et al. 2022, Liu et al. 2023a). Two *Kirschsteiniotheliales* species have also been identified as human pathogens from Japan and Morocco (Nishi et al. 2018, Guegan et al. 2021).

History

Kirschsteiniothelia was described by Hawksworth (1985). The phylogenetic placement of this genus was uncertain due to its polyphyletic nature and classified as *Dothideomycetes* genus *incertae sedis* (Lumbsch & Huhndorf 2010). Because of the asexual morph linkage and morphology, Barr (1993a) placed *Kirschsteiniothelia* in *Pleomassariaceae*. Schoch et al. (2006) showed in their phylogenetic tree, that *Kirschsteiniothelia aethiops* did not cluster with *Pleosporaceae*, which supported the removal of *Kirschsteiniothelia* to a new family. After many phylogenetic treatments of this genus, Boonmee et al. (2012) introduced *Kirschsteiniotheliaceae* to accommodate the species of *Kirschsteiniothelia* in *Pleosporales*. Gené et al. (2017) introduced *Kirschsteiniotheliales* to accommodate *Kirschsteiniotheliaceae*.

General description

Dendryphiopsis is an asexual genus, which has been linked to *Kirschsteiniothelia aethiops* (Hughes 1953). Several phylogenetic studies recognized and validated the asexual and sexual morphs (Boonmee et al. 2012, Hyde et al. 2013, Wijayawardene et al. 2014a). The phylogenetic analysis of Boonmee et al. (2012) found that the type species of *Kirschsteiniothelia*, *K. aethiops*, grouped with *Dendryphiopsis atra* which is the type species of *Dendryphiopsis*. Later, Wijayawardene et al. (2014a) proposed *Kirschsteiniothelia* to be used in preference to *Dendryphiopsis* (Figs. 45, 46, 47).
Sexual morph: *Ascomata* superficial, globose to subglobose, unilocular, heavily pigmented. *Asci* bitunicate, fissitunicate. *Ascospores* ellipsoidal, dull green, brown to dark brown, 1–2-septate Asexual morph: *Conidiophores* mononematous, straight to slightly curved, branched, septate, darkened. *Conidia* broadly ellipsoid-obovoid, septate, light to dark brown.

Families included in ***Kirschsteiniotheliales***

Kirschsteiniotheliaceae Boonmee & K.D. Hyde

Kirschsteiniotheliales genera *incertae sedis*
Brachysporiella Bat.
Taeniolella S. Hughes

Evolution

Species of *Kirschsteiniotheliales* inhabit terrestrial and aquatic environments. Understanding the details of their evolutionary history remains limited (Silva et al. 2022). Research should involve studying their phylogenetic relationships, morphological traits, and genetic data. Phylogenetic studies, in particular, have been critical in determining the evolutionary relationships of *Kirschsteiniotheliales*. The estimated divergence time of *Kirschsteiniotheliales* is reported to be around 221 MYA (Hongsanan et al. 2020b). In regards to morphology, *Kirschsteiniotheliales* species share traits with the species of *Dothideomycetes*. Extensive morphological research on *Kirschsteiniotheliales* species can shed light on their evolutionary adaptations and ecological roles (Hyde et al. 2013).

Justification of order and problems

Currently, LSU, SSU and ITS are the common genetic markers which have been used in many studies to construct phylogenetic trees for *Kirschsteiniotheliales* (Boonmee et al. 2012, Bao et al. 2018, Sun et al. 2021a, Silva et al. 2022).

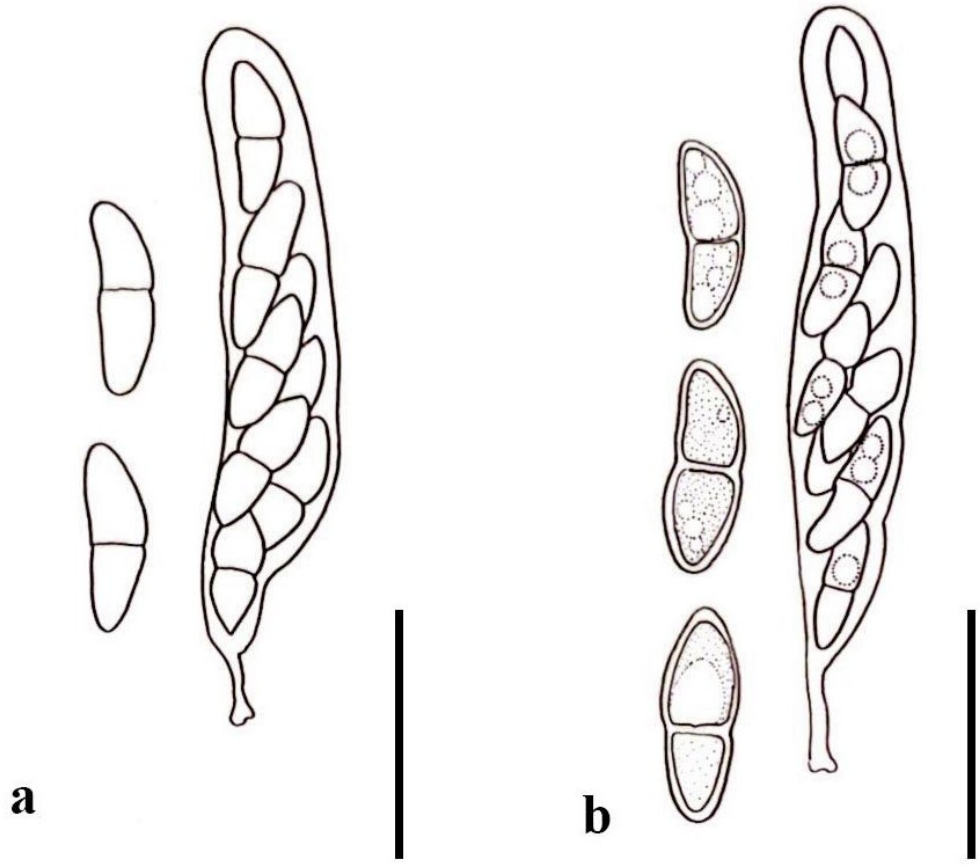


Figure 45 – Asci and ascospores morphology of *Kirchsteiniotheliales.* a *Kirschsteiniothelia emarceis*. b *Kirschsteiniothelia lignicola* (redrawn from Boonmee et al. 2012). Scale bars: a, b = 30 μm.

Significance

Ecological and economic roles

Many *Kirschsteiniothelia* species are found in tropical areas. They are frequently found on decaying wood (Boonmee et al. 2012, Su et al. 2016a). Bao et al. (2018) reported several *Kirschsteiniotheliales* species from both terrestrial and aquatic habitats. According to updated data, the members of this order have been reported from a wide range of habitats, including rotting wood, herbaceous debris, soil, water, and as human pathogens (Guegan et al. 2021). Many

Kirschsteiniotheliales species have been discovered in Asia (Boonmee et al. 2012, Su et al. 2016a, Bao et al. 2018, Nishi et al. 2018, Sun et al. 2021a, Silva et al. 2022) and Europe (Hernández-Restrepo et al. 2017, Rodríguez-Andrade et al. 2019). The first recorded case of *Kirschsteiniothelia* infection presented as ankle bursitis was reported by Nishi et al. (2018). Further phylogenetic research by Guegan et al. (2021) indicated that the taxon that caused chromoblastomycosis belonged to *Kirschsteiniotheliales*. However, due to their infrequent involvement in human infections and the challenges associated with their slow growth *in vitro*, there is limited available data on the susceptibility of *Kirschsteiniotheliales* to antifungal agents.

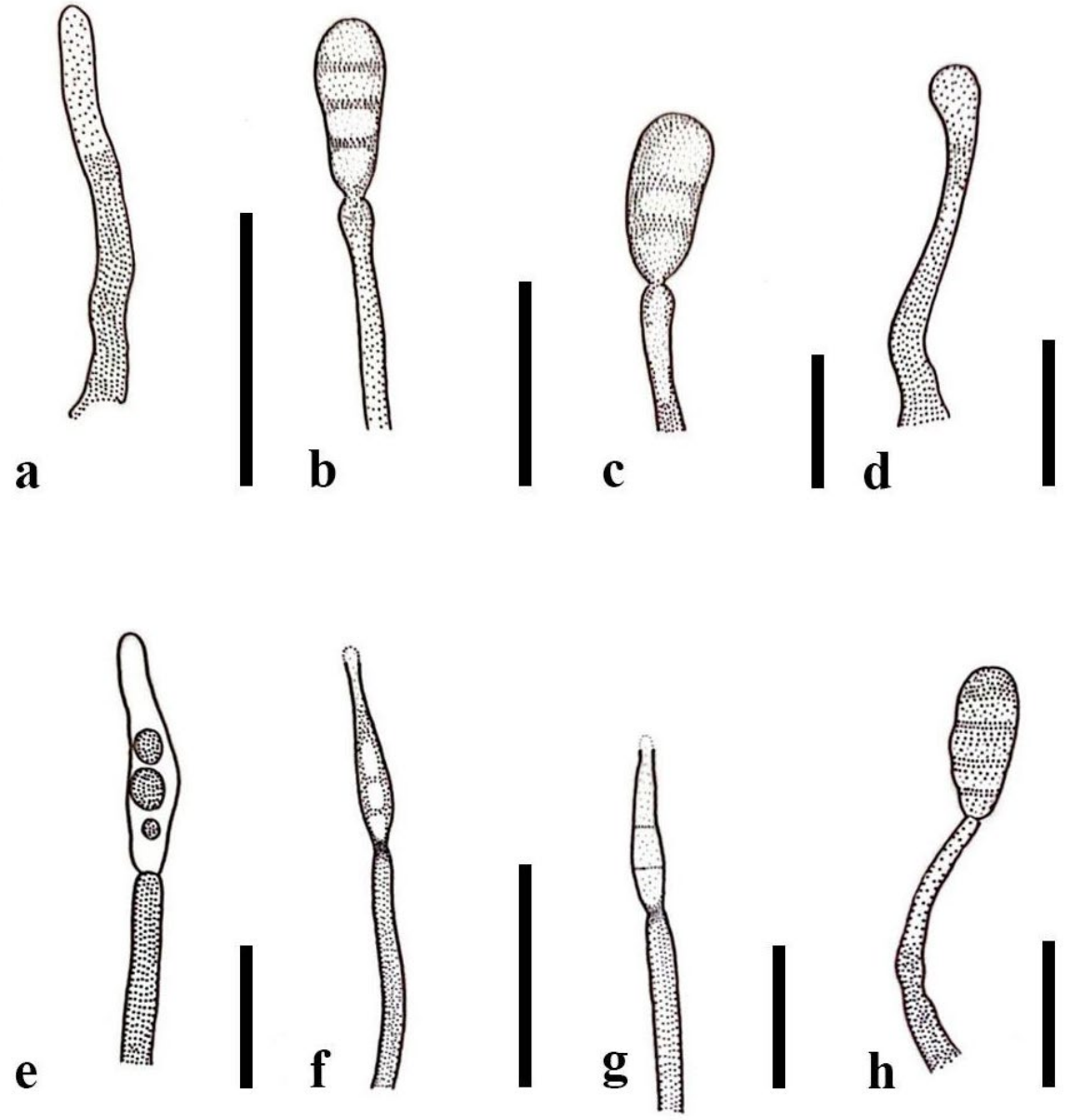


Figure 46 – Conidiophores morphology of *Kirachsteiniotheliales*. a *Kirschsteiniothelia emarceis.* b *Kirschsteiniothelia lignicola.* c *Kirschsteiniothelia lignicola.* d *Kirschsteiniothelia thailandica.* e *Kirschsteiniothelia fluminicola.* f *Kirschsteiniothelia cangshanensis.* g *Kirschsteiniothelia aquatica.* h *Kirschsteiniothelia rostrata* (redrawn from Boonmee et al. 2012, Bao et al. 2018, Silva et al. 2022). Scale bars: a = 100 μm, b = 50 μm, c, d = 20 μm, e, h = 30 μm, f, g = 40 μm.

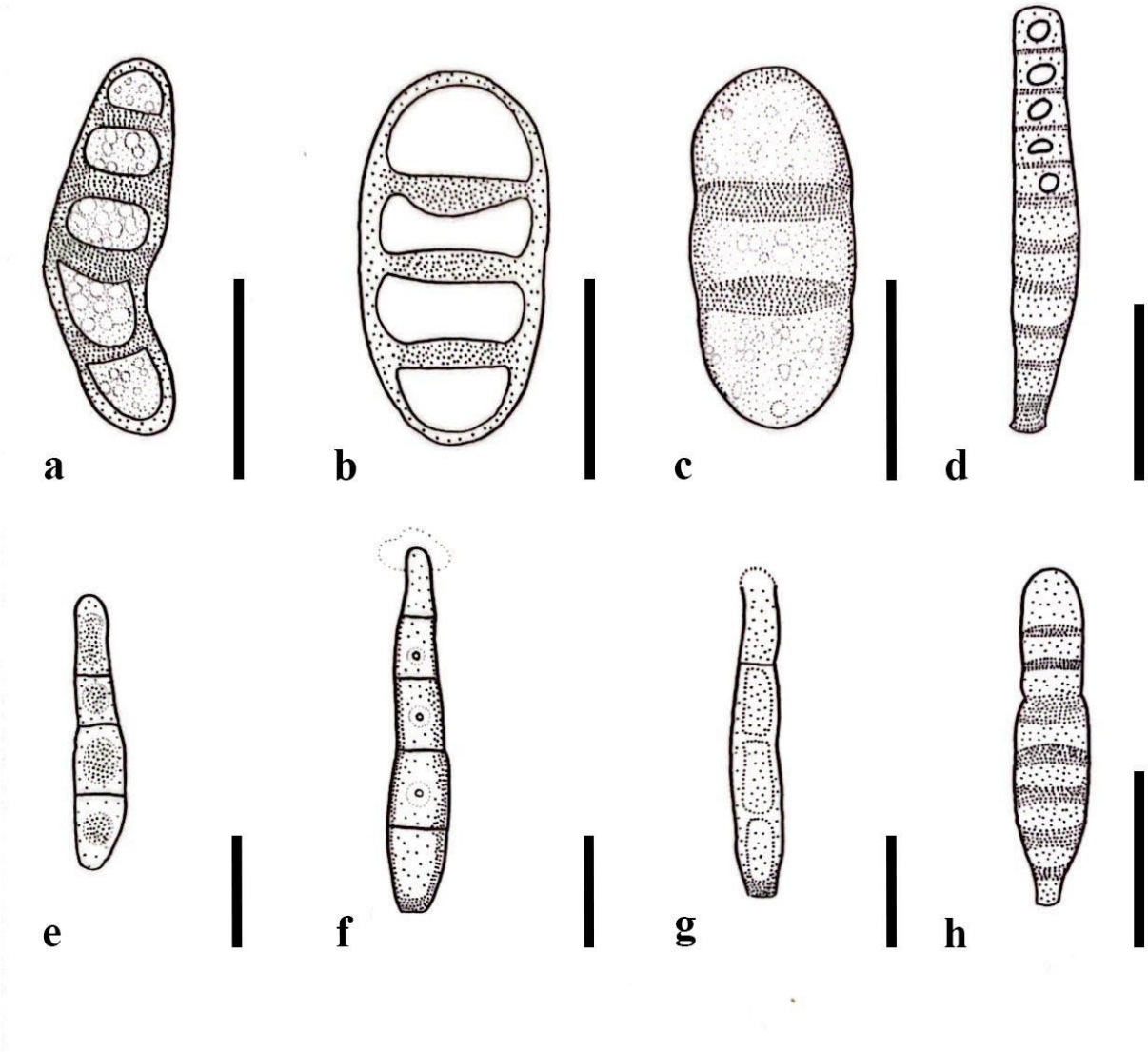


Figure 47 – Conidia morphology of *Kirachsteiniotheliales*. a *Kirschsteiniothelia emarceis.* b, c *Kirschsteiniothelia lignicola.* d *Kirschsteiniothelia thailandica*. e *Kirschsteiniothelia fluminicola.* f *Kirschsteiniothelia cangshanensis.* g *Kirschsteiniothelia aquatica.* h *Kirschsteiniothelia rostrata*. (redrawn from Boonmee et al. 2012, Bao et al. 2018, Silva et al. 2022). Scale bars: a, b, c, d = 20 µm, e, f, g = 10 µm, h = 25 µm.

Chemical diversity

Poch et al. (1992) reported five bioactive compounds from cultures of a *Kirschsteiniothelia* species. Bugni et al. (2004) isolated *Kirschsteiniothelia maritima* from the marine environment and found ascochital, an aldehyde compound which inhibits *Bacillus subtilis* growth. However, only a few investigations on secondary metabolites from this fungal group have been conducted, and the chemical diversity of *Kirschsteiniotheliales* members has yet to be determined.

Other relevant data and future recommendations

Further studies are needed to understand the evolutionary drivers and ecological significance of *Kirschsteiniotheliales*.

***Lineolatales* Crous, Spatafora, Haridas & I.V. Grig. Studies in Mycology 96: 151 (2020)**

Subphylum *: Pezizomycotina*
Class : *Dothideomycetes*

Subclass : *Pleosporomycetidae*

Introduction

Lineolatales is an aquatic group in *Dothideomycetes*, containing only a single genus *Lineolata*, occurring on mangrove substrata and widely reported from different geographical locations (Hyde & Lee 1998, Schmit & Shearer 2003). Haridas et al. (2020) generated a high confidence whole-genome-based phylogenetic tree, which they analyzed by using 101 *Dothideomycetes*. According to their results of reclassification of newly sequenced whole-genome data, the family *Lineolataceae* and *Lineolatales* were established under the subclass *Pleosporomycetidae* with high bootstrap support.

History

Lineolatales was introduced by Haridas et al. (2020) and is typified by family *Lineolataceae* and accommodates a single species *Lineolata rhizophorae*, which was first described with its basionym *Didymosphaeria rhizophorae* in the family *Didymosphaeriaceae*, *Melanommatales* (Kohlmeyer & Kohlmeyer 1967, 1979). Later, Kohlmeyer & Volkmann-Kohlmeyer (1990b) established *Lineolata* to accommodate *Lineolata rhizophorae*, which morphologically differs from species in *Didymosphaeria* by its superficial ascomata with a colored peridium, a hamathecium with gelatinous matrix, asci with apical ring-like structure around the ocular chamber, ornamented ascospores and the absence of a clypeus. However, *Lineolata* was placed in the family *Didymosphaeriaceae* of *incertae sedis*. Jones et al. (2009) assigned *Lineolata* to the family *incertae sedis* in *Pleosporales* based on phylogenetic analysis. Suetrong et al. (2009) sequenced three strains of *Lineolata rhizophorae* obtained from different geographic locations, and indicated *Lineolata* phylogenetically belongs among the group of *Dothideomycetes* of *incertae sedis*. A recent sequence of whole-genomes of *Lineolata rhizophorae* was done by Haridas et al. (2020), the order *Lineolatales* was established to accommodate the single family *Lineolataceae* and typified by the genus *Lineolata* based on the molecular evidence.

General description

Lineolataceae contains only one genus *Lineolata*, characterized by its obpyriform, immersed to superficial ascomata, 8-spored, cylindrical, short pedunculate, non-amyloid, with multi-layered refractive ring, fissitunicate asci and uniseriate, 1-septate, ellipsoidal, brown with surface sculpturing ascospores (Kohlmeyer & Kohlmeyer 1967,1979, Kohlmeyer & Volkmann-Kohlmeyer 1990b, Haridas et al. 2020). To compare with other marine didymosphaeria-like species, species in *Lineolataceae* are observed as ascomata superficial or only partly immersed on the substrate, with ascospores ornamented and striate (Kohlmeyer & Volkmann-Kohlmeyer 1990b). Asexual morphs of species in the order *Lineolatales* are undetermined (Fig. 48).

Sexual morph: *Ascomata* obpyriform, immersed to superficial, ostiolate, papillate, subcarbonaceous to subcoriaceous, periphysate, and dark brown to black, pseudoparaphyses trabeculate, in a gelatinous matrix. *Peridium* thick, bitunicate, an outer layer pseudostromatic, with irregular brown cells, almost hyphoid near the substrate, a thin inner layer, with hyaline, compressed cells forming an angular texture. *Pseudoparaphyses* trabeculate, embedded in a gelatinous matrix. *Asci* 8-spored, cylindrical, short pedunculate, non-amyloid, with multi-layered refractive ring, fissitunicate. *Ascospores* uniseriate, 1-septate, ellipsoidal, brown with surface sculpturing (adapted from Kohlmeyer & Volkmann-Kohlmeyer 1990b). Asexual morph: Undetermined.

Families included in *Lineolatales*

Lineolataceae Crous, Spatafora, Haridas & I.V. Grig.

Evolution

Haridas et al. (2020) revealed that, within *Dothideomycetes*, two gene clusters are predominantly associated with pathogens (pathogen-related genes, PRG), while four others are primarily found in presumed saprobes (saprobe-related genes, SRG). Despite being a marine saprobe, *Lineolata rhizophorae* lacks all six of these gene clusters in its genome. This absence might suggest

unique evolutionary adaptations specific to its marine environment. There has been no comprehensive evolutionary study on the divergence within the *Lineolataceae* or the *Lineolatales*, pointing to a significant gap in our understanding of their evolutionary history.

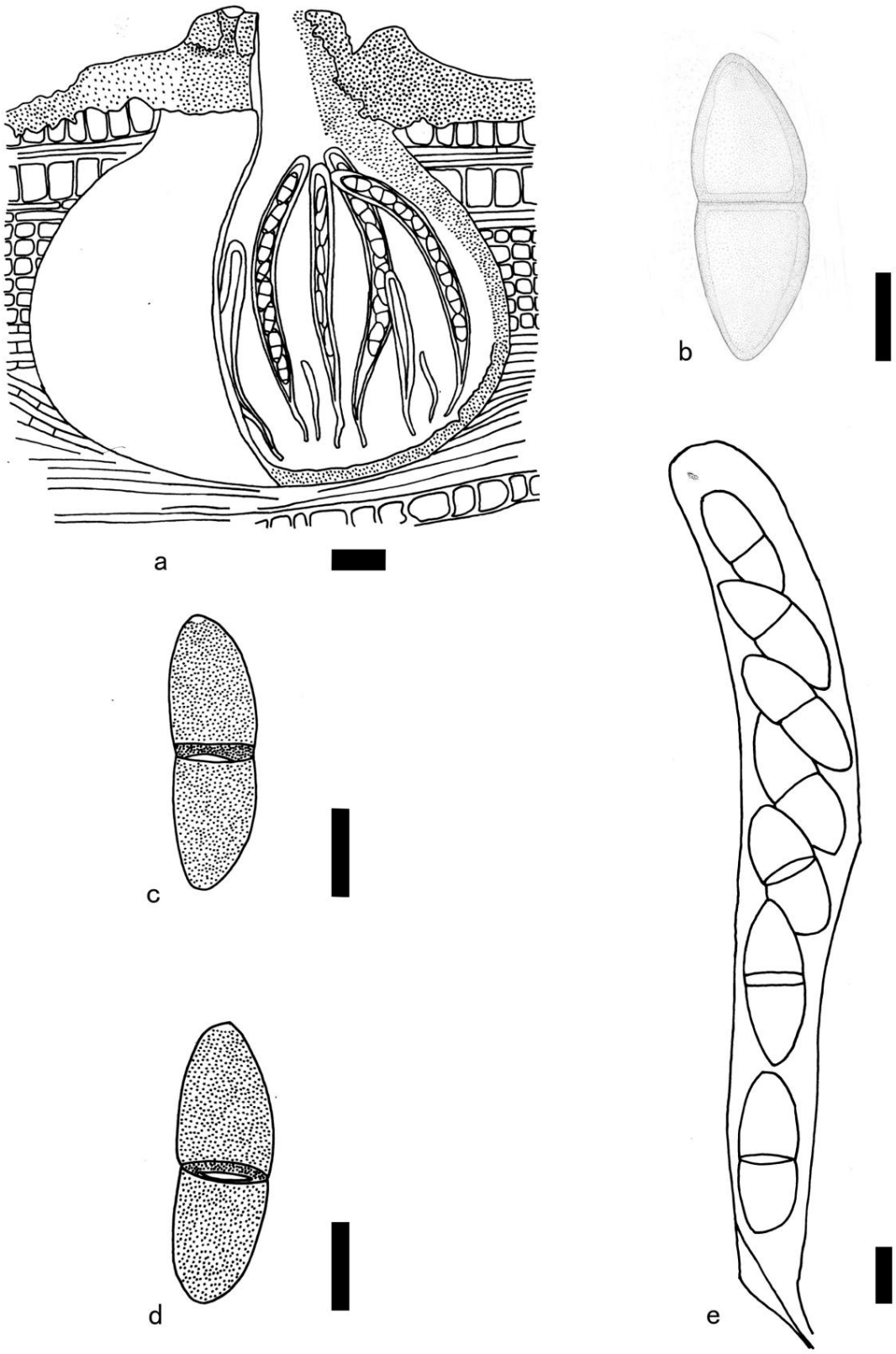


Figure 48 – Morphology of *Lineolatales* (*Lineolata rhizophorae*). a Ascomata immersed on host. b–d Ascospores. e Ascus (redrawn from Kohlmeyer & Kohlmeyer 1967). Scale bars: a = 20 µm, b–e = 10 µm.

Justification of order and problems

The order *Lineolatales* contains only a single family *Lineolataceae,* accommodating one genus with a single species and supported by molecular phylogeny along with morphological evidence.

Significance

Ecological and economic roles

Lineolata rhizophorae was reported as a marine saprobe on driftwood, it may degrade lignocellulosic masses in marine environments.

Chemical diversity

The structure of an alkali-extracted water-soluble polysaccharide has been isolated from the cell wall of *Lineolata rhizophorae* (Giménez-Abián et al. 2007).

***Lembosinales* Crous, Fungal Systematics and Evolution 5: 91 (2019) [2020]**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

The order *Lembosinales* belongs to *Dothideomycetes*, which accommodates only a single genus, *Lembosina*. Species in this order are common and widespread, and many species have been described based on the identity of the host plant (Müller & von Arx 1962, Reed & Farr 1993, Mibey & Hawksworth 1997, Sivanesan & Shivas 2002). Crous et al. (2019b) provided the first molecular data for *Lembosina* and found that it formed a distinct lineage next to *Lichenoconiales*. Thus, they introduced *Lembosinales* and *Lembosinaceae* to accommodate this lineage.

History

Lembosinales was established by Crous et al. (2019b) and is typified by the family *Lembosinaceae*. *Lembosina* was placed in *Leptopeltidaceae* and *Asterinaceae* by von Arx & Müller (1975) and Hawksworth et al. (1995), respectively. Hyde et al. (2013) placed this genus in *Aulographaceae*. However, Crous et al. (2019b) indicated that *Lembosina* based on *L. aulographoides*, does not cluster with any known family or order based on their LSU single gene phylogenetic analysis, and therefore placed it in its own family and order.

General description

Lembosinaceae contains only one genus *Lembosina*, which morphologically characterized by its ascomata thyriothecial or hysterothecial, linear, rarely y-shaped, solitary, gregarious, superficial, loose on host surface, black, opening with linear fissures. Upper wall comprising a thin layer of mostly neatly arranged dark cells, which are branched at the outer rim, base is poorly developed. Asci are 8-spored, bitunicate, subglobose to oblong with ascospores are 2–4-seriate, 1-septate, hyaline, becoming brown with age, with basal protrusion (Crous et al. 2019b). Asexual morphs of species in the order *Lembosinales* are undetermined (Fig. 49).

Sexual morph: *Ascomata* thyriothecial or hysterothecial, linear, rarely y-shaped, solitary, gregarious, superficial, loose on host surface, black, opening with linear fissures. *Upper wall* comprises a thin layer of mostly neatly arranged dark cells, which are branched at the outer rim, base poorly developed. *Hamathecium* comprises, sparse, filiform pseudoparaphyses. *Asci* 8-spored, bitunicate, subglobose to oblong. *Ascospores* overlapping 2–4-seriate, 1-septate, with an upper cell slightly wider and shorter than the lower cell, hyaline, becoming brown with age, with basal protrusion (adapted from Crous et al. 2019b). Asexual morph: undetermined.

Families included in *Lembosinales*

Lembosinaceae Crous, Spatafora, Haridas & I.V. Grig.

Evolution

The recent evolutionary study on *Lembosinales* was reported by Hongsanan et al. (2020a), with the divergence time of *Lembosinales* estimated as 253 MYA.

Justification of order and problems

The order *Lembosinales* contains only a single family *Lembosinaceae,* accommodating one genus. The order *Lembosinales* is interesting in the class *Dothideomycetes* as it is a single-family group, and phylogenetically distinct from other orders in this class. The classification and exploration of species in *Lembosinales* are expected in future studies.

Significance

Ecological and economic roles

Lembosinales species are considered host-specific on plants in tropical and sub-tropical regions (Müller & von Arx 1962, Sivanesan & Shivas 2002). *Lembosina* species are reported to cause black leaf spots on indigenous plants from Kenya (Mibey & Hawksworth 1997).

Chemical diversity

The chemical diversity of species in *Lembosinales* has not been reported.

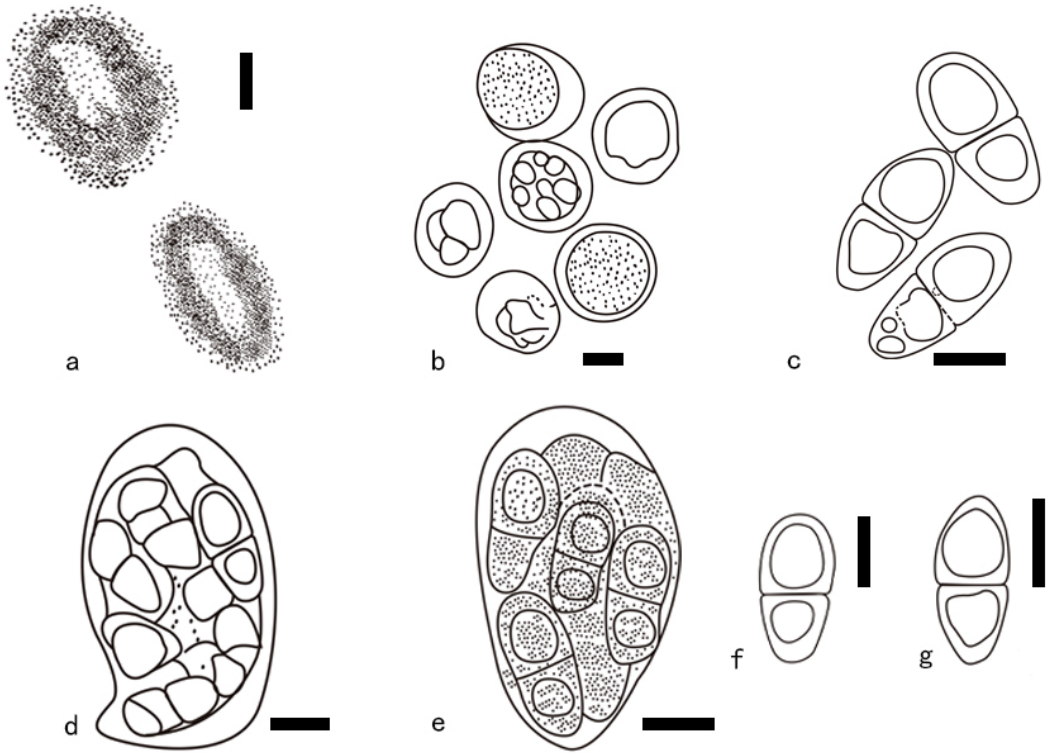


Figure 49 – Morphology of *Lembosinales* (*Lembosina aulographoides*). a Hysterothecioid ascomata on host surface. b Asci viewed from above. c, f, g Ascospores. d Young asci. e Asci when mature (redrawn from Hongsanan et al. 2020a). Scale bars: a = 100 µm, b–f = 10 µm.

Lichenotheliales **K. Knudsen, Muggia & K.D. Hyde, Fungal Diversity 63: 8 (2013)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Lichenotheliales was erected by Hyde et al. (2013) to accommodate a single family *Lichenotheliaceae* in *Dothideomycetes*. *Lichenotheliaceae* was introduced to accommodate *Lichenothelia* and *Lichenostigma* (Eriksson & Hawksworth 1986b, c). Henssen (1987) provided a detailed study of the *Lichenothelia* and accepted 20 species, including 18 new species.

History

Lichenothelia was established to accommodate two rock inhabiting taxa that were originally placed in *Microthelia* (Hawksworth 1981). The genus was placed in *Dothideales* and showed similar ascus morphology to *Lecanorales*. Ertz et al. (2014) established a new order *Lichenostigmales,* based on the sequencing of the type species *Lichenostigma maureri* along with morphology. *Lichenothelia* mainly differs from *Lichenostigma* by division through the formation of septa, whereas in *Lichenostigma,* these cells are spherical and multiply by "budding" (Ertz et al. 2014). Presently, the order accommodates a single genus, *Lichenothelia*.

General description

Sexual morph: *Thallus* endolithic or epilithic when saxicolous, episubstratic or endokapylic when lichenicolous, black, dispersed or continuous, areolate or not, rarely effigurate or frequently producing black superficial hyphae, branching or not, sometimes connecting scattered stromata; meristematic growth frequent. *Ascomata* perithecial and with interascal filaments or fertile stromata without an ostiole and with asci forming in pseudoparenchymatous locules. *Asci* globose to broadly clavate, bitunicate, sometimes K/I + bluish around the outer layers or apex of the ascus. Interascal gel amyloid or not. *Ascospores* hyaline or brown, 8 per ascus (but often few mature), 1-septate to muriform. Asexual morph: *Macroconidia* black, originating from the surface of superficial hyphae, varying in shape and number of cells. *Pycnidia* immersed in vegetative stromata, conidia hyaline, simple, rod-shaped or unknown (adapted from Hyde et al. 2013) (Fig. 50).

Families included in *Lichenotheliales*

Lichenotheliaceae Henssen

Evolution

The taxa are adapted for various extreme environments such as exposed rocks, or saltpans or acidic sites and deserts (Selbmann et al. 2015). The fungi that grow on exposed rocks develop stress tolerance through their high melanin content and thick cell walls to withstand harsh climate changes. In deserts, these rock inhabiting fungi might face low availability of energy-rich carbon sources. Thus, they might gain these from neighbouring algae and cyanobacteria (Selbmann et al. 2015). Hongsanan et al. (2020a) reported the divergence time for *Lichenotheliales* as 265 MYA.

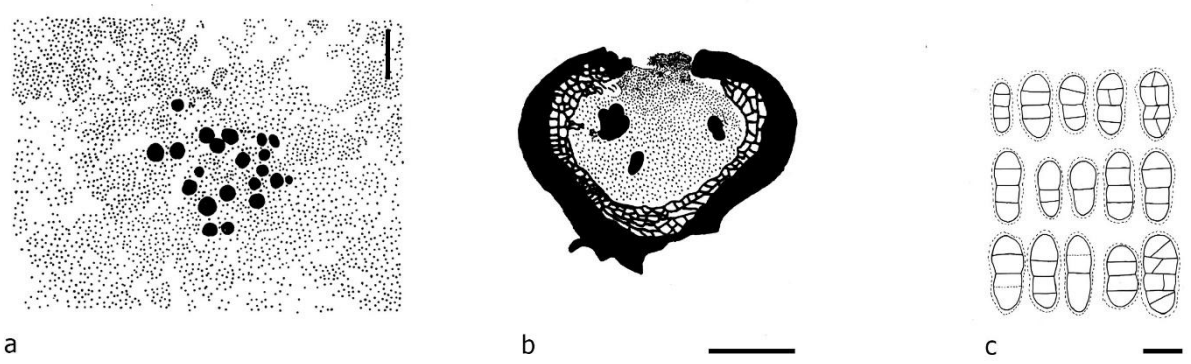


Figure 50 – Morphology of *Lichenotheliales*. a Fertile stromata of *Lichenothelia arida* (redrawn from Muggia et al. 2015). b section through ascoma of *Lichenothelia ilamensis* (redrawn from

Hawksworth 1981). c Ascospores of *Lichenothelia scopularia* (redrawn from Hawksworth 1981). Scale bars: a = 500 µm, b = 30 µm, c = 10 µm.

Significance

Ecological and economic roles

Members of *Lichenothelia* are reported as lichens, borderline lichens, and rock-inhabiting fungi (Henssen 1987, Muggia et al. 2015, Ametrano et al. 2019b) and are distributed worldwide, including desert regions (Henssen 1987, Ametrano et al. 2019b).

Chemical diversity

The chemical diversity of *Lichenotheliales* is poorly explored and needs further studies.

Other relevant data and future recommendations

Endococcus was introduced in the early stages of lichenology, and had various taxonomic placements in the past. Triebel (1989) treated the genus under *Dothideales*. Later, Jayasiri et al. (2016) transferred this genus to *Lichenotheliaceae* based on the morphological characteristics, such as perithecioid ascomata with widely porate ostioles, globose to broadly clavate asci and hyaline or brown with 1-septate ascospores. However, this classification was not accepted in further studies and the genus was placed in *Verrucariales* (Diederich et al. 2018, Hafellner 2019). However, the phylogeny of the genus is not fully resolved and needs further studies for species identification (Muggia et al. 2015).

Microthyriales **G. Arnaud, Les Astérinées: 85 (1918)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Microthyriales is one of the important orders consisting of epifoliar taxa appearing as small, inconspicuous, black spots on host leaves (Wu et al. 2011). It is a poorly known monotypic order and belongs to *Dothideomycetes*. Taxa of *Microthyriales* are mainly characterized by having superficial, flattened, ostiolate thyriothecia, with the cells of the upper wall radiating in parallel arrangement of the poorly developed lower wall (Marasinghe et al. 2022b, 2023).

History

Saccardo (1883c) established *Microthyriaceae* with the type genus *Microthyrium.* Theissen (1913) accommodated it in *Hemisphaeriales* including taxa with unilocular ascomata with radiating arranged cells. *Microthyriales* was introduced by Arnaud (1918) to accommodate *Microthyriaceae* and *Microthyriopsidaceae*. Luttrell (1973) included 11 families (*Asterinaceae*, *Aulographaceae*, *Brefeldiellaceae*, *Leptopeltidaceae*, *Micropeltidaceae*, *Microthyriaceae*, *Munkiellaceae*, *Parmulariaceae*, *Stephanothecaceae*, *Schizothyriaceae* and *Trichopeltinaceae*) in *Hemisphaeriales*. von Arx & Müller (1975) transferred *Microthyriaceae* from *Hemisphaeriales* to *Dothideales* and referred it to *Pseudosphaeriineae*. Then, Barr (1987a) placed it in *Melanommatales* and subsequently, in *Dothideomycetes* families *incertae sedis* by Lumbsch & Huhndorf (2010). *Aulographaceae* and *Leptopeltidaceae* were later added by Kirk et al. (2008b) in *Microthyriales* based on morphology and mentioned that *Microthyriales* is probably a polyphyletic order. Hyde et al. (2013) placed *Aulographaceae* in *Asterinales* and *Leptopeltidaceae* in *Dothideomycetes,* family *incertae sedis*. However, the later studies with advanced molecular approaches showed that *Microthyriales* clustered as a distinct clade within *Dothideomycetes* with high support (Hongsanan & Hyde 2017, Wijayawardene et al. 2018, 2020, Marasinghe et al. 2022a, b, 2023).

Wu et al. (2011) revisited *Microthyriaceae* and accepted seven genera (*Arnaudiella*, *Calothyriopsis*, *Caribaeomyces*, *Microthyrium*, *Palawania*, *Paramicrothyrium* and *Seynesiella*). Hyde et al. (2013) accepted *Microthyriaceae* and *Micropeltidaceae* in *Microthyriales*. However,

Hongsanan & Hyde (2017) excluded *Micropeltidaceae* from *Microthyriales* and placed in *Lecanoromycetes*. Wijayawardene et al. (2018) listed nine genera in *Microthyriaceae*. Later, Hongsanan et al. (2020a) and Wijayawardene et al. (2020) accepted 11 genera in *Microthyriales* and six genera in *Microthyriales* placed in *incertae sedis*. However, an additional two aquatic hyphomycetous genera were added to this order by Zheng et al. (2022). Hyde et al. (2024b) accept 18 genera in *Microthyriaceae* and eight genera are accepted under *Microthyriales incertae sedis*.

General description

The sexual morphs of *Microthyriaceae* are usually characterized by having superficial, flattened ostiolate thyriothecia with upper wall consisting of radially arranged cuboid or angular cells. Asci of this family are bitunicate, fusiform or obclavate to cylindrical-clavate or fissitunicate and contain hyaline to brown, 1-septate ascospores often with cilia (Kirk et al. 2008b, Wu et al. 2011, Hyde et al. 2013, Hongsanan et al. 2020a). Asexual morphs of *Microthyriaceae*/*Microthyriales* are ecologically similar to their respective sexual morphs, with similar host-specificity and distribution patterns (Yen et al. 2018). They usually occur on other fungi (*Hansfordiella* and *Isthmospora*), on wood and litter (*Zalerion*) or on leaves (*Xenogliocladiopsis*) in terrestrial or aquatic ecosystems (Seifert et al. 2011) (Figs. 51, 52, 53).

Sexual morph: *Thyriothecia* superficial, orbicular, flattened, dark brown to brown, ostiolate, basal plate poorly developed. *Upper wall* brown, comprising radially arranged cells of *textura prismatica*, often darkened at the ostiole and tapering at the margin. *Hamathecium* presence or absence of pseudoparaphyses. *Asci* 8-spored, bitunicate, fissitunicate, cylindrical to obpyriform, with or without a pedicel, with or without an ocular chamber at the tip. *Ascospores* overlapping 1–3-seriate, hyaline or brown, fusiform to ellipsoidal, usually 1-septate, with cilia or appendages. Asexual morph: Coelomycetous *mycelium* consisting of hyaline to pale brown, smooth to verruculose, branched, septate hyphae. *Conidiophores* micronematous or macronematous, *Conidiogenous cells* mono- to polyblastic, holothallic, integrated, terminal, smooth or verruculose, determinate or sympodial, clavate, subcylindrical, narrow cylindrical to cylindrical, ampulliform or ovoid. *Ramoconidia* pale brown, verruculose, subcylindrical to fusoid-ellipsoid, aseptate, giving rise to branched chains of conidia. *Conidia* solitary or in branched chains, thallic-arthric or radial on compact heads, acrogenous or acropleurogenous, verruculose, cylindrical, cylindrical-obclavate, obclavate, subcylindrical to ellipsoid, obclavate, pale brown, aseptate to multi-septate, sometimes rostrate; hilum inconspicuous, truncate, sometimes thinned or thickened; conidia in *Hamatispora* consisting of a main axis and lateral branches; main axis hook-shaped with a long tail bearing lateral branches; lateral branches straight, developing from different cells of the helicoid part of the main axis. *Chlamydospores* in *Keqinzhangia* are globose, terminal, solitary or short catenulate, subhyaline (adapted from Marasinghe et al. 2022b, 2023).

Families included in *Microthyriales*

Microthyriaceae Sacc.

Microthyriales genera *incertae sedis*
Antidactylaria Z.F. Yu, M. Qiao & R.F. Castañeda
Heliocephala V. Rao, K.A. Reddy & de Hoog
Mitopeltis Speg.
Neoscolecobasidium Crous
Parazalerion Madrid, Gené & Cano
Pseudosoloacrosporiella Crous
Seynesiella G. Arnaud
Thyriodictyella Cif.

Evolution

Hongsanan et al. (2016b) stated that epifoliar fungi evolved at least in Permian (298.9 to 252.17 MYA) and concluded that *Zeloasperisporiales* and *Microthyriales* lineages have evolved later

than other epifoliar orders (*Asterinales*, *Meliolales* and *Capnodiales*).There is no study about the evolution of *Microthyriales* due to the lack of molecular data (Hongsanan et al. 2016b). Numerous microthyriaceous fossil taxa have been described from the Cretaceous and Cenozoic deposits worldwide (Cookson 1947, Dilcher 1965, Alvin & Muir 1970, Phadtare 1989, Phillips & Rember 2004, Ding et al. 2011, Du et al. 2012). They are probably the most studied fossil fungi and the earliest record of microthyriaceous thyriothecia is dated to the Late Permian of India (Jha & Aggarwal 2011). Dilcher (1965) mentioned that microthyriaceous fungi had a fairly modern aspect during the Eocene. Taylor et al. (2015a) stated that some of microthyriaceous fossils are similar to the chlorophycean green algal fossils. Germlings of microthyriaceous fungi have been recorded from various localities around the world. Several recent studies have been carried out to estimate the divergent time of *Microthyriales*. Hongsanan et al. (2016b) also estimated a quite similar crown date for *Microthyriales* as 181 MYA while the minimum age for *Microthyrium* was estimated as 54 MYA by Samarakoon et al. (2019).

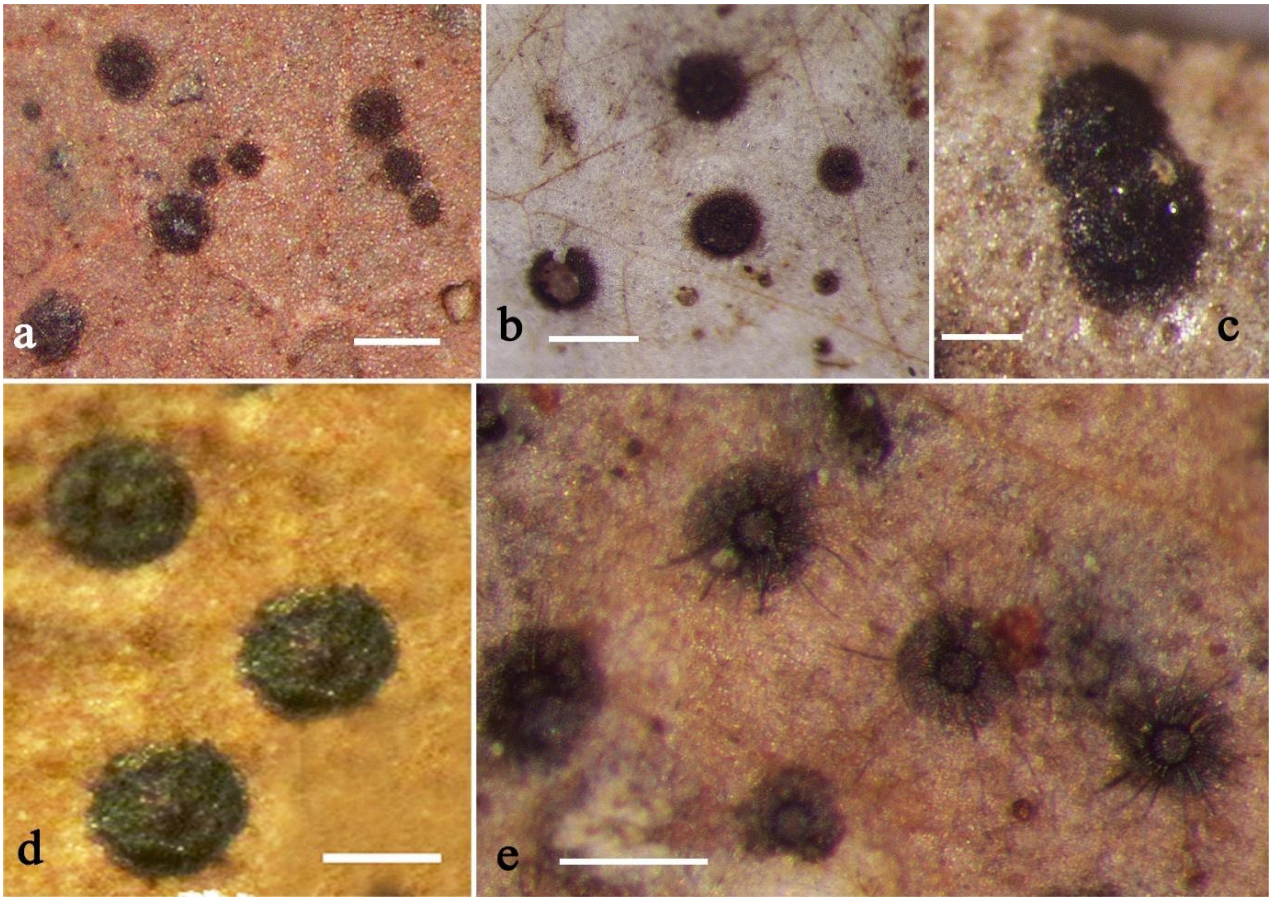


Figure 51 – Appearance of thyriothecia on the host surface. a *Microthyrium* sp. b *Pseudomicrothyrium* sp. c *Tothia* sp. d *Tumidispora* sp. e *Chaetothyriothecium* sp. Scale bars: a-d = 100 µm, e = 150 µm.

Justification of order and problems

There are many taxonomic confusions available in *Microthyriales* and many species are only known from their morphology. Therefore, many of those studies has led to misinterpretations due to phenotypic plasticity (Doidge 1942, Müller & von Arx 1962, Luttrell 1973, Barr 1987a, Hofmann 2010). During the last two decades, morpho-molecular approaches have been used as the primary research tool for species identification of *Microthyriaceae*. Wu et al. (2011), revisited *Microthyriaceae* and provided a phylogeny for this group. Many aquatic hyphomycetes have been identified in *Microthyriaceae,* reflecting its highly diversified ecological niches (Zheng et al. 2022). These taxa are difficult to culture on artificial media and direct DNA extraction is not always

successful due to their tiny fruiting structures. Some genera of this order have not been sequenced yet and fresh collections of their type species are needed to obtain molecular data.

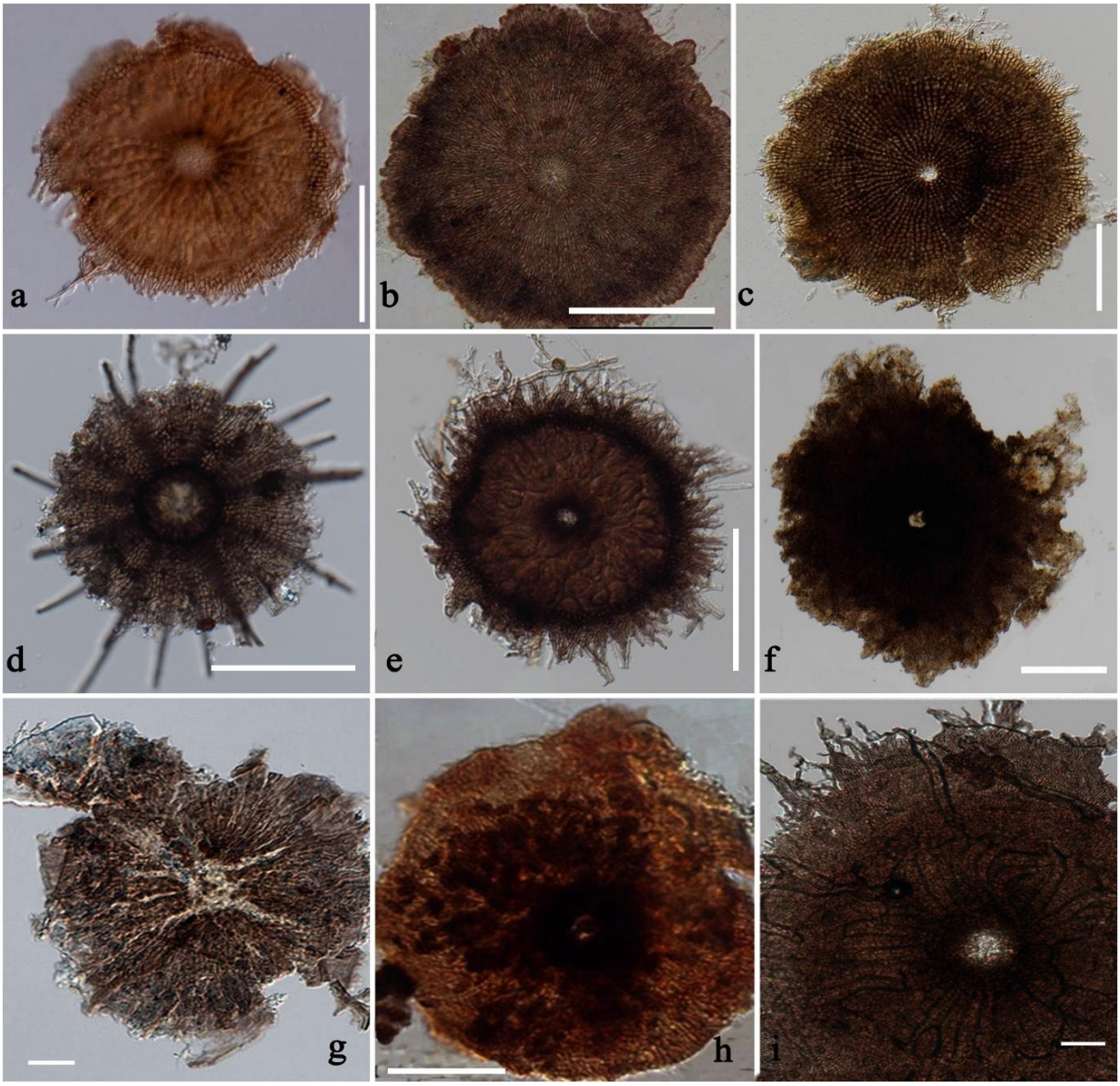


Figure 52 – Thyriothecial morphology of *Microthyriales*. a *Microthyrium* sp. b *Tumidispora* sp. c *Paramicrothyrium* sp. d *Chaetothyriothecium* sp. e *Pseudomicrothyrium* sp. f *Tothia* sp. g *Mitopeltis* sp. h. *Arnaudiella* sp. i *Thyriodictyella* sp. (Source from Ariyawansa et al. 2015 (b), Wu et al. 2011 (h) and Zeng et al. 2019 (g, i). Scale bars: a, c–f, h = 50 μm, b = 100 μm, g = 20 μm.

Significance

Ecological and economic roles

Members of this order are usually superficial or subcuticular, submerged decaying leaves and stems in terrestrial or aquatic habitats (Wu et al. 2014a). Doidge (1942) mentioned that microthyriaceous species are common in tropical and subtropical areas and they are rarely found in temperate regions (Ellis 1976a, 1977). They are usually reported as epiphytes, pathogens or saprobes (Hyde et al. 2013, Hongsanan et al. 2015b). The ecological role and the host-specificity of microthyriaceous taxa are not clear. They colonize living leaves and release ascospores on fallen decaying leaves. These fungi prefer coriaceous leaves of evergreen plants, as they apparently provide a better substrate for fungi to complete their life cycle (Eriksson 1974, Kirk & Spooner 1989, Flessa

et al. 2012, Worobiec & Worobiec 2013, Marasinghe et al. 2022b, 2023). Occurrences of microthyriaceous fungal thyriothecia in various developmental stages are correlated with humid, tropical to subtropical climates (Dilcher 1965, Kalgutkar & Jansonius 2000, Tripathi 2009, Du et al. 2012, Paruya et al. 2017, Marasinghe et al. 2022b, 2023). This order contains aquatic and saprobic hyphomycetous taxa with large, tetraradiate and branched spores which help them disperse easily for colonization on the litter patches (Dang et al. 2007). They help to decompose plant litter in the nutrient recycling of forest ecosystems (Bärlocher & Boddy 2016).

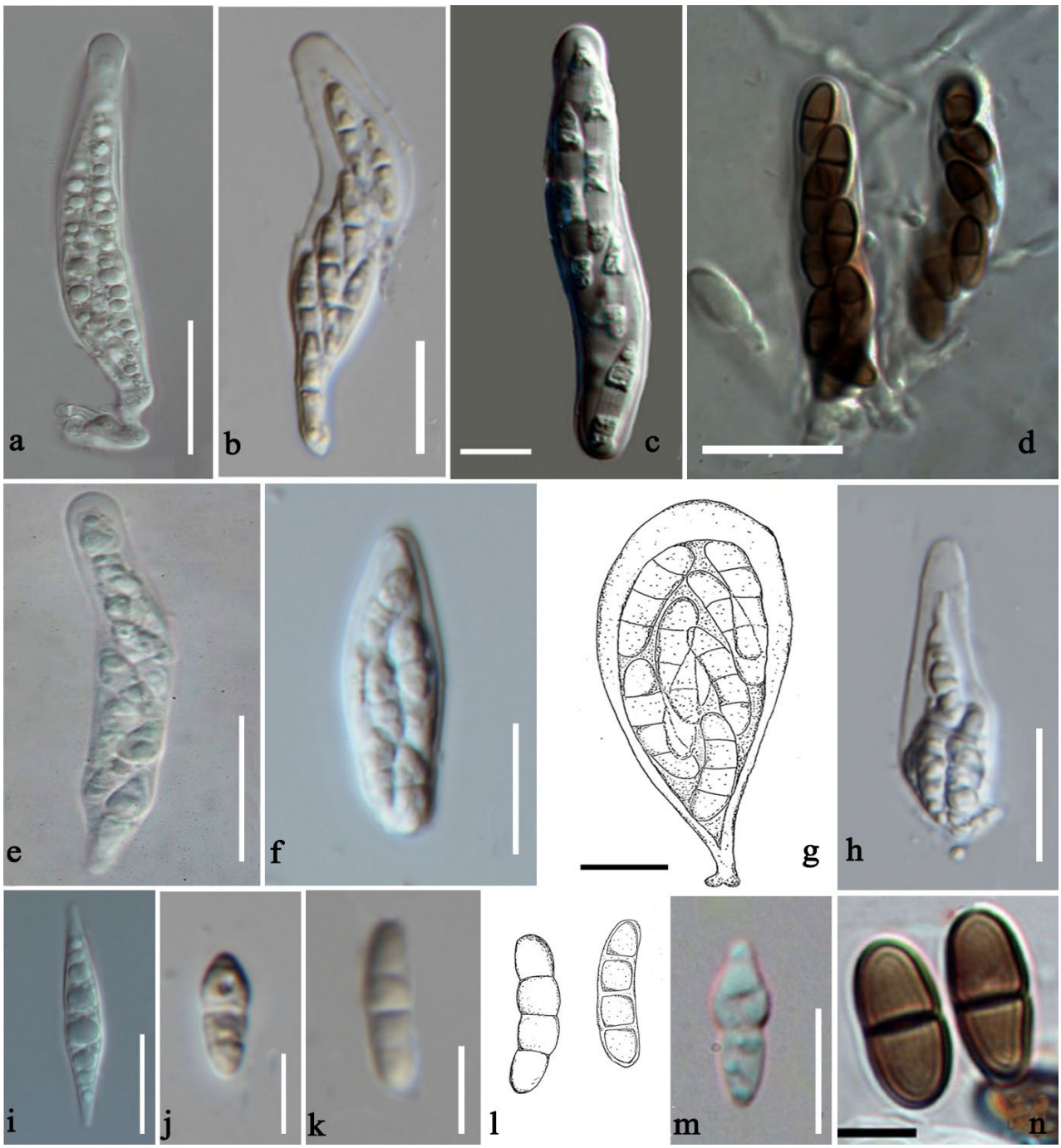


Figure 53 – Asci and ascospores morphology of *Microthyriales*. a, i *Microthyrium* sp. b, k *Tothia* sp. c *Thyriodictyella* sp. d, n *Arnaudiella* sp. e, m *Tumidispora* sp. f, j *Chaetothyriothecium* sp. g, l *Mitopeltis* sp. h, j *Pseudomicrothyrium* sp. (Adapted from Ariyawansa et al. 2015 (e, m), Wu et al. 2011 (d, n) and Zeng et al. 2019 (c)). Scale bars: a–c, f–h, i–k, m, n = 10 µm, d, e = 20 µm.

Chemical diversity

No relevant studies are available for the chemical diversity of *Microthyriales*.

Other relevant data and future recommendations

Microthyriaceae species have widely distributed all over the world and most of them lack molecular data (Wu et al. 2011, Tennakoon et al. 2023). Some genera (*Arnaudiella*, *Calothyriopsis* and *Seynesiella)* have never been sequenced and are accommodated in uncertain placements in *Microthyriales*. Therefore, it is important to recollect representative species of these genera and obtain molecular data to confirm their placements in *Microthyriales*. Studies regarding ecological and pathogenic aspects of microthyriaceous fungi are lacking. Extensive sampling from different habitats and hosts are needed to increase the understanding of these fungi. The sexual and asexual connection of microthyriaceous taxa is poorly known and needs molecular approaches to support future studies.

Minutisphaerales **Raja, Oberlies, Shearer & A.N. Mill. Mycologia 107(4): 854 (2015)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Minutisphaerales is a small order with only two genera and approximately 20 species. Raja et al. (2015a) established the order in the class *Dothideomycetes*. The order formed a monophyletic clade in phylogenetic analysis based on LSU, SSU, and MCM7 sequences (Raja et al. 2015a). However, the monophyletic nature has recently been questioned (Jayasiri et al. 2018a). Based on morphological characteristics and phylogenetic analyses of the LSU, SSU, RPB2, and TEF1-α, *Minutisphaerales* is divided into two families, *Acrogenosporaceae* and *Minutisphaeraceae* (Raja et al. 2015a, Jayasiri et al. 2018a). The type family *Minutisphaeraceae* accommodates a monophyletic group *Minutisphaera* (Raja et al. 2015a) and the taxa are distinguished by apothecioid or pseudothecioid, erumpent to superficial ascomata with ostioles, a thin-walled peridium and clavate, fusiform to ellipsoid, multiguttulate ascospores with a gelatinous sheath. Taxa of *Acrogenosporaceae* are characterized by hysterothecial ascomata with thick-walls, a prominent sunken slit and hyaline or moderately pigmented, 1-celled, stipitate, ascospores (Raja et al. 2015a, Jayasiri et al. 2018a). *Acrogenosporaceae* includes a single genus *Acrogenospora* (Jayasiri et al. 2018a). *Minutisphaerales* are found in terrestrial and freshwater habitats on decaying wood, submerged wood, bark, and bamboo culms (Dong et al. 2020).

History

The study of *Minutisphaerales* began when Ferrer et al. (2011) discovered freshwater taxa with small ascomata and fissitunicate asci, which were also commonly reported in *Dothideomycetes*. Until 2011, all freshwater fungi were placed in two orders: *Pleosporales* and *Jahnulales* (Ferrer et al. 2011). *Minutisphaera* was introduced to accommodate *Minutisphaera fimbriatispora* based on their morphological characters and the phylogeny of LSU and SSU sequence data. The genus clustered in the same clade with *Farlowiella carmichaeliana* (Ferrer et al. 2011). *Minutisphaera* differed from *Jahnulales* in its large vegetative hyphae and did not fit into any orders of *Dothideomycetes* (Shearer et al. 2009). Thus, the familial and ordinal placement of the new genus remained obscure. Raja et al. (2013) introduced another species *Minutisphaera japonica* based on morphological characters and phylogenetic analysis of SSU and LSU sequences. Later, Raja et al. (2015a) described two new species (*Minutisphaera parafimbriatispora* and *M. aspera*) based on the phylogeny of LSU, SSU and MCM7 sequence data, and morphological features. The author further found that all the *Minutisphaera* clustered together in a strongly supported clade, but they had no phylogenetic affinities with other taxonomic groups of *Dothideomycetes*. Subsequently, the order

Minutisphaerales and the family *Minutisphaeraceae* were established. These taxa formed a sister group with *Farlowiella carmichaeliana*.

Farlowiella is a hysterothecioid genus classified as *incertae sedis* in *Pleosporomycetidae*, with *Acrogenospora* as the anamorphic state (Goh et al. 1998b, Boehm et al. 2009b). Later, it was considered as a synonym of *Acrogenospora* (Rossman et al. 2015b). Jayasiri et al. (2018a) investigated the phylogenetic position of *Acrogenospora* species using combined multigene phylogenetic analysis of LSU, SSU, TEF1-α, and RPB2, along with morphological characters. *Acrogenospora* formed a sister group to *Minutisphaeraceae* but showed morphological differences. Therefore, a new family *Acrogenosporaceae* was established within *Minutisphaerales* to accommodate *Acrogenospora* species (Jayasiri et al. 2018a).

General description

The term "hysteriaceous," "hysteriform", or "hysterothecioid" ascomycete refers to fungi with lirelliform ascomata, also known as hysterothecia (Clements & Shear 1931). *Minutisphaeraceae* have pseudothecioid or apothecioid ascomata with ostioles, whereas *Acrogenosporaceae* have hysterothecial ascomata with a prominent sunken split. Peridium is thick in the *Acrogenosporaceae* but thin in the *Minutisphaeraceae*. The ascospores of *Minutisphaeraceae* are multi guttulate with a gelatinous sheath, and can be fusiform, clavate, or ellipsoid whereas aseptate, stalky, hyaline, or slightly pigmented ascospores are found in *Acrogenosporaceae* (Jayasiri et al. 2018a). The asci of *Acrogenospora* are thin-walled, obtuse at the apex, and short pedicellate, whereas *Minutisphaera* has bitunicate asci that are rounded at the apex, and lack a pedicel. The hyphomycete asexual morph of *Acrogenospora* is well known. However, no asexual morph has been reported in *Minutisphaera* (Dong et al. 2020). *Acrogenospora* species are also distinguished by conidiophore and conidial dimensions, as well as conidial surface and shape (Bao et al. 2020, Dong et al. 2020). The shape and size of the ascospores are used to differentiate *Minutisphaera* species (Dong et al. 2020).

Sexual morph: *Ascomata* apothecioid or pseudothecioid, small, with irregularly curved, dark brown to black hyphal-like structures around the ostiole. *Pseudoparaphyses* septate, with or without enlarged pigmented tips. *Asci* obclavate to broadly cylindrical, oval, eight-spored, fissitunicate. *Ascospores* clavate to broadly oblong, hyaline or pale brown, septate, smooth- or rough-walled, with or without numerous filamentous appendages radiating around the mid-septum and with or without gelatinous sheath. Asexual morph: *Conidiophores* mononematous, macronematous, brown, simple with multiple percurrent proliferations. *Conidiogenous cells* terminally or intercalary, monoblastic. *Conidia* ellipsoid, globose or obovoid, olivaceous to dark brown conidia (adapted from Hongsanan et al. 2020a) (Fig. 54).

Families included in *Minutisphaerales*

Acrogenosporaceae Jayasiri & K.D. Hyde

Minutisphaeraceae Raja, Oberlies, Shearer & A.N. Mill

Evolution

Fissitunicate asci and ascospore sheaths are found in terrestrial ascomycetes, which supports the hypothesis that freshwater *Dothideomycetes* evolved from terrestrial ancestors (Dhanasekaran et al. 2006, Dong et al. 2020). The presence of fissitunicate asci are an essential character for ascospore discharge and survival in aquatic habitats, as ascospores must be ejected through air or possibly in water (Dhanasekaran et al. 2006). Gelatinous sheaths, appendages, and ornamentation of ascospores are thought to be responsible for spore attachment to substrates and dispersal in water (Jones 2006, Dong et al. 2020). Members of the *Minutisphaerales* have some morphological similarities to *Pleosporales* and *Patellariales*, but phylogenetic analysis of LSU, SSU, and MCM7 sequences places them in a strongly supported monophyletic clade (Raja et al. 2015a). Despite having homoplasy with other orders of *Dothideomycetes*, they have evolved in a distinct lineage. According to Hongsanan et al. (2020a), the divergence time for *Minutisphaerales* is estimated as 224 MYA (stem age).

Justification of order and problems

Although *Alascospora evergladensis* (from *Pleosporales*) and *Minutisphaera* have morphological similarities, their phylogenetic relationships are unclear due to a lack of sequences for *A. evergladensis*. New collections of *Alascospora evergladensis* could shed light on the boundaries of *Minutiphaerales* (Raja et al. 2015a). It is not clear whether *Acrogenospora sphaerocephala* or *A. megalospora* are an asexual morph of *Farlowiella carmichaeliana*. The phylogenetic analysis of *Acrogenospora* species revealed that *A. sphaerocephala* does not belong to the same clade as *A. carmichaeliana* and forms a distinct clade within *Acrogenosporaceae* (Bao et al. 2020).

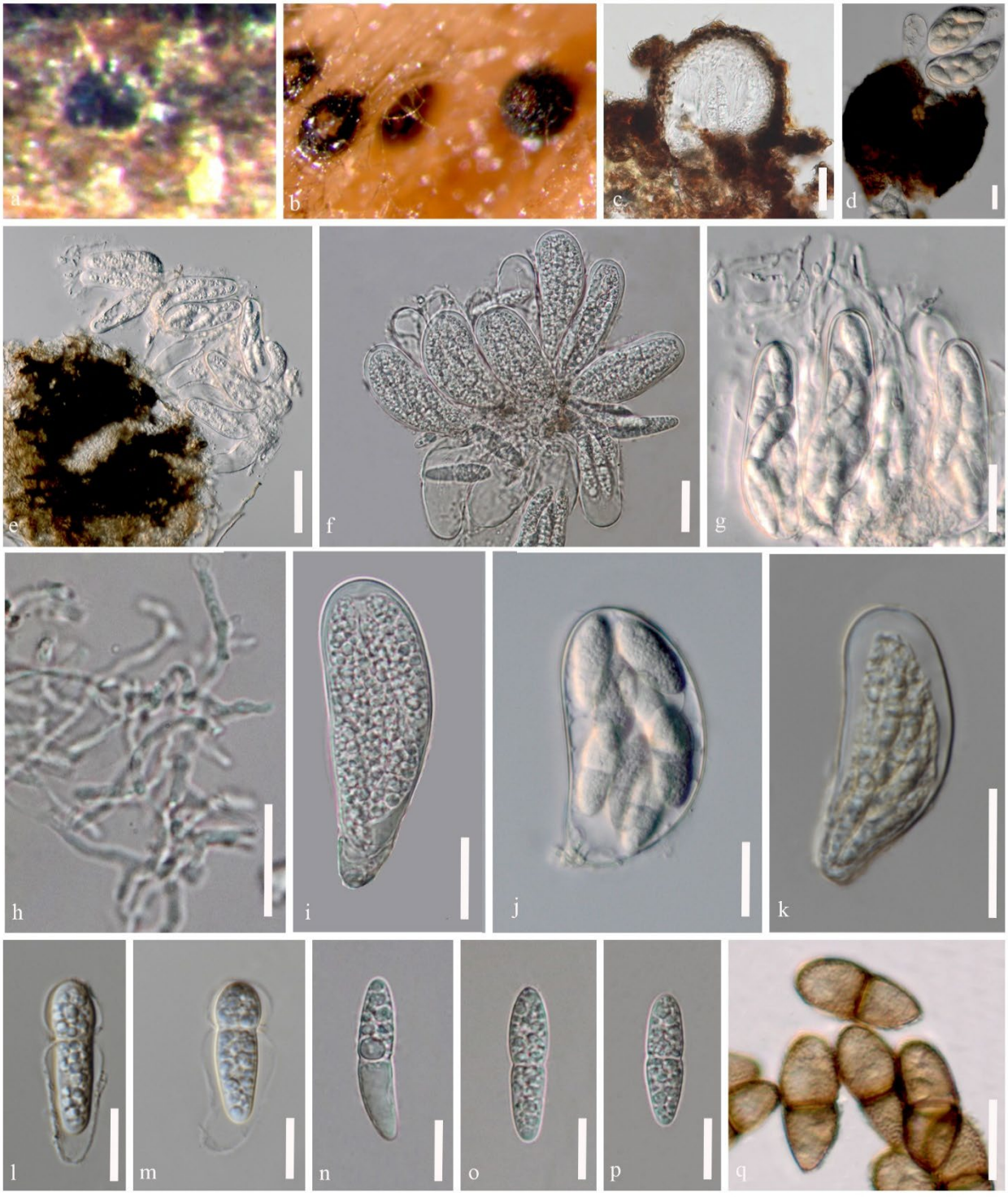


Figure 54 – Sexual morph of *Minutisphaerales*. a, b Ascomata on submerged wood (a *Minutisphaera aquaticum*, b *M. parafimbriatispora*). c Sections of ascoma (*M. aquaticum*). d, e Squash mount of

ascoma (d *M. aspera*, e *M. parafimbriatispora*). f, i–j Asci (f *M. aquaticum,* i *M. aquaticum*, j *M. aspera*, k *M. thailandensis*). g Asci and Paraphyses (*M. parafimbriatispora*). h Paraphyses (*M. aquaticum*). l–q Ascospores (l, m *M. thailandensis*, n–p *M. aquaticum*, q *M. aspera*). Scale bars: c = 30 µm, d = 50 µm, e–k = 20 µm, l–p = 10 µm.

Significance

Ecological and economic roles

Some species of this order have been isolated from submerged wood in freshwater. This indicates that they can serve an ecological function in nutrient cycling and organic matter decomposition in freshwater habitats (Simonis et al. 2008). Recently, it has been observed that *Acrogenospora terricola* infects seeds in a terrestrial environment (Harrington et al. 2022). Additionally, their high ITS sequence similarity to endophytes suggests that they may potentially be endophytes inside the roots of trees (Raja et al. 2015a).

Acrogenospora sphaerocephala has been shown to decolorize Reactive Red in 11 and Acid Blue in 113 dyes. Therefore, this species has the potential to be used for wastewater purification as a dye decolorization treatment in the leather and textile industries (Yang et al. 2016b). Secondary metabolites produced by some species of this order have shown antimicrobial activity against human pathogenic bacteria (*Staphylococcus aureus* and *Mycobacterium smegmat*) (Raja et al. 2015a). They may also have antimicrobial activity against other fungal and bacterial species that grow on submerged wood in aquatic habitats (Raja et al. 2015a). Identification of fungi of this order and investigation of their metabolites are critical for the waste recycling industry, the production of compost required in the agricultural industry, and the development of new antibiotics in the pharmaceutical industry.

Chemical diversity

Minutisphaera aspera and *M. parafimbriatispora* produce six secondary metabolites that are dipeptides and aromatic polyketides. Both species produce an aromatic polyketide (isosclerone [5], while the metabolites produced by *M. aspera* include some dipeptides (Cyclo-[R]-Pro-[S]-Phe, Cyclo-[S]-Pro-[S]-Leu, Cyclo-[S]-Ala-[S]-Phe, and Cyclo-[S]-Pro-[S]-Phe). Two polyunsaturated fatty acids (polyunsaturated palmitic acid and (E)-hexadec-9-en-1-ol) were identified as the major metabolites in *M. parafimbriatispora* (Raja et al. 2013).

Other relevant data and future recommendations

Nine species, including seven new species, have been identified in research on the identification of *Acrogenospora* species in Yunnan Province, China. It appears that this genus is very diverse, so more research into species identification in this genus is essential (Bao et al. 2020). Based on the phylogenetic tree of SSU, LSU, TEF1-α, and RPB2 and morphological data, the phylogenetic position of *A. carmichaeliana*, *A. basalicellularispora* and *A. verrucispora* is unclear. More taxa might belong to this group. Further collections and phylogenetic studies are required to resolve these uncertainties (Bao et al. 2020). Despite the potential importance of *A. sphaerocephala* for dye decolorization (Yang et al. 2016b), no research on the secondary metabolites of *Acrogenospora* spp. has yet been conducted. Given the ability of some fungi to live as endophytes and saprobes (Bärlocher 2006) and the high similarity of the ITS sequences of *M. aspera* to those of an endophyte in *Pleosporales* (Raja et al. 2015a), more research into their ecological role is recommended.

Monoblastiales Lücking, M.P. Nelsen & K.D. Hyde, Fungal Diversity 63: 8 (2013)

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Monoblastiales is a mostly lichenized order and was introduced by Hyde et al. (2013) to accommodate a single family *Monoblastiaceae*. The order differs in having net-like physes and

euseptate ascospores with few septa and poor secondary chemistry from other lichenized orders of *Dothideomycetes,* including *Strigulales* and *Trypetheliales,* respectively. Further, the order differs in macroconidia arranged in a gelatinous matrix from both orders (Hyde et al. 2013).

History

Monoblastiaceae was introduced by Watson (1929) to accommodate lichenized genera *Coccotrema*, *Haplopyrenula*, *Lepolichen* and *Monoblastia* and were characterized by crustaceous or foliose thallus with *Trentepohlia* or allied alga, simple perithecia with an apical pore and 2-8 simple ascospores per ascus. Eriksson (1981) suggested that the family formed a part of *Pertusariaceae* in *Lecanoromycetes*. However, later studies argued for retaining a separate family (Harris 1990, 1995, Aptroot 1991a, Eriksson & Hawksworth 1993a) and the natural circumscription of the family was provided by Harris (1990, 1995). In the six gene phylogenetic analyses conducted by James et al. (2006), *Monoblastiaceae* represented by *Anisomeridium polypori* was recovered in *Dothideomycetes*. The family also formed a separate clade within *Dothideomycetes* that were represented by the lichenized genera (Nelsen et al. 2009). Nelsen et al. (2011a) showed the sister relationship of *Funbolia* and *Heleiosa* with *Monoblastiaceae* in their phylogenetic analyses but with weak statistical support. Hyde et al. (2013) established a new order to accommodate *Monoblastiaceae,* including the genera *Acrocordia*, *Anisomeridium*, *Caprettia*, *Megalotremis*, *Monoblastia* and *Trypetheliopsis* and the order recovered in the basal lineage of *Dothideomycetes*. *Eriomycetaceae* was later established to accommodate *Funbolia*, *Heleiosa*, *Phellinocrescentia* and *Pseudopassalora* with a newly established genus *Eriomyces* (Hyde et al. 2020b). Except for *Eriomyces,* all other genera were treated under *Dothideomycetes*, genera *incertae sedis*. However, in the phylogenetic analyses of Hyde et al. (2020b), the lichenized members were mostly overlooked when they established the new family, and consequently, Hongsanan et al. (2020a) treated *Eriomycetaceae* as a synonym of *Monoblastiaceae*.

General description

The subtle morphological differences were reported among the genera of *Monoblastiaceae*. *Funbolia* and *Pseudopassalora* are reported in their hyphomycetous asexual morphs (Crous et al. 2011a, c) whereas, other non-lichenized genera are reported as pycnidial anomorphic states. However, based on shared morphological similarities between other sexual and asexual members, both lichenized and non-lichenized members are included in *Monoblastiales* (Hongsanan et al. 2020a) .

Sexual morph: *Ascomata* perithecial, distinct or reduced involucrellum and *psoroplectenchymatous* excipulum, branched and anastomosing, thin, net-like physes. *Asci* fissitunicate, ocular chamber and fluorescent ring- or cap-structures. *Ascospores* ellipsoid- fusiform, 1-septate (rarely aseptate or 3-septate), euseptate, hyaline to rarely brownish. Asexual morph: Conspicuous conidiomata. *Conidia* produced in conspicuous conidiomata, with the macroconidia typically clustered in groups or masses in a distinct gelatinous matrix (adapted from Hongsanan et al. 2020a) (Figs. 55, 56).

Families included in *Monoblastiales*

Monoblastiaceae Walt. Watson (=*Eriomycetaceae* Huanraluek & K.D. Hyde)

Evolution

Hongsanan et al. (2020a) reported that the divergence time for *Monoblastiales* is estimated as 230 MYA (stem age).

Justification of order and problems

The generic type *Monoblastia* lacks molecular data and was mostly supported by morphological and anatomical characters with the extant lichenized members of the family. In the recent phylogenetic analysis conducted by Hongsanan et al. (2020a), *Anisomeridium-Megalotremis-Trypthelіopsis* together formed a clade and the relationship to the generic type is unknown. Another genus, *Caprettia,* also lacks molecular data and was placed in *Monoblastiaceae* based on

hamathecium and ascus structure, ascospore type, and the peculiar conidiomata and conidia (Hongsanan et al. 2020a). Thus, further studies with molecular data are required to resolve the phylogeny of the members.

Significance

Ecological and economic roles

The taxa are mostly reported as lichenized on bark, rarely on rocks or leaves, rarely non-lichenized and saprobic on leaves or bark. They are usually found in terrestrial, lowland to montane tropical to subtropical habitats, with few species extending into temperate regions and in one case (*Heleiosa*) growing on leaves of *Juncus* in salt marshes (Crous et al. 2011a, c). *Phellinocrescentia* reported on the sporocarp of a *Phellinus* species as a hyperparasite (Crous et al. 2014b).

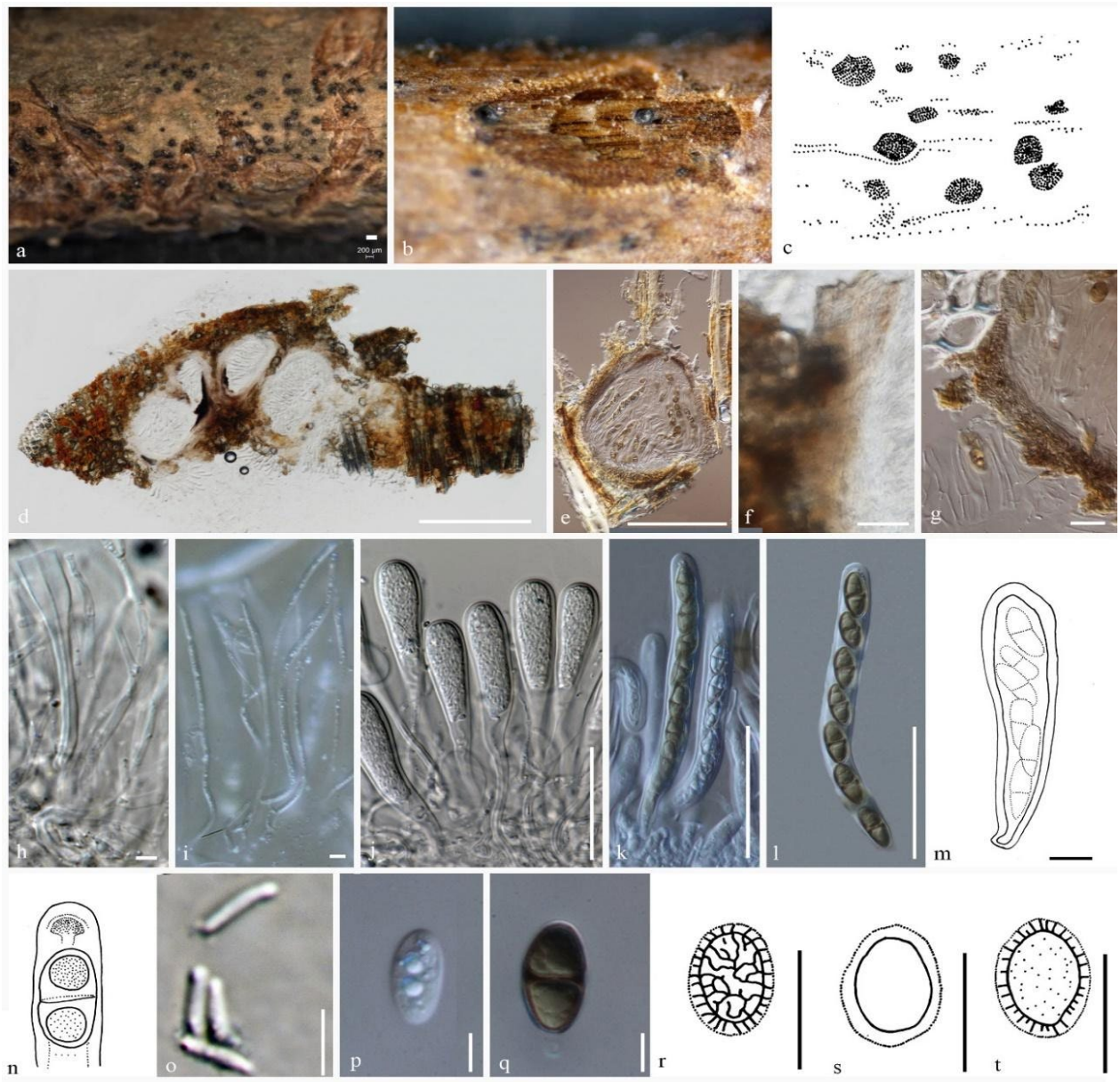


Figure 55 – Sexual morph of *Monoblastiales*. a–c Host substrate (a *Eriomyces heveae*, b *Neoheleiosa lincangensis*, c *Acrocordia gemmate*). d, e Vertical section though ascomata (d *Eriomyces heveae*, e *Neoheleiosa lincangensis*). f, g Peridium (f *Eriomyces heveae*, g *Neoheleiosa lincangensis*). h, i Paraphyses (h *Eriomyces heveae*, i *Neoheleiosa lincangensis*). j–m Asci (j *Eriomyces heveae*, k, l *Neoheleiosa lincangensis*, m *Anisomeridium guangdongensis*). n Ascus apex (*Acrocordia gemmata*). o–t Ascospores (o *Eriomyces heveae*, p, q *Neoheleiosa lincangensis*, r, s *Monoblastia pellucida*, t

Monoblastia rappii). (redrawn from Aptroot 1991b, Hongsanan et al. 2020a, Zhang et al. 2020c). Scale bars: a = 200 µm, d, e = 100 µm, f = 30 µm, g, r–t = 10 µm, j–l = 50 µm, h, i, o–q = 5 µm.

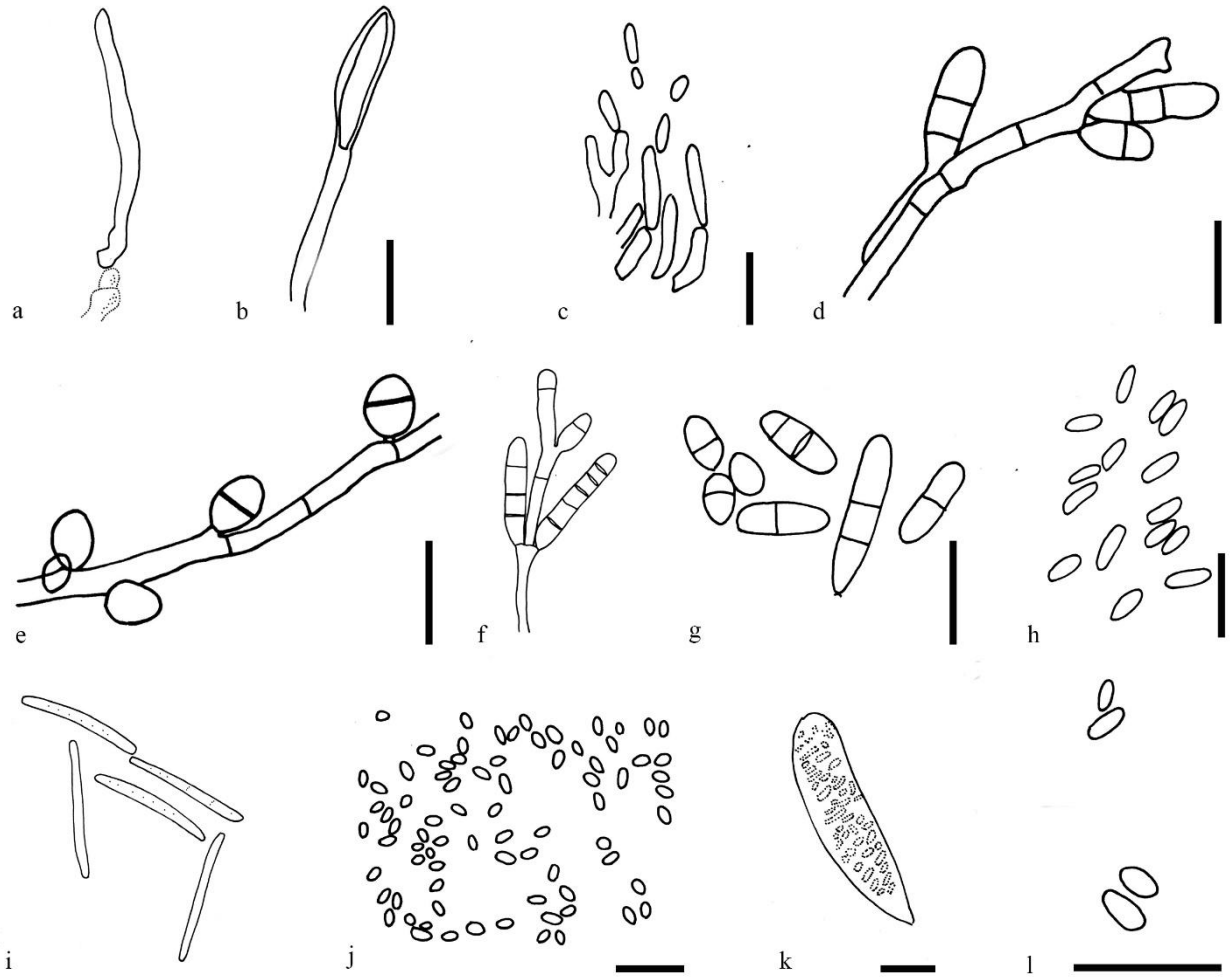


Figure 56 – Asexual morph of *Monoblastiales*. a, b Conidiogenous cells giving rise to conidia (a *Haudseptoria typhae*, b *Pseudopassalora gouriqua*). c Conidiophores with conidiogenous cells (*Italiofungus phillyreae*). d–g Conidiophores giving rise to dimorphic conidia (*Funbolia dimorpha*). h–l Conidia (h *Italiofungus phillyreae*, i *Haudseptoria typhae*, j *Phellinocrescentia guianensis*, k, l *Anisomeridium guangxiensis*) (Crous et al. 2011a, c, 2014b, 2020d, 2021c, Zhang et al. 2020c). Scale bars: a–j = 10 µm, k, l = 20 µm.

Chemical diversity

Lichexanthone and anthraquinone pigments are reported in a few species but secondary substances are not commonly reported (Hongsanan et al. 2020a, Wijayawardene et al. 2021c).

***Murramarangomycetales* Crous, Persoonia 39: 385 (2017)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Murramarangomycetales was introduced by Crous et al. (2017a) to accommodate a new family *Murramarangomycetaceae* and the monotypic genus *Murramarangomyces* based on morphological characterization along with phylogenetic analyses.

History

Studies on *Murramarangomycetales* began with fungal collections from leaves of *Corymbia maculate* (*Myrtaceae*) in Australia. An asexual morph represented a species that formed leaf spots that are circular, hypophyllous, and dark brown (Crous et al. 2017a). The species showed distinct morphological features from other *Dothideomycetes* orders and formed a sister clade to *Acrospermales* and was phylogenetically closely related to *Venturiales*. Thus, a new order, family and genus *Murramrangomyces* were established to accommodate the new species *M. corymbiae*. Several black and round, hysterothecia were also observed when they isolated *M. corymbiae* but the sexual asexual link was not established at that time. Later, Crous et al. (2019d) synonymized *M. corymbiae* under *Phaeothyriolum corymbiae* by treating the latter as the sexual morph of *M. corymbiae. Phaeothyriolum* presently accommodates seven species with *P. eucalyptinum* as the type and the genus was accepted under *Dothideomycetes* in genera *incertae sedis* (Wijayawardene et al. 2017a).

General description

Murramarangomycetales is characterized by having creeping hyphae that give rise to aggregated brown clusters of phialidic conidiogenous cells which form hyaline, smooth, aseptate conidia and the sexual morph is produced in thyriothecial ascomata.

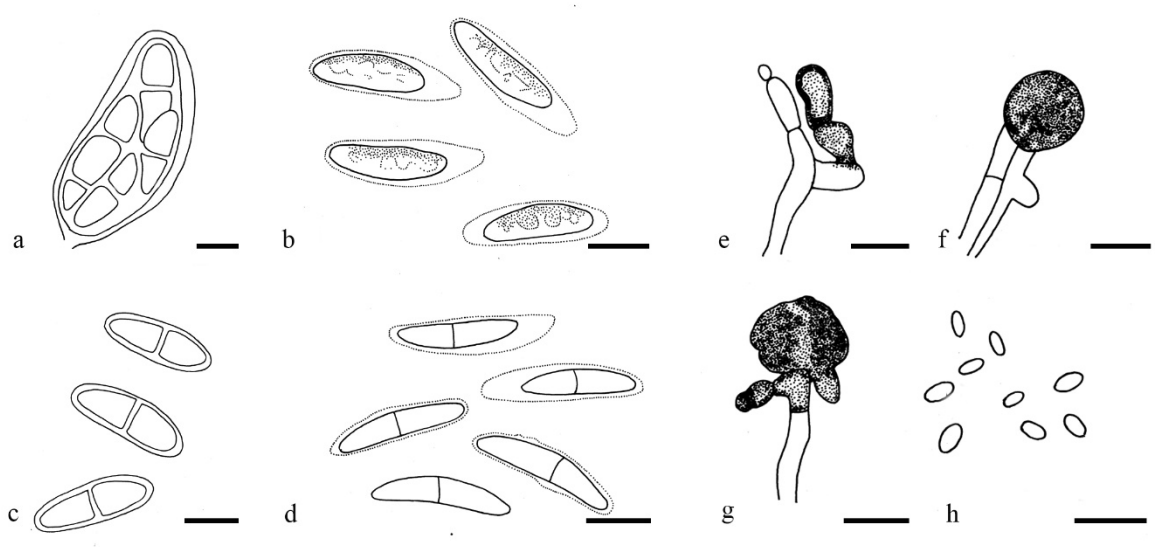


Figure 57 – Morphology of *Murramarangomycetales*. a Ascus (*Phaeothyriolum amygdalinum*). b–d Ascospores (b *P. eucalyptorum*, c *P. amygdalinum*, d *P. dunnii*). e Mycelium becoming fertile conidiogenous cells. f, g Conidigenous cell aggregated in caulifower-like form. h Conidia (e–h *P. corymbiae*) (drawn from Crous et al. 2019d, redrawn from Hongsanan et al. 2020a). Scale bars: = 10 μm.

Sexual morph: Leaf spots circular, indistinct, confined to one side of the leaf. *Mycelium* interepidermal, brown, septate, branched, giving leaf spots a red-purple appearance without any superficial mycelium being present, mycelium aggregating in substomatal cavity, giving rise to suprastomatal ascomata, either on living leaves, or on leaf litter. *Ascomata* thyriothecial, in radial orientation or clusters, circular, brown, superficial, flattened, with lobed, smooth to irregular margin of *textura epidermoidea* or *angularis*. *Asci* ellipsoid-obclavate, pedicellate, 8-spored, with small ocular chamber. *Pseudoparaphyses* hyaline, septate, anastomosing or not, hypha-like, dissolving at maturity, or persistent. *Ascospores* tri- to multiseriate, hyaline, 1-septate, guttulate, granular, slightly constricted at median septum or not, fusoid-ellipsoid to obovoid, encased in prominent mucoid sheath that is mostly absent at maturity, becoming brown (adapted from Crous et al. 2019d, Hongsanan et al. 2020a). Asexual morph: Leaf spots circular, hypophyllous, dark brown. *Mycelium* consisting of hyaline, smooth, hyphae, irregular, constricted at septa, forming brown, thick-walled cells that

become fertile conidiogenous cells, aggregated in cauliflower-like clusters of doliiform to globose, brown conidiogenous cells, phialidic, giving rise to solitary conidia. *Conidia* in slimy mass, aseptate, hyaline, smooth, and bacilliform (adapted from Crous et al. 2017a, Hongsanan et al. 2020a) (Fig. 57).

Families included in *Murramarangomycetales*

Murramarangomycetaceae Crous.

Evolution

Hongsanan et al. (2020a) estimated the divergence time for *Murramarangomycetales* as 151 MYA (stem age).

Justification of order and problems

The order presently accommodates a single genus *Phaeothyriolum*. *Murramarangomycetales* recovered as a sister clade to *Acrospermales* when the order was established. However, Crous et al. (2019d) indicated that four species of *Phaeothyriolum* clustered together within *Dothideomycetes*, but its placement was not assigned. The order formed a sister clade to *Natipusillales* in the phylogenetic analyses conducted by Hongsanan et al. (2020a). However, the inclusion of all *Phaeothyriolum* in the molecular analyses can provide a better understanding of the closely related orders in *Dothideomycetes*.

Significance

Ecological and economic roles

Species of this order are found in *Corymbia* plantations and *Corymbia* forests in eastern Australia, and have been reported to cause spots on living leaves (Crous et al. 2019d, Hongsanan et al. 2020).

Chemical diversity

No relevant studies are available for the chemical diversity of *Murramarangomycetales*.

***Muyocopronales* Mapook, Boonmee & K.D. Hyde, Phytotaxa 265(3): 230 (2016)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Mapook et al. (2016a) introduced the *Muyocopronales* to accommodate *Muyocopronaceae* that was introduced by Luttrell (1951a). *Muyocopronales* belongs to *Dothideomycetes incertae sedis* and comprises only one family *Muyocopronaceae* with ten genera that have over 80 species (Wijayawardene et al. 2022a, Hyde et al. 2024b). The type genus *Muyocopron* was introduced by Spegazzini (1881b) and the members of this taxa have superficial, solitary or scattered, coriaceous ascomata appearing as circular, scattered, flattened, brown to dark brown spots covering the host, without a subiculum, with a poorly developed basal layer and an irregular margin (Mapook et al. 2016a).

In phylogenetic analyses, members listed under *Muyocopronales* formed a distinct clade with another two orders namely; *Acrospermales* and *Dyfrolomycetales* which also share similar morphology (Mapook et al. 2016a, Hongsanan et al. 2020a, Pem et al. 2024). However, morphologically, *Muyocopronales* can be separate from those two orders by having superficial, flattened, carbonaceous, brittle ascomata, pseudoparaphyses that are longer than the asci, narrow cylindrical, long asci, and ellipsoidal to ovate, filiform, multi-septate, unicellular ascospores (Mapook et al. 2016a, Hongsanan et al. 2020a, Pem et al. 2024). *Dyfrolomycetales* also differ from *Acrospermales* and *Muyocopronales* by having immersed, coriaceous ascomata and uniseriate, broadly fusiform multi-septate ascospores (Mapook et al. 2016a, Hongsanan et al. 2020a). Members

of *Muyocopronales* are generally found as saprobes on the surface of dried twigs and rarely on leaves (Mapook et al. 2016a).

History

Luttrell (1951a) introduced *Muyocopronaceae* and listed under the order *Hemisphaeriales* based on having a pleospora-type of centrum as in the majority of *Microthyriaceae*, *Hemisphaeriaceae*, and *Polystomellaceae* (Eriksson 1981). Later, Lumbsch & Huhndorf (2007) synonymized the members of this family (*Muyocopron*) under *Microthyriaceae*. However, Hyde et al. (2013) formally described and accepted as a distinct family with a single genus under *Dothideomycetes* family *incertae sedis*. Hyde et al. (2013) also provided detailed descriptions with illustrations for the genus *Muyocopron*. Based on the morpho-molecular data, Mapook et al. (2016a) introduced *Muyocopronales* to accommodate *Muyocopronaceae*. Mapook et al. (2016b) also introduced *Palawaniaceae* (*Dothideomycetes* family, *incertae sedis*) and based on morphology, phylogeny and divergence time and suggested that this family should be listed under *Muyocopronales*. Hongsanan et al. (2020a) listed this family again under *Dothideomycetes* families *incertae sedis* until the sequence of type species is available. Therefore, currently, only one family is listed under *Muyocopronales* (Hongsanan et al. 2020a, Wijayawardene et al. 2022a)

Crous et al. (2018a) listed three known genera under *Muyocopronaceae* (*Muyocopronales*) *viz*. *Arxiella*, *Leptodiscella*, and *Paramycoleptodiscus* that were previously listed under *Dothideomycetes incertae sedis*, *Ascomycota incertae sedis* and *Acrospermales incertae sedis*. Furthermore, they introduced a new monotypic genus *Neocochlearomyces* under *Muyocopronaceae*. Consequently, four new genera (*Muyocopromyces*, *Neomycoleptodiscus*, *Pseudopalawania* and *Setoapiospora*) were introduced to this family (Hernãndez-Restrepo et al. 2019, Hyde et al. 2020b, Mapook et al. 2020b, Worobiec et al. 2020).

General description

Most of the genera in *Muyocopronaceae* (*Muyocopronales*) (*Arxiella*, *Leptodiscella*, *Muyocopromyces*, *Neocochlearomyces*, *Paramycoleptodiscus* and *Neomycoleptodiscus*) are only known in their asexual morphs (Crous et al. 2018a, Hernãndez-Restrepo et al. 2019, Hongsanan et al. 2020a, Worobiec et al. 2020) whereas some genera are only known in their sexual morphs (*Pseudopalawania* and *Setoapiospora*) (Mapook et al. 2020b, Hyde et al. 2020b). *Muyocopron* (type genus of *Muyocopronaceae*) was previously known from their sexual morphs when introducing the order (Mapook et al. 2016a). Later, Hernãndez-Restrepo et al. (2019) defined both sexual and asexual characters of *Muyocopron* and provided a comprehensive description to *Muyocopronales*.

Sexual morph: *Ascomata* pseudo-thyriothecial, superficial, coriaceous, and circular, flattened, brown to dark brown spots covering the host, without subiculum, with a poorly developed basal layer. *Ostiole* central and without setose or hairy appendages. *Peridium* consists of two layers, the outer layer is composed of black-brown pseudoparenchymatous cells of *textura epidermoidea*, and the inner layer is composed of pale brown cells of *textura angularis*. *Hamathecium* consists of pseudo paraphyses. *Asci* 8-spored, bitunicate, and cylindrical to pyriform and with or without an ocular chamber. *Ascospores* oval to obovoid with obtuse ends, aseptate, and hyaline. Asexual morph: Sporodochium-like conidiomata, if present. *Conidiophores* typically reduced to conidiogenous cells. *Conidiogenous cells* (*Arxiella*, *Leptodiscella*) solitary or aggregated, mono- or polyblastic, sympodial, and often denticulate, (*Mycoleptodiscus*, *Neocochlearomyces*, *Neomycoleptodiscus*, *Paramycoleptodiscus*) phialidic, globose to ampulliform. *Conidia* one-celled or septate, lunate, falcate, fusiform or fusoid-ellipsoid, curved to geniculate, generally with terminal and/or lateral appendages and mostly hyaline. *Appressoria* (if present) ellipsoid to oblong-oval or obovoid, narrowly clavate or subcylindrical, sometimes uncinate, occasionally sigmoid or bluntlybifurcate, straight or curved, brown. *Black sclerotia* frequently seen in culture (adapted from Hernãndez-Restrepo et al. 2019) (Figs. 58, 59, 60, 61).

Families included in *Muyocopronales*

Muyocopronaceae K.D. Hyde

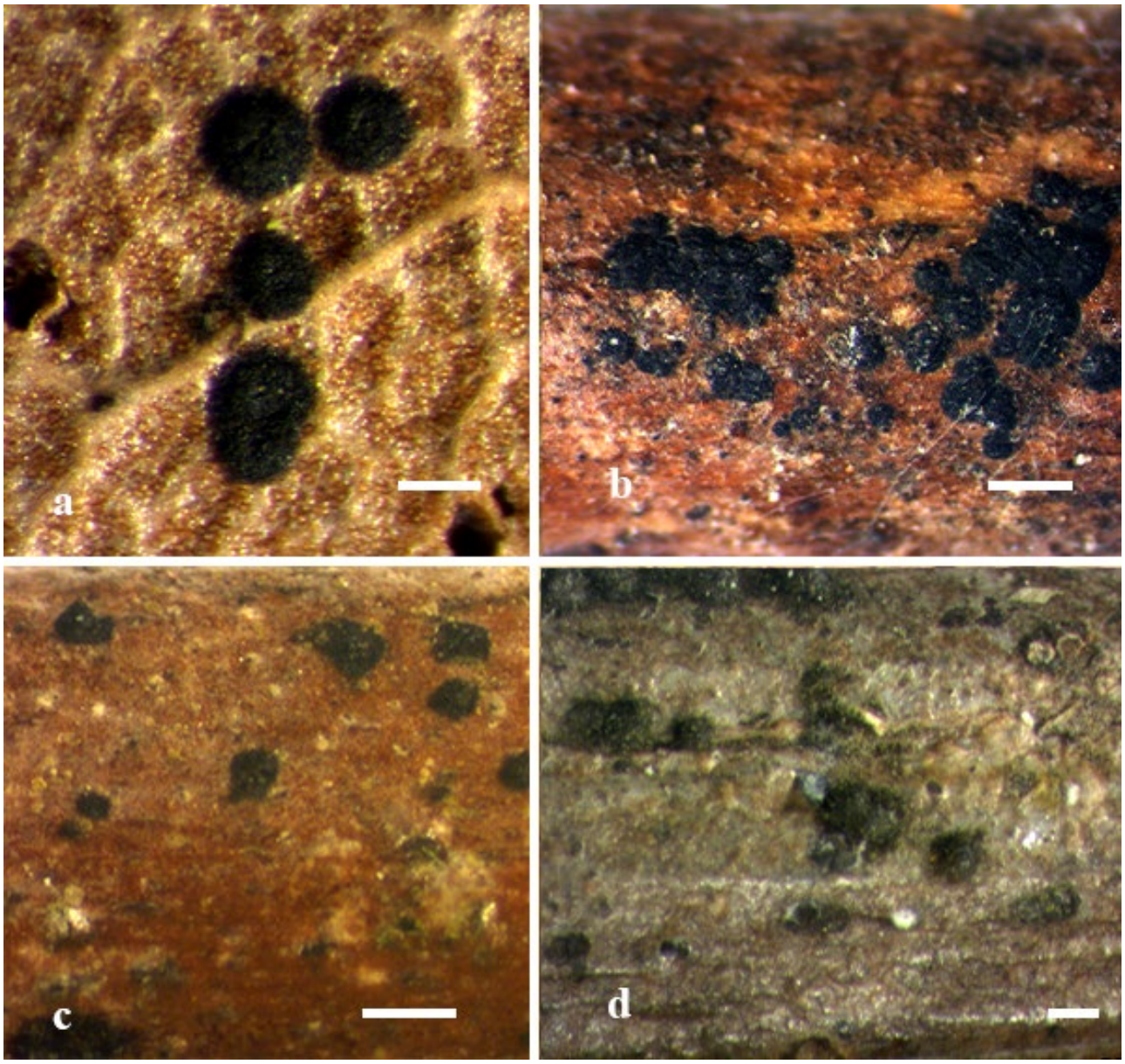


Figure 58 – Ascomata morphology of *Muyocopronales* on substrate. a *Muyocopron lithocarpi*. b *Muyocopron dipterocarpi*. c *Pseudopalawania siamensis*. d *Setoapiospora thailandica*. Scale bars: a = 200 μm, b, c, d = 500 μm.

Evolution

With the help of fossil evidence from Ascomycetes, several estimations of the divergence periods in fungi have been published (Hongsanan et al. 2016b, Pérez Ortega et al. 2016). According to Visscher et al. (1996) and Shen et al. (2011), the Permian-Triassic extinction event (252 MYA) was linked to the ancient fungal spore record. The number of marine and terrestrial fungi is considered to have evolved during this time. However, more than 95% of land plants disappeared in this period (Labandiera & Sepkoski 1993, Eshet et al. 1995, Mapook et al. 2016b). Furthermore, Benton (1988) and Ryder et al. (1996) report that 34% of marine genera disappeared, along with numerous amphibians and land vertebrates, after the Triassic-Jurassic extinction (201.3 MYA). According to the results of the molecular clock and divergence time estimates of Mapook et al. (2016b), the maximum clade credibility (MCC) tree indicates the divergence estimates at 319 MYA (247−400), in the Carboniferous for *Dothideomycetes* and *Lecanomycetes*. The estimated crown dates of *Muyocopronales* during the Cenozoic at 52 MYA (38−66) and the split between *Muyocopronales* and *Palawaniaceae* is estimated at 172 MYA (130−218), during the Jurassic (Mapook et al. 2016b).



Figure 59 – Ascomata morphology of *Muyocopronales*. a *Muyocopron dipterocarpi*. b *Muyocopron lithocarpi*. c, d *Setoapiospora thailandica*. e *Pseudopalawania siamensis*. f *Muyocopron dipterocarpi*. Scale bars: a–e = 100 μm, f = 50 μm.

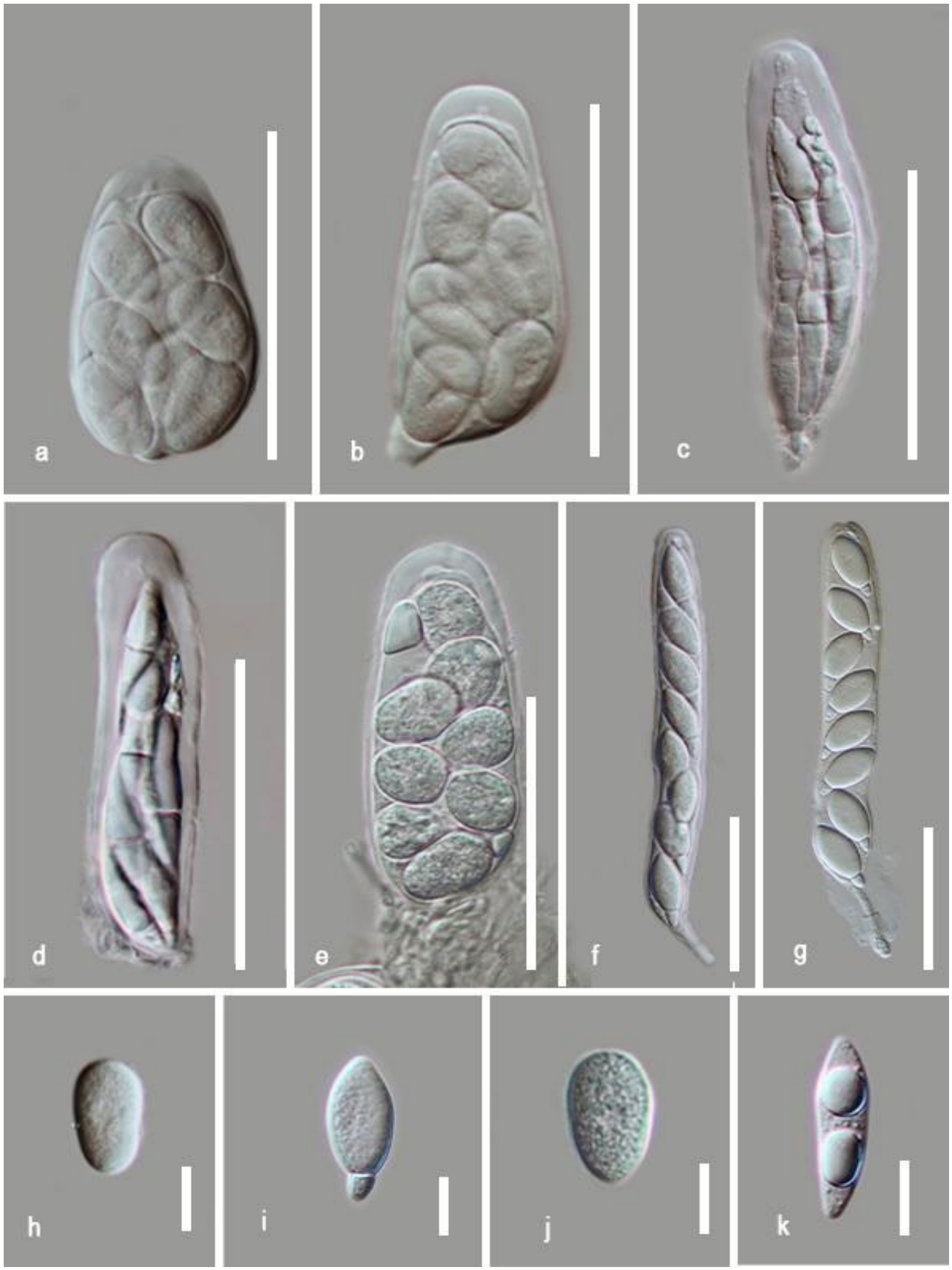


Figure 60 – Asci and ascospores morphology of *Muyocopronales*. a, b *Muyocopron lithocarpi*. c,d *Pseudopalawania siamensis*. e *Muyocopron dipterocarpi*. f, g *Setoapiospora thailandica*. h *Muyocopron lithocarpi*. i *Setoapiospora thailandica*. j *Muyocopron dipterocarpi*. k *Pseudopalawania siamensis*. Scale bars: a–g = 50 μm, h–k = 10 μm.

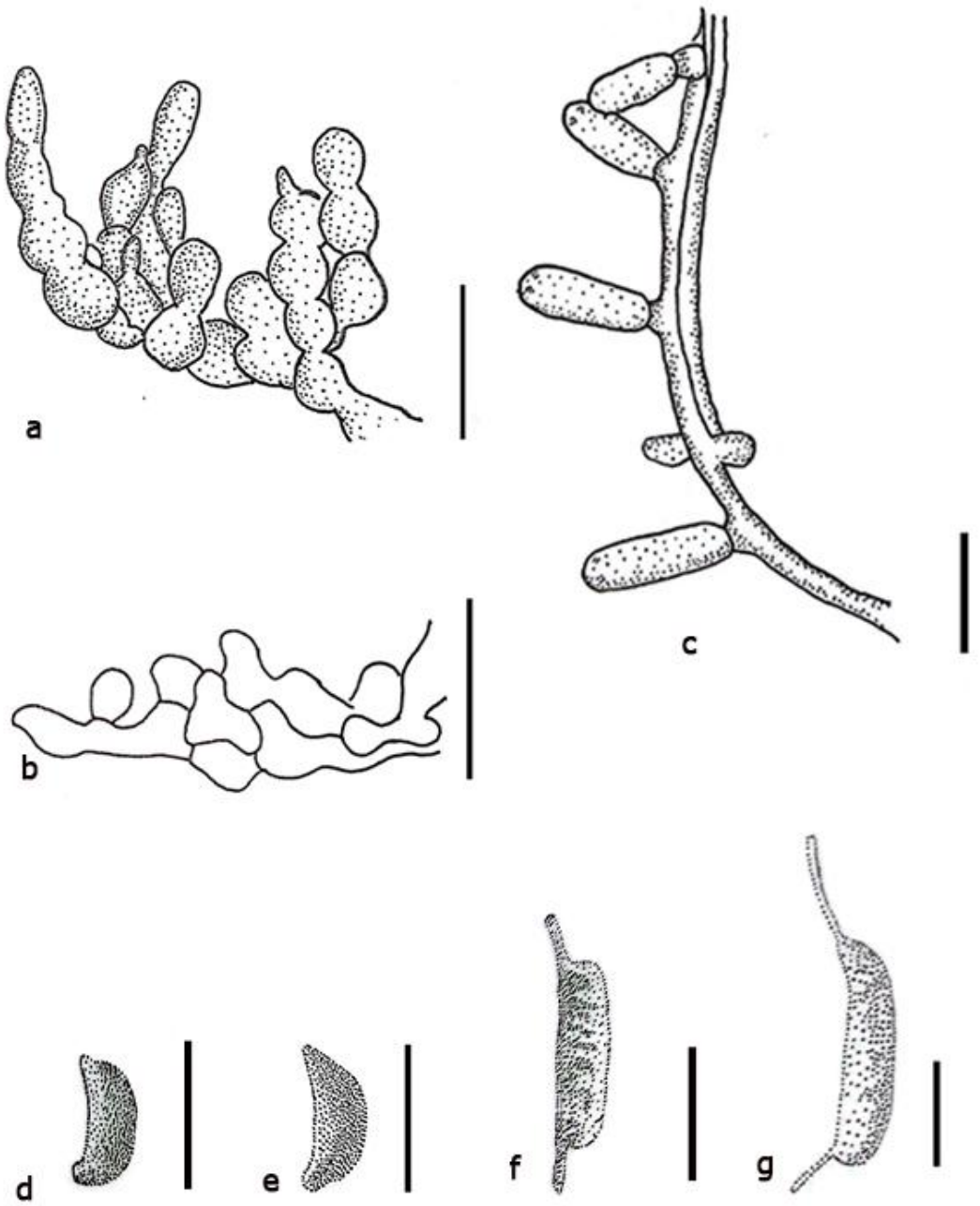


Figure 61 – Conidiomata, Conidiogenous cell and conidia morphology of *Muyocopronales*. a *Arxiella dolichandrae*. b, c *Leptodiscella rintelii*. d, e *Arxiella dolichandrae*. f *Leptodiscella rintelii*. g *Neomycoleptodiscus venezuelense* (redrawn from Crous et al. 2014b, Crous et al. 2018a, Hernández-Restrepo et al. 2019). Scale bars: a–g = 10 μm.

Furthermore, the estimated crown date for *Pleurotremataceae* is 55 MYA (38–74) in the early Cenozoic, and the family shares a common ancestor with *Palawaniaceae* and *Muyocopronales* at 192 MYA (145–243) in the early Jurassic. Additionally, Mapook et al. (2016b) show the family *Acrospermales* has an estimated crown date in the Cretaceous of 124 MYA (90−160) and it shares the most common ancestor with *Pleurotremataceae*, *Palawaniaceae*, and *Muyocopronales* at 215 MYA (164−272) in the late Triassic.

Significance

Ecological and economic roles

Most of the members of this order have been reported as saprobes on dried twigs and are less common on leaves, and thus are involved in the decomposition of organic matter and nutrient

recycling (Hongsanan et al. 2020a). Some species are reported as pathogenic on plants and opportunistic pathogens on animals, lignicolous, foliicolous, and soil-borne (Hernández-Restrepo et al. 2019). *Muyocopromyces* was introduced as a fossil genus to accommodate *M. quilonensis* which was previously placed in *Callimothallus*. *Callimothallus quilonensis* was previously reported as *Microthyriaceous germlings* and *Phragmothyrites eocaenica* in different places of India. *Phragmothyrites eocaenica* was used for the formation of some sindhu drugs (Worobiec et al. 2020).

Chemical diversity

Pseudopalawania siamensis (*Pseudopalawania*, *Muyocopronaceae*, *Muyocopronales*) contains some metabolic compounds that can act as antimicrobial agents for some microbes, and some metabolic compounds shows moderate cytotoxic effects on HeLa and mouse fibroblast cell lines, which makes them less attractive as candidates for development of selectively acting antibiotics (Mapook et al. 2020b). The study of bioactive compounds and chemical profiling for members of *Muyocopronales* is very few, and further studies are needed to identify the chemical diversity of *Muyocopronales*.

Mycosphaerellales **P.F. Cannon, Ainsworth & Bisby's Dictionary of the Fungi, Edn 9 (Wallingford): 343 (2001)**

Based on *Pseudosphaeriales* subord. *Mycosphaerellineae* Nannf. *Nova Acta R. Soc. Sci. upsal.* ser. 4, 8(2): 38 (1932), on *Mycosphaerellaceae* Lindau, in Engler & Prantl, *Nat. Pflanzenfam.* Teil. I (Leipzig) 1(1): 421 (1897), on *Mycosphaerella* Johanson, *Öfvers. K. Svensk. Vetensk.-Akad. Förhandl.* 41(no. 9): 163 (1884) [1884–1885] = *Ramularia* Unger, *Exanth. Pflanzen* (Wien): 119 (1833)

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Dothideomycetidae*

Introduction

Mycosphaerellales is a large order in *Ascomycota* comprising thousands of species. The order was introduced by Kirk et al. (2001), though later again placed under *Capnodiales* (Kirk et al. 2008a) due to a lack of molecular data to clearly separate the two orders. Ecologically, however, they are quite distinct, with *Capnodiales* representing families of sooty moulds, while *Mycosphaerellales* predominantly represents saprobes and plant pathogens. Abdollahzadeh et al. (2020) recently revalidated *Mycosphaerellales* as a separate order based on LSU, TEF1-α and RPB2 sequence data, accommodating eight families formerly treated in *Capnodiales*: *Cystocoleaceae*, *Dissoconiaceae*, *Extremaceae*, *Mycosphaerellaceae*, *Neodevriesiaceae*, *Phaeothecoidiellaceae*, *Schizothyriaceae* and *Teratosphaeriaceae*. Members of *Mycosphaerellales* have a cosmopolitan distribution. They predominantly occur in terrestrial habitats and have diverse lifestyles such as epiphytes, ectophytes, endophytes, saprobes, plant and animal pathogens, mycoparasites, lichenized and rock-inhabiting fungi (Schoch et al. 2009a, Schoch & Grube 2015, Ametrano et al. 2019a). They include numerous important plant pathogens and quarantine organisms, with a huge impact on agriculture, horticulture and forestry (Crous 2009).

History

Capnodiales was established for three families of sooty moulds, namely *Antennulariaceae*, *Capnodiaceae* and *Coccodiniaceae* (Woronichin 1925). Hawksworth et al. (1995) treated *Mycosphaerellaceae* as a family in *Dothideales*, while Kirk et al. (2001) introduced a separate order *Mycosphaerellales* for this family, but later again placed it under *Capnodiales* (Kirk et al. 2008a). Schoch et al. (2006) transferred *Mycosphaerellaceae* and *Piedraiaceae* to the *Capnodiales* and resurrected the *Cladosporiaceae*, making the *Capnodiales* the second-largest order of *Dothideomycetes*. Although there were ample data available for the plant pathogenic families placed in *Mycosphaerellales* (formerly treated as *Capnodiales*), this was not the case for the sooty mould

genera (*Capnodiales sensu stricto*). Abdollahzadeh et al. (2020) revalidated *Mycosphaerellales* as a separate order based on LSU, TEF1-α and RPB2 sequence data, and included eight families formerly treated in *Capnodiales*: *Cystocoleaceae*, *Dissoconiaceae*, *Extremaceae*, *Mycosphaerellaceae*, *Neodevriesiaceae*, *Phaeothecoidiellaceae*, *Schizothyriaceae* and *Teratosphaeriaceae*. In a later study, Crous et al. (2022a) also added *Phillipsiellaceae* to *Mycosphaerellales*.

Mycosphaerellales is based on the family *Mycosphaerellaceae*, which was introduced in Engler & Prantl (1897) with *Mycosphaerella* as generic type. The family initially included 14 genera based on morphological characteristics: *Achorodothis*, *Brunneosphaerella*, *Cymadothea*, *Euryachora*, *Gillotia*, *Melanodothis*, *Mycosphaerella*, *Placocrea*, *Polysporella*, *Pseudostigmidium*, *Sphaerellothecium*, *Sphaerulina*, *Stigmidium* and *Wernerella* (Lumbsch & Huhndorf 2010).

Mycosphaerellaceae is recognized by having characteristic brown to black pseudothecial ascomata that can be immersed or superficial, embedded in host tissue or erumpent, having ostiolar periphyses, but lacking interascal tissue at maturity. Ascospores are hyaline, but in some cases slightly pigmented at maturity (Barr 1987b), mostly lack a mucilaginous sheath (Crous 1998), and are predominantly 1-septate, although some taxa with 3-septate ascospores have been recorded (Crous et al. 2003). With the advent of molecular tools, *Mycosphaerellaceae* was shown to be polyphyletic (Crous et al. 2007a, 2009a, e), and split into several families, namely *Schizothyriaceae* (Batzer et al. 2008), *Cladosporiaceae* (Schubert et al. 2007, Dugan et al. 2008, Bensch et al. 2012, 2015), *Dissoconiaceae* and *Teratosphaeriaceae* (Crous et al. 2009b, Li et al. 2012, Quaedvlieg et al. 2014, Crous et al. 2022a). Hyde et al. (2013) re-circumscribed the genera in *Mycosphaerellaceae* and accepted 46 genera in this family. Subsequent authors have included many genera in *Mycosphaerellaceae* based on molecular data along with morphological characteristics of their asexual morphs (Quaedvlieg et al. 2014, Bakhshi et al. 2015, Crous et al. 2016a, 2017a, 2019a, Guatimosim et al. 2016, Videira et al. 2016, 2017, Hyde et al. 2017, Thambugala et al. 2017b, Hassan & Chang 2019, Crous et al. 2022a). Videira et al. (2017) revised the *Mycosphaerellaceae*, revealing many well-known genera to be paraphyletic, with several synapomorphic characters having evolved more than once within the family. As a consequence, several old generic names including *Cercosporidium*, *Fulvia*, *Mycovellosiella*, *Phaeoramularia* and *Raghnildiana* were resurrected, and 32 additional new genera were described. Videira et al. (2017) accepted 120 genera based on phylogenetic data in the family, but many accepted cercosporoid genera remain unresolved pending fresh collections and DNA sequence data. Hongsanan et al. (2020a) recognised 112 genera in *Mycosphaerellaceae* based on molecular data, and regarded 107 genera as doubtful pending further studies.

General description

Sexual morph: *Ascomata* pseudothecial, small, immersed in plant tissue, becoming erumpent, solitary to aggregated with weakly developed basal stroma, black papillate, with lysigenous, periphysate ostiole; peridium usually of thin-walled, pseudoparenchymatous cells. *Hamathecial* tissue dissolving at maturity. *Asci* ovoid to broadly ellipsoid, fissitunicate, with ocular chamber, not bluing in Melzer. *Ascospores* hyaline, transversely septate, sheath mostly lacking. Asexual morph: hyphomycetous or coelomycetous. *Hyphomycetous morphs* frequently with subcylindrical to obclavate, pigmented to hyaline conidia, on pigmented to hyaline fasciculate conidiophores arising from basal stroma, with or without conspicuous scars. *Conidia* pigmented to hyaline, 0–multi-septate, usually euseptate, in a few genera distoseptate, solitary or in fragmenting chains. *Coelomyceous morphs* pycnidial, with hyaline to pigmented conidiogenous cells that proliferate percurrently or sympodially. *Conidia* pigmented to hyaline, 0–multi-septate. *Synasexual morphs* common in several genera (Figs. 62, 63).

Families included in *Mycosphaerellales*

Aeminiaceae J. Trovão, I. Tiago & A. Portugal
Cystocoleaceae Locq. ex Lücking, B.P. Hodk. & S.D. Leav.
Dissoconiaceae Crous & de Hoog

Extremaceae Quaedvl. & Crous
Mycosphaerellaceae Lindau
Neodevriesiaceae Quaedvl. & Crous
Phaeothecoidiellaceae K.D. Hyde & Hongsanan (= *Nowamycetaceae* Crous)
Phillipsiellaceae Höhn.
Schizothyriaceae Höhn. ex Trotter, Sacc. D. Sacc. & Traverso
Teratosphaeriaceae Crous & U. Braun
Xenodevriesiaceae Crous

Mycosphaerellales genera *incertae sedis*
Brunneomycosphaerella Dissan., Jian K. Liu & K.D. Hyde
Mucomycosphaerella Quaedvl. & Crous
Neohortaea Quaedvl. & Crous
Ramopenidiella Crous & R.G. Shivas

Evolution

Studying whole-genome data of 101 *Dothideomycetes* genomes, Haridas et al. (2020) concluded that the ancestral ecological character state of *Dothideomycetes* is saprobic, and that plant pathogenicity evolved six to eight times within *Dothideomycetes*, corroborating the findings of Schoch et al. (2009a), who demonstrated numerous transitions from saprobic life histories to plant pathogens and lichens and multiple transitions from terrestrial to aquatic habitats. By employing ancestral reconstruction analysis, Abdollahzadeh et al. (2020) revealed that saprobic lifestyle is a primitive state within *Capnodiales sensu lato* and several transitions have occurred to evolve lichenised, plant and human parasitic, ectophytic (sooty blotch and flyspeck) and more recently epiphytic (*Capnodiales sensu stricto*) lifestyles. Within *Mycosphaerellales*, the *Mycosphaerella* sexual morph (Aptroot 2006) has radiated throughout the *Mycosphaerellaceae*, where it is linked to various hyphomycete and coelomycete asexual genera (Videira et al. 2017).

Justification of order and problems

The monophyly of *Mycosphaerellales* is well-supported as distinct from *Capnodiales* (Abdollahzadeh et al. 2020). However, other than *Capnodiaceae*, *Neoantennariellaceae* and *Readerielliopsidaceae*, several other families of *Capnodiales* (*e.g., Aeminiaceae*, *Antennulariellaceae*, *Euantennariaceae*, *Johansoniaceae* and *Metacapnodiaceae)* are not known from DNA sequence data, and thus the monophyly of these families awaits verification.

Significance

Ecological and economic roles

There are various important plant pathogens in temperate and tropical regions of food and fibre crops, as well as ornamentals, some of quarantine importance. Also significant in food spoilage, as postharvest pathogens, and in the indoor environment. Members of *Mycosphaerellales* include taxa that are biotrophic, necrotrophic or saprobic, frequently endophytic, occurring on various plant tissues, but also in rocks or soil (Crous et al. 2009b). Genera in *Mycosphaerellaceae* and *Teratosphaeriaceae* are especially well-known as plant pathogens, of which the far majority tend to have narrow host ranges (Crous et al. 2009b, Videira et al. 2017). In most of these cases, these plant pathogens can also be isolated as latent pathogens (or endophytes) from apparently healthy tissue. The trigger mechanism that induces one lifestyle over the other is poorly understood, though some of the weakly aggressive pathogens are chiefly found sporulating on senescent host tissues. Furthermore, chance isolations from non-hosts have been ascribed to the pogo-stick hypothesis (Crous & Groenewald 2005), where a specific pathogen can infect and sporulate on older lesions as a secondary coloniser, in search of its ideal host. In this manner, it has been observed that up to six or more different species could colonise the lesion of a well-known primary pathogen (Crous 1998), enabling them to sporulate and disperse onwards, in search of their ideal hosts.

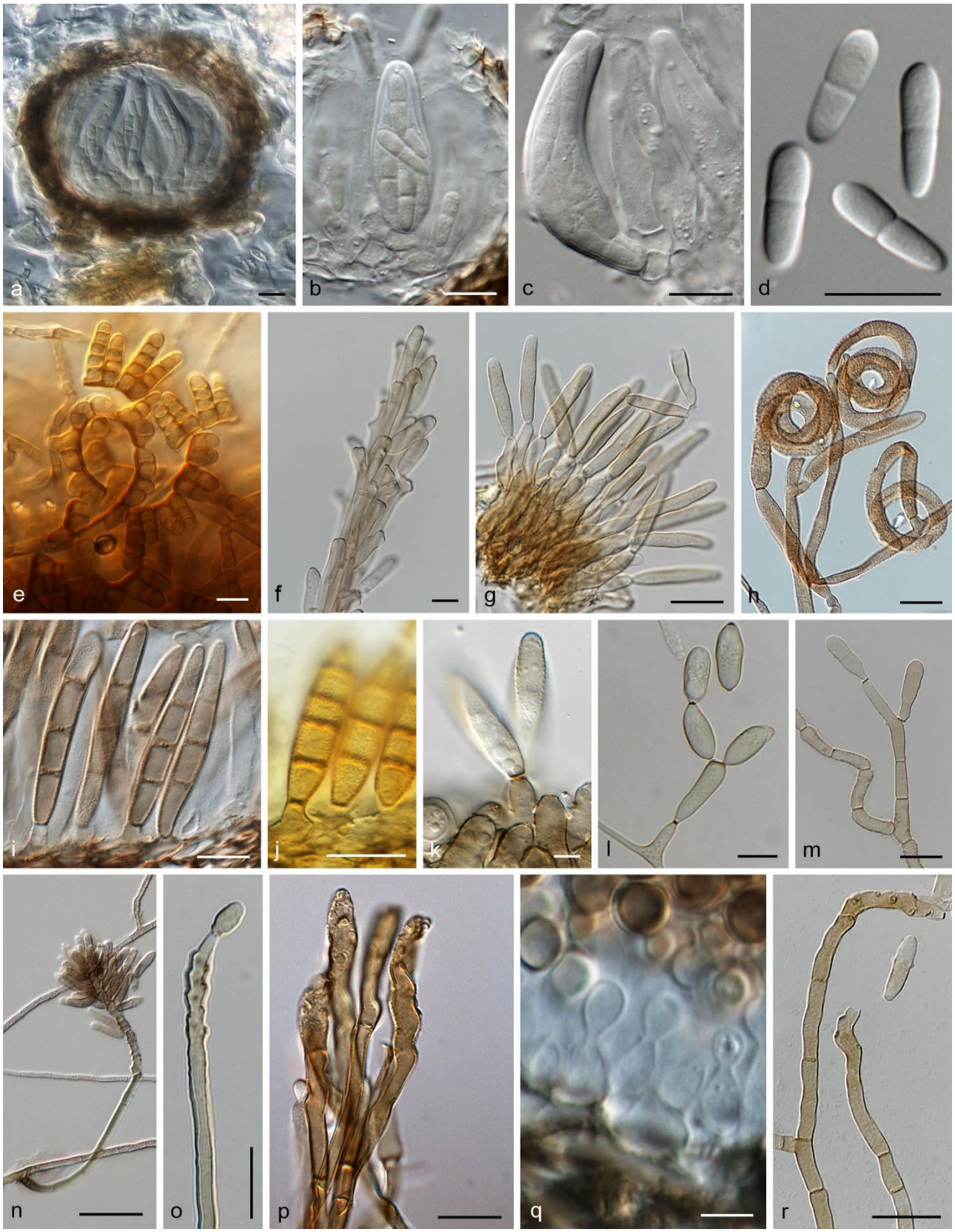


Figure 62 – Morphology of *Mycosphaerellales.* a–d *Pallidocercospora crystallina*. a Transverse section though ascoma. b, c Asci. d Ascospores. e Conidia of *Nothotrimmatostroma bifarium*. f Synnema of *Mycovellosiella cajani*. g–r Conidiogenous cells and conidia. g *Cercosporidium chaetomium*. h *Laocoon paradoxus*. i *Sonderhenia eucalyptorum*. j *Sonderhenia radiata*. k *Camptomeris leucaenae*. l *Fulvia fulva*. m *Phaeoramularia gomphrenicola*. n *Zasmidium elaeocarpi*.

o *Zasmidium elaeocarpi*. p *Passalora bacilligera*. q *Readeriella pseudocallista*. r *Cercosporidium chaetomium*. Scale bars = 10 µm.



Figure 63 – Conidial morphology of *Mycosphaerellales*. a *Distocercospora dioscoreae*. b *Mycovellosiella cajani*. c *Passalora bacilligera*. d *Sonderhenia eucalypticola*. e *Sonderhenia*

eucalyptorum. f *Suberoteratosphaeria pseudosuberosa*. g *Sonderhenia radiata*. h *Readeriella pseudocallista*. i, j *Readeriella eucalyptigena*. k Conidia of *Cibiessia* synasexual morph. l, m Nothostrasseria synasexual morph of *R. dendritica*. n, o *Readeriella eucalypti*. p, q *Readeriella menaiensis*. r *Readeriella callista*. s *Readeriella patrickii*. Scale bars = 10 µm.

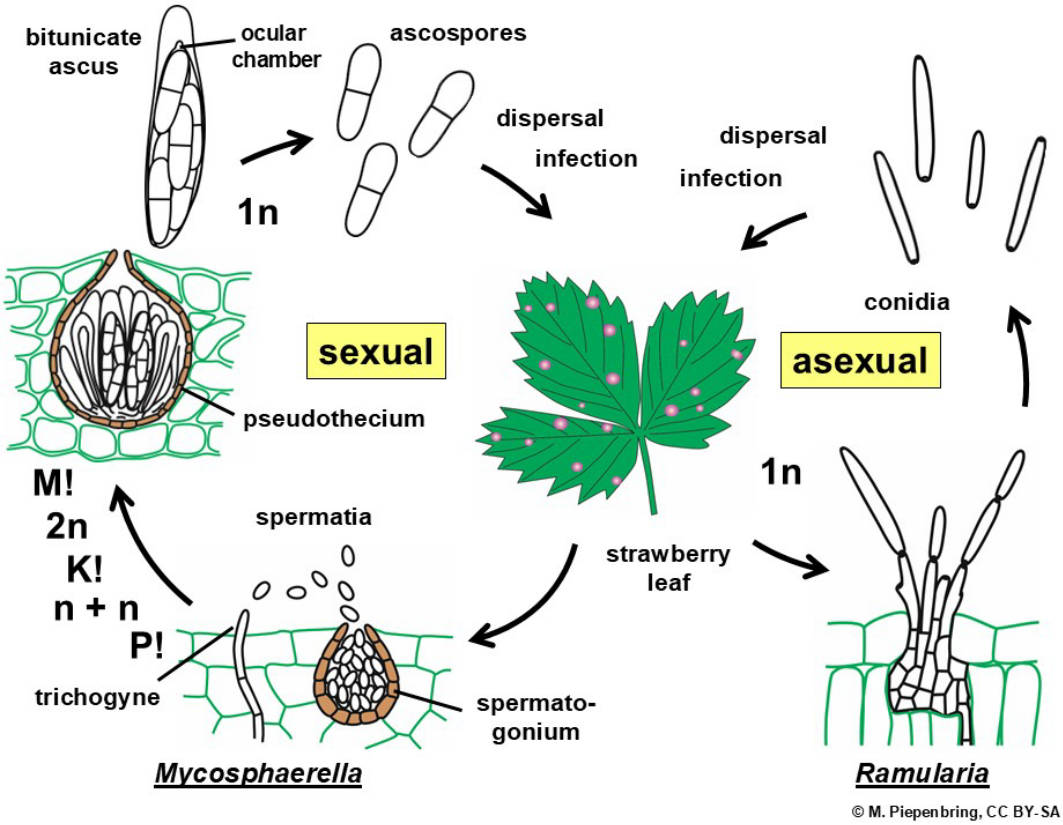


Figure 64 – Sexual and asexual life cycles of *Mycosphaerellales* (From Mycological teaching diagrams by Meike Piepenbring (2023)). Abbreviations: 1n = haploid, 2n = diploid, P! = plasmogamy, K! = karyogamy, M! = meiosis. Black and white circles represent haploid nuclei of different mating types, circles of both colors represent diploid nuclei.

Several plant pathogens are associated with diseases of major economic importance on a wide range of crops (Quaedvlieg et al. 2013, 2014, Videira et al. 2017, and see Supplementary Table in Crous et al. 2021e). For Europe, see e.g., https://www.eppo.int/index, but note that several of the names used are listed under the incorrect "*Mycosphaerella*" morph, or under one of the synonyms.

Other relevant data and future recommendations

Nearly all plant hosts are associated with one or several species of *Mycosphaerellales*, the majority of which will not be known from culture of DNA phylogeny. Because taxa in the order are notorious for producing different morphs once cultivated, cultures should always be established from a single ascospore or conidial propagules. Unfortunately, many taxa will remain sterile in culture, hence, colonised host material is essential to facilitate morphological description. Furthermore, for some genera, especially in the *Mycosphaerellaceae*, the conidial morphology is frequently atypical in culture, rendering host material preferable for species description and morphological comparisons. When slow-growing in culture, rich media such as oatmeal agar or V8 agar are recommended, while sporulation is also preferable on rich media, or on a poor medium such as synthetic nutrient-poor agar (Crous et al. 2019c). Cultures easily lose their ability to sporulate, and plant pathologists interested in pathogenicity trials should ensure that they have a large -80 °C stock collection, as sub-culturing leads to loss of sporulation and virulence. Lastly, disease symptoms and general

morphology can be misleading, and European and American names most often do not apply to the same disease symptoms and taxa occurring in Africa, Asia or Latin America (Crous et al. 2013a).

Myriangiales **Starbäck, Bihang til Kongliga Svenska Vetenskaps-Akademiens Handlingar. 25(1):1-68**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Dothideomycetidae*

Introduction

Myriangiales was introduced by Starbäck (1899), centered on species that possess crustose ascostromata and muriform ascospores in *Dothideomycetes* (Hyde et al. 2013). These species appear as saprobes, pathogens or epiphytes on leaves and branches, bark of plants (Dissanayake et al. 2014, Jayawardena et al. 2014), while some are rock-inhabiting (Ruibal et al. 2009). Presently, *Myriangiales* comprises with two families: *Elsinoaceae* and *Myriangiaceae*. *Elsinoaceae* is a family of plant pathogens that cause anthracnose and scab. Many traditional revisions have placed *Elsinoaceae* in synonymy with *Myriangiaceae*. However, Höhnel (1909) was persuaded that the previous represented a distinct family. Eriksson (1981) approved and continued two different families with *Myriangiaceae* mainly saprobic on branches and *Elsinoaceae* limited to foliar pathogens. In *Elsinoaceae*, the pseudoascostromata produce whitish, crust-like spots on leaves with a small number of asci in each locule. Asci are globose and mostly 4–5 asci are embedded in one locule. Species of *Schizothyriaceae* Höhn. have similar characters in the shape of the asci to those in *Myriangiaceae* but vary as asci form in a single hymenial layer and not in locules dispersed in an ascostromata or pseudostromata (Hyde et al. 2013).

Myriangiaceae is a family of saprobes, but with particular genera being parasitic and epiphytic on leaves. The family was introduced by Nylander (1854) and comprised two species, *Myriangium duriaei* Mont. and Berk. and *M. curtisii* Berk. and Mont. Millardet (1870) assigned the family near the *Tuberaceae*. Numerous traditional revisions have placed *Elsinoaceae* in synonymy with *Myriangiaceae*, but Höhnel (1909) was influenced that the previous comprised a distinct family.

History

Starbäck (1899) introduced the order *Myriangiales* whereas *Myriangium duriaei* was proposed as the type species (Miller 1938). Phylogenetic studies centered on multigene analysis have designated that *Myriangiales* constantly clusters with *Dothideomycetes* (Schoch et al. 2009b, Zhang et al. 2011a). Kirk et al. (2008a) integrated three families, *Cookellaceae*, *Elsinoaceae* and *Myriangiaceae* in *Myriangiales*, whereas Lumbsch & Huhndorf (2010) established only *Elsinoaceae* and *Myriangiaceae* in the order centered on phylogenetic results, whereas *Cookellaceae* was treated as *Dothideomycetes incertae sedis*. This classification was followed in subsequent studies (Hyde et al. 2013, Dissanayake et al. 2014, Jayawardena et al. 2014, Wijayawardene et al. 2014a, Dai et al. 2017, Wijayawardene et al. 2017a, 2018, 2020, Hongsanan et al. 2020b, Jiang et al. 2020a).

The order *Myriangiales* has two families, *Elsinoaceae* and *Myriangiaceae*, that contain two and 11 genera, correspondingly (Dissanayake et al. 2014, Jayawardena et al. 2014, Dai et al. 2017). The latest revision of *Myriangiaceae* by Dissanayake et al. (2014) added six genera to the family based on morphological characteristics (*Ascostratum*, *Butleria*, *Dictyocyclus*, *Hemimyriangium*, *Micularia*, and *Zukaliopsis*). Molecular data from genera in *Myriangiaceae* are emerging, and only two *Myriangium* species, *M. duriaei* (CBS 260.36) and *M. hispanicum* (CBS 247.33), currently have SSU, LSU, RPB2, and TEF1-α sequences accessible (Jayawardena et al. 2014). The similar condition seemed to be the case in the *Elsinoaceae*, which was reevaluated by Jayawardena et al. (2014) who expelled eight genera (*Beelia*, *Butleria*, *Hemimyriangium*, *Hyalotheles*, *Micularia*, *Saccardinula*, *Stephanotheca* and *Xenodium*) and encompassed only *Elsinoe* and *Molleriella* in this family. Prior to the study by Fan et al. (2017), the accessible molecular dataset for *Elsinoe* (asexual morph *Sphaceloma*) shown to be relatively sparse (Swart et al. 2001, Summerell et al. 2006, Crous et al.

2015d, 2016a). Fan et al. (2017) revised the taxonomy of *Elsinoe* based on morphological data and combined analyses of ITS, LSU, RPB2 and TEF1-α DNA sequence data which were used to reconstruct the backbone phylogeny of the genus *Elsinoe*. Fan et al. (2017) introduced eight new species leading to a total of 75 *Elsinoe* species sustained by molecular data. Diverse authors have considered the association between *Elsinoaceae* and *Myriangiaceae*, but based on morphological structures and phylogenetic analyses, the two families were established as dissimilar within the order *Myriangiales* (Schoch et al. 2006, 2009b, Lumbsch & Huhndorf 2007, 2010, Boehm et al. 2009b, Hyde et al. 2013, Jayawardena et al. 2014, Fan et al. 2017).

General description

The order is considered by pulvinate, asymmetrical ascostromata in which the asci are occasionally organized in one or more layers in locules. Locules have single or multiple asci inside each locule. Asci are globose, with minute pedicels and indistinct ocular chambers. Ascospores which are irregularly organized are liberated only by the breakup of the stromatal layers over them. Asexual states are coelomycetous. They are acervular coelomycetous fungi with polyphialidic conidiogenous cells, such as the *Sphaceloma* asexual morph of *Elsinoe*.

Sexual morph: *Ascostromata* superficial, scattered, solitary or aggregated, coriaceous to sub-carbonaceous, semi-immersed or immersed to erumpent, generally dark, globose to oval, sometimes surrounded by the remains of the ruptured epidermis, multi- loculate, locules generally in the upper layer or scattered throughout the ascostromata. *Loculues* with single ascus, ostiolate. *Ostiole* minute or asci pushed out through pseudoparenchymatous cells. *Paraphyses* absent. *Cells of ascostromata* comprising pseudo-parenchymatous cells of pale yellow to brown pigmented *textura angularis*, *textura globulosa* or *textura intricata*. *Asci* 8-spored, bitunicate, fissitunicate, globose to subglobose, apedicellate or with a minute pedicel, apically rounded with indistinct ocular chamber. *Ascospores* hyaline to subhyaline or brown, oblong, or fusiform with slightly acute ends, with 1–9-transverse septa, with 0–5-longitudinal septa, muriform, smooth-walled to verruculose, rarely having a sheath. Asexual morph: coelomycetous "Sphaceloma". *Lesions* circular, dark brown raised margin, cream-brown. *Acervuli* subepidermal, pseudoparenchymatous. *Conidiophores* hyaline to pale-brown, polyphialidic. *Conidiogenous cells* formed directly from the upper cells of the pseudoparenchyma, monophialidic to polyphidalic, integrated or discrete, determinate, hyaline to pale brown, lacking a thickened region around the phialide channel. *Conidia* hyaline, unicellular, ellipsoidal, aseptate, biguttulate (adapted from Dissanayake et al. 2014) (Fig. 65).

Families included in *Myriangiales*

Elsinoaceae Höhn. ex Sacc. & Trotter
Myriangiaceae Nyl.

Myriangiales genus *incertae* sedis
Dictyonella Höhn.

Evolution

Further studies are needed to assess the evolutionary relationship of *Myriangiales*.

Justification of order and problems

The family *Myriangiaceae* is comparatively less well collected and studied among *Dothideomycetes* and comprises genera which are saprobic, epiphytic and parasitic on the bark, leaves and branches of numerous plants. Due to absence of molecular data for most of the species exist in this family, upcoming studies are greatly needed in reassessing this family.

Significance

Ecological and economic roles

Most of the species of *Myriangiales* are phytopathogens. Several are causing scab and spot anthracnose on numerous plants, comprising some economically significant crops such as avocado,

citrus, grapevines, and ornamentals such as poinsettias, field crops and woody hosts. Disease symptoms are frequently simply detectable, and stated to as signature- bearing infections, for the cork-like appearance of older diseased tissues with scab-like presence.

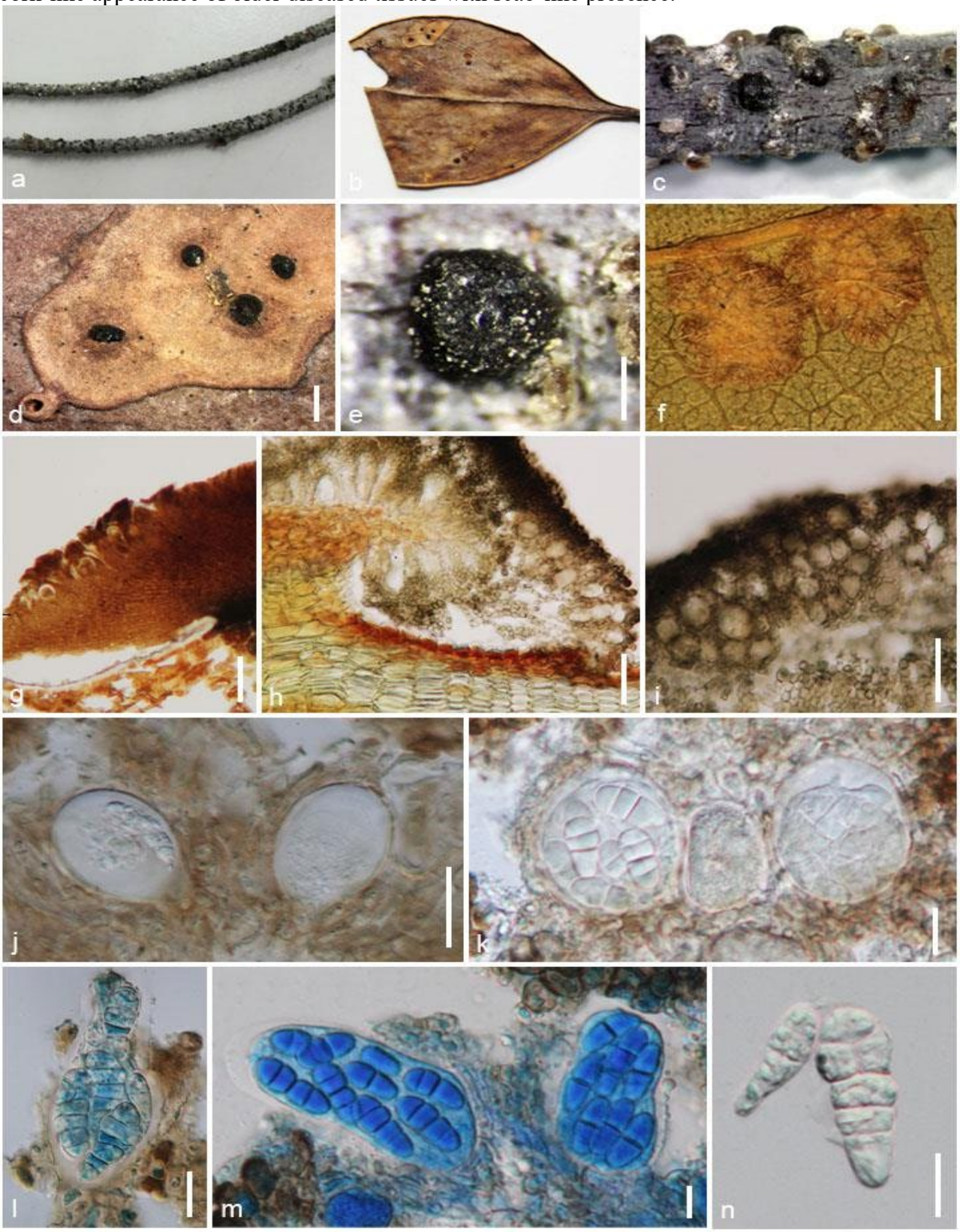


Figure 65 – Sexual morph of *Myriangiales* a–f Ascostromata on host substrate. g–i Cross section of ascostroma. j Immature asci. k Immature and mature asci. l, m Mature asci stained with cotton blue. n Ascospores. Scale bars: d–f = 200 µm, g–i = 50 µm, j–n = 10 µm.

In some *Elsinoe*-host associations, the subsequent symptoms are well defined as spot anthracnose. Furthermore, the diseased plants may also demonstrate mild to severe distortions of diseased organs. Species of *Elsinoe* are simply recognized for their symptom-marker cork-like necrotic tissues. These are frequently raised, displaying cracks, and therefore are stated as scabs. The symptoms that result from infection are dissimilar and are frequently known anthracnose (such as in infected grapevines) (Barrus & Horsfall 1928, Jenkins 1947, Farr et al. 1989, Pan 1994, Phillips 1994, Gottwald 1995). Spot anthracnose was another name endorsed by Jenkins (1947). Several hosts progress strict distortions of diseased organs, such as stem extension in cassava, or twisting of diseased stems of *Bidens* spp. (Guatimosim et al. 2015b).

Though scab symptoms are easily recognized, inspection of specimens collected in the field is frequently unsatisfying due to the absence of fertile structures. In addition, isolation of *Elsinoe* in pure culture can be very challenging because of their slow growth and subsequent cultures easily becoming overgrown by impurities. Though numerous species of the scab fungus have been defined under *Elsinoe* or *Sphaceloma*, only a few causes significant diseases (Holliday 1980). Economically significant diseases comprise avocado scab caused by *Elsinoe perseae*, citrus scab caused by *E. fawcettii* and *E. australis*, bean scab caused by *E. canavaliae* and *E. phaseoli*, grape spot anthracnose caused by *E. ampelina*, and cassava super elongation caused by "*Sphaceloma manihoticola*" (Jenkins 1925, Shear 1929, Jenkins 1931, Bruner & Jenkins 1933, Bitancourt & Jenkins 1936a, b, Boedijn 1961, Tan et al. 1996) (Fig. 65). In many cases the main impact is on the appearance of the harvested product, and its market adequacy rather than on crop efficiency (Swart et al. 2001). On the positive side, several *Elsinoe* species cause devastating diseases on significant agricultural and environmental weeds and are valuable species in this regard. Some instances are the scab fungi attacking alligator weed (*Alternanthera philoxeroides*), giant sensitive plant (*Mimosa diplotricha*), beggar tick (*Bidens pilosa*) (Guatimosim et al. 2015b), and wild poinsettia (*Euphorbia heterophylla*) (Barreto & Evans 1998, Nechet et al. 2004).

Other relevant data and future recommendations

In future studies of *Myriangiales*, especially *Elsinoe*, fresh specimens should be collected to help clarify species concepts of taxa currently lacking types linked to multigene DNA data. It is often problematic to detect typical sexual structures in many of these taxa characterized by old specimens, and strains soon become sterile in culture. Phylogenetically, the association between the two main subclades and the position of the type species *Elsinoe canavaliae*, also needs explanation. This epitypification, supplemented by DNA data of related genera such as *Molleriella* and *Myriangium*, will significantly improve the knowledge of the evolutionary relationships within the order (Fan et al. 2017).

Mytilinidiales E. Boehm, C.L. Schoch & Spatafora, Mycological Research 113(4): 468 (2009)

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Pleosporomycetidae*

Introduction

Mytilinidiales comprises 11 genera and 88 species. Mytilinidioid etymologically refers to *Mytilus*, a genus of mussels (Duby 1861). Their conchate nature, with appearance of bivalve shells or wedge-shaped and rigid, brittle, or carbonaceous hysterothecia and thin-walled, scleroparenchymatous peridium are characteristic features of this group. The ascospores are didymosporous, phragmosporous, or dictyosporous (Boehm et al. 2009a, b). Asexual genera in the order are mainly coelomycetous and less frequently hyphomycetous (Boehm et al. 2009a, b). Taxa are commonly temperate in distribution, and found in wood, bark, resin, cones, scales, needles, seeds, and roots of gymnosperms (Boehm et al. 2009b).

History

Mytilinidiales was proposed by Boehm et al. (2009b) to accommodate *Mytilinidiaceae*, with *Mytilinidion* as the type genus. This family was separated from *Pleosporales* based on its morphological characters and high statistical support in a four-gene phylogeny. These indicated that *Mytilinidiales* has a monophyletic origin. Studies on mytilinidioid taxa began with the description of two genera: *Actidium* and *Lophium* by Fries (1815, 1818). Both genera were included in *Pyrenomycetes* (Fries 1823). Chevalier (1826) classified *Lophium* in *Hysteriaceae* (*Hysterineae*) by its black, bilabiate, and erumpent perithecium (actually hysterothecium). Duby (1861) described *Mytilinidion* with *M. aggregatum* as the type species in the Tribe *Hystérinées* in the family of *Hypoxylées*. Duby (1861) included in this group in *Lophium* and *Ostreichnion* and proposed two sections, namely *Lophiées* and *Hystériées* to accommodate mytilinidioid forms, separating them from the other hysterothecioid genera. Kirschstein (1924) proposed *Mytilinidiaceae* (as *Mytilidiaceae*) and included *Bulliardella*, *Mytilinidion* (as *Mytilidion*), *Ostreion* and *Lophium*.

Boehm et al. (2009 a, b) and Hyde et al. (2013) made a historical review of the classification of mytilinidioid fungi. Previously, *Mytilinidiales* was classified in the Tribe *Hystérinées* or in the family *Hysteriaceae* due to perceived similarities in ascomata morphology; specifically on having longitudinal dehiscence. Zogg (1962) proposed two families in *Hysteriales*: *Hysteriaceae sensu stricto* to accommodate thick-walled hysterioid forms, and proposed a new family *Lophiaceae* to accommodate thin-walled, mytilinidioid forms (Boehm et al. 2009 a, b, Hyde et al. 2013). Barr & Blackwell (1980) described a new genus *Quasiconcha* in *Lophiaceae* (*Melanommatales*). Later, *Lophiaceae* was synonymized with the earlier name *Mytilinidiaceae* and this family was accepted in later studies (Boehm et al. 2009 a, b, Boonmee et al. 2012, Hyde et al. 2013, Wijayawardene et al. 2014a, Jayasiri et al. 2018a). *Halokirschsteiniothelia* was included in *Mytilinidiales* based on DNA sequence data, but differs from the hysterothecioid genera of *Mytilinidiales* by having hemispherical to subglobose ascomata with a small papillate ostiole and by its marine habitat (Boonmee et al. 2012).

Boehm et al. (2009a, b) used molecular analyses of hysterioid and mytilinidioid fungi. Multi-gene phylogenies provided strong support for the monophyly of both *Hysteriaceae* and *Mytilinidiaceae*, within *Pleosporomycetidae*. However, the sequence data indicated that both families were not closely related within the subclass whereas many *Hysteriaceae* genera were recovered as polyphyletic. After numerous transfers, *Mytilinidion*, *Lophium* and *Quasiconcha* formed a monophyletic clade within *Mytilinidiaceae*, which led to the establishment of a new order *Mytilinidiales* (Boehm et al. 2009b, Hyde et al. 2013).

General description

Mytilinidiales taxa form both sexual and asexual morphs. Lohman (1932) noted that spore germination in the subgenus *Mytilinidion* is polar, with the terminal cells germinating first.

Sexual morph: *Ascomata* hysterothecia globoid to obovoid to strongly laterally compressed, erect, oyster-shaped (conchate) or hatchet-shaped (dolabrate), standing on edge, with lateral walls more or less convent and extended vertically to a prominent longitudinal keel or cristate apex, Carbonaceous consistency, persistent and fragile dehiscent; with a longitudinal cleft (Barr 1990a, Boehm et al. 2009b). *Black peridium* formed by thin-walled scleroparenchymatous cells (Boehm et al. 2009a), rarely multi-layered (Hongsanan et al. 2020b). *Hymenium* is formed by a hamathecium of narrow, trabecular pseudoparaphyses, embedded in a gel matrix, which are often scarce or nonexistent at maturity (Boehm et al. 2009b). *Ascospores* bipolar symmetry in the contour, unicellular with a transverse septum or several transverse and longitudinal ones resembling a dyctiospore, ellipsoidal, fusiform, cylindrical, straight, curved, umbonate, filiform (scolecospores) range from hyaline to yellowish pigmented to reddish-brown (adapted from Barr 1987b, 1990a, Boehm et al. 2009a, b) (Figs. 66, 67, 68). Asexual morph: primarily coelomycetous and less frequently hyphomycetous. In coelomycetous fungi, *Conidiomata* immersed to erumpent, black, elongated, lens-shaped, opening by regular or irregular rupture. In hyphoycetous, mycelium is mostly superficial consisting of branched, septate, smooth to strongly verruculose, echinulate, verrucose or strongly verrucose, subhyaline to pale brown hyphae. *Conidiophores* hyaline to dark brown, smooth to verrucose, poorly

developed or undifferentiated to macronematous, simple to branched, septate, thin to thick walled, produced directly of the hyphae or into the pycnidia chamber. .



Figure 66 – Morphology of *Mytilinidiales* a, b, c, d *Lophium* sp. e, f *Mytilinidion* sp. Scale bars: a, b = 200 µm, c, d = 500 µm, e, f = 200 µm.



Figure 67 – Asci and ascospores of *Mytilinidiales*. a *Mytilinidion australe.* b *Mytilinidion didimospora*. c *Mytilinidion mexicanum.* d *Mytilinidion thujarum.* e *Lophium mytilinum*. f *Ostreola consiosata*.

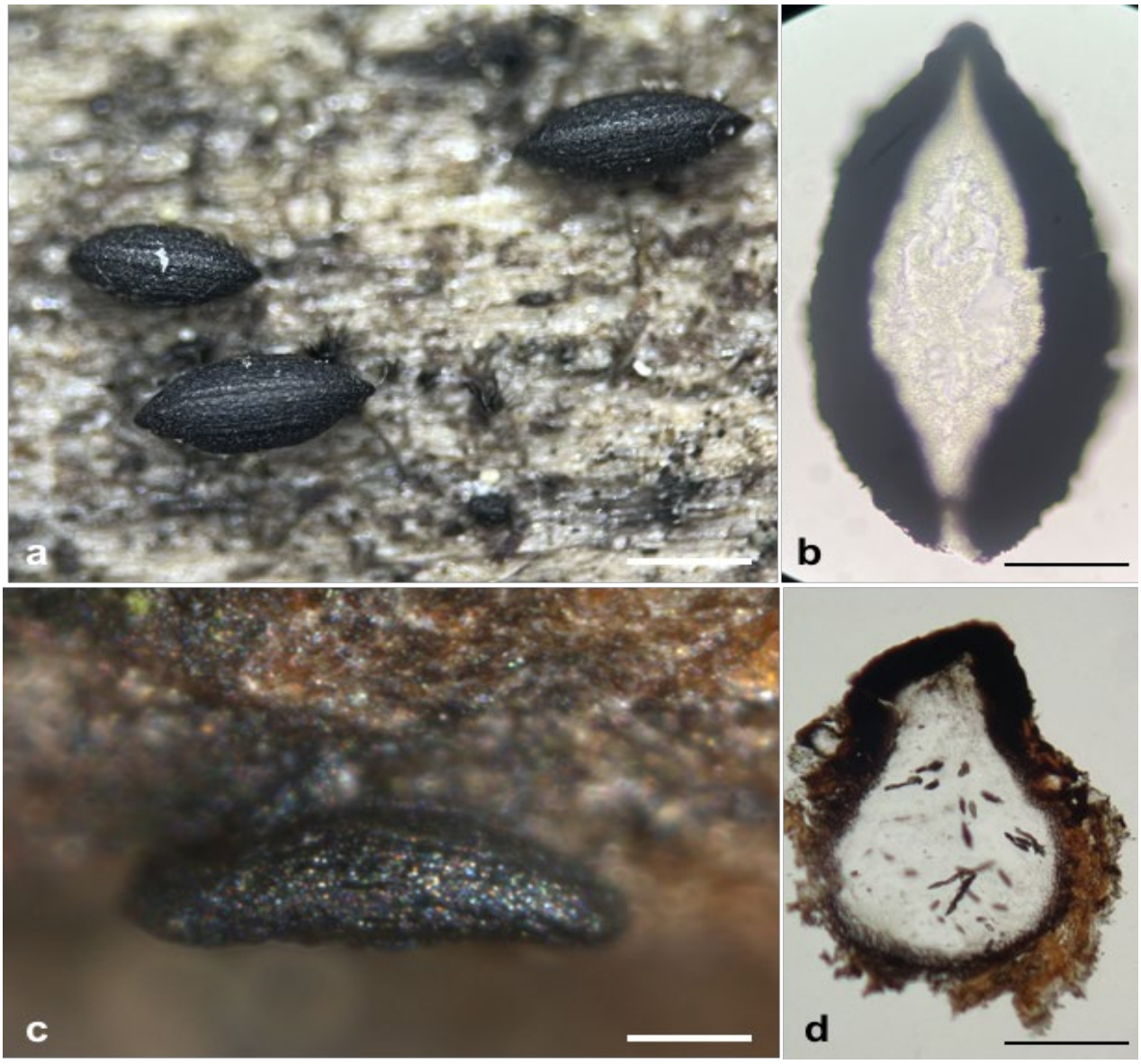


Figure 68 – *Mytilinidiales* a, b, *Lophium* sp. c, d, *Mytilinidion* sp. Scale bars: a = 300 µm, b, d = 100 µm, c = 200 µm.

Conidiogenous cells hyaline to dark brown, smooth to verrucose, terminal or lateral, subcylindrical, phialidic with minute periclinal thickening. *Conidia* solitary or catenulate, amerosporous, phargmosporous to muriform (dyctiosporous), hyaline to dark brown, smooth to verrucose, elongate to cylindrical.

Families included in *Mytilinidiales*

Mytilinidiaceae Kirschst. (=*Lophiaceae* H. Zogg ex Arx & E. Müll. 1975)

Evolution

Mytilinidiales have a close association with *Hysteriales* in the morphology of hysterothecia. However, phylogenetic studies have shown that the ascoma shell-like form is a homoplastic character with convergent origins at different times. Each order is considered monophylogenetic so the character states are considered synapomorphies among the hysteriaceous taxa. The divergence of *Mytilinidiales* is estimated to have been 219 MYA (Hongsanan et al. 2020b).

Justification of order and problems

Bulliardella is a sexual morph of a mytilinoid taxa that was synonymized under *Actidium* because its type species, *B. baccarini*, was considered as *A. baccarini*. However, this has not been complemented with molecular data, and the two species have been considered as separate which needs molecular data for confirmation. *Taeniolella* is a polyphyletic taxon (Ertz et al. 2016) with a taeniolella-like anamorph linked to *Mytilinidion gemmigenum* (Minter & Holubová-Jechová 1981). However, its phylogenetic affiliation within *Mytilinidiales* has not been verified (Heuchert et al. 2018).

Significance

Ecological and economic roles

Mytilinidiales have been mostly found on bark and fallen branches of trees in temperate forests at altitudes above 2500 meters above sea level in the Northern and Southern Hemispheres. However, a greater number of records are from the Northern Hemisphere. Conifers are the main hosts,specifically on branches and bark. The tropical forests are little studied, and they are apparently very diverse in this group of fungi.

Chemical diversity

There are no records on the chemical diversity in *Mytilinidiales*.

***Natipusillales* Raja, Shearer, A.N. Mill. & K.D. Hyde, Fungal Diversity 63 (1): 9 (2013)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Natipusillales, a group of saprobic fungi, are exclusively freshwater inhabitants. Their distribution is limited to South and North America, with collection sites in Costa Rica, Ecuador, and Peru (Ferrer et al. 2011, Raja et al. 2012, Shearer et al. 2015). Molecular data have supported the placement of these taxa within this order. Since its introduction, the type genus *Natipusilla* has been noted as a later earlier name for *Ascominuta* due to their morphological similarities (Hyde et al. 2013, Shearer et al. 2014). However, the placement of *Ascominuta* remains unresolved due to a lack of molecular data.

Calabon et al. (2025) generated sequence data for *Ascominuta lignicola*, which was collected from submerged decaying wood in Thailand. BLASTn analysis revealed high similarity to members of *Natipusilla*. Furthermore, phylogenetic analysis demonstrated that *A. lignicola* clustered with other strains of *Natipusilla*. These findings supported the reclassification of *Natipusilla* within the genus *Ascominuta*.

History

The monotypic order *Natipusillales*, established by Hyde et al. (2013), encompasses the freshwater ascomycetous family *Natipusillaceae*. *Natipusillales* comprises a single genus, *Natipusilla*, which was first described by Ferrer et al. (2011). The type species, *Natipusilla decrospora*, was isolated from submerged wood in swamps in Ecuador. Ferrer et al. (2011) described two additional species, *N. limonensis* and *N. naponensis*, isolated from a stream in Costa Rica and swamps in Ecuador, respectively. *Natipusilla bellaspora* was later described by Raja et al. (2012) from a stream in Peru.

Natipusilla and *Minutisphaera*, two freshwater fungal genera, exhibit striking morphological similarities, including minute ascomata, bitunicate asci, and ascospores adorned with gelatinous appendages. To elucidate their evolutionary relationships, Raja et al. (2013) conducted a phylogenetic analysis using combined SSU and LSU gene sequences. While the morphological resemblance between the two might suggest a close evolutionary relationship, the phylogenetic analysis revealed that *M. japonica* is not closely related to *Natipusilla* species. This result provides

strong evidence for the distinctness of *Natipusillaceae* as a separate family, further emphasizing the importance of molecular data in fungal taxonomy. Hyde et al. (2013) noted a morphologically similar genus, *Ascominuta*, a freshwater fungus also, that it might be an earlier name for *Natipusilla*. However, due to the lack of molecular data for *Ascominuta*, its phylogenetic relationship with *Natipusillaceae* remains uncertain. Shearer et al. (2014) further suggested that *Ascominuta* could be phylogenetically related to members of the *Natipusillaceae*. This hypothesis was later confirmed by Calabon et al. (in press) through a morpho-phylogenetic analysis of *Ascominuta lignicola*.

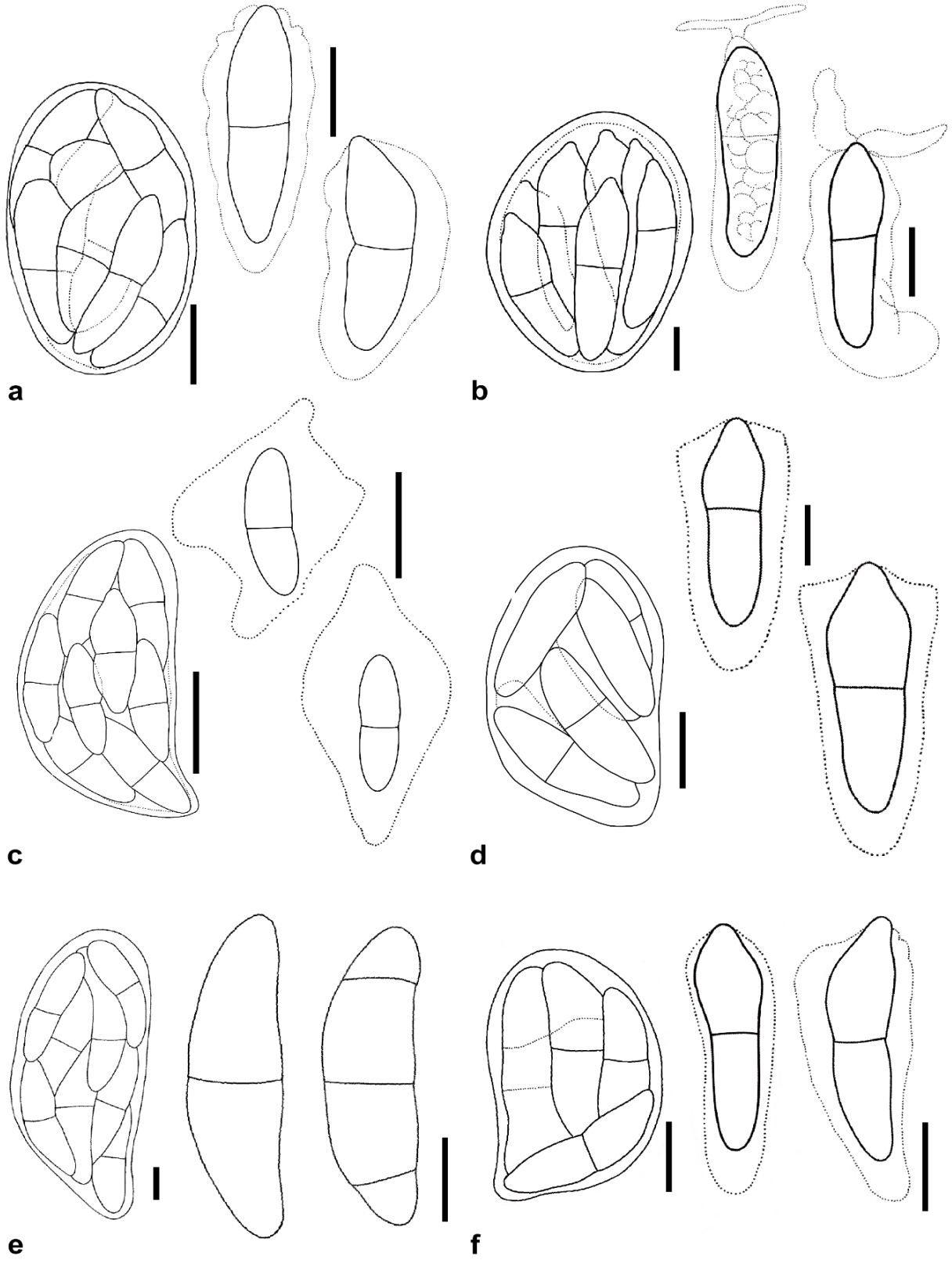


Figure 69 – Sexual morph of *Natipusillales*. a Asci and ascospores of a *Ascominuta bellaspora*. b *A. decorospora*. c *A. lignicola*. d *A. limonensis*. e *A. naponensis*. f *A. ovalispora*. (Drawn and redrawn from Calabon et al. 2025). Scale bars: a–f = 20 µm.

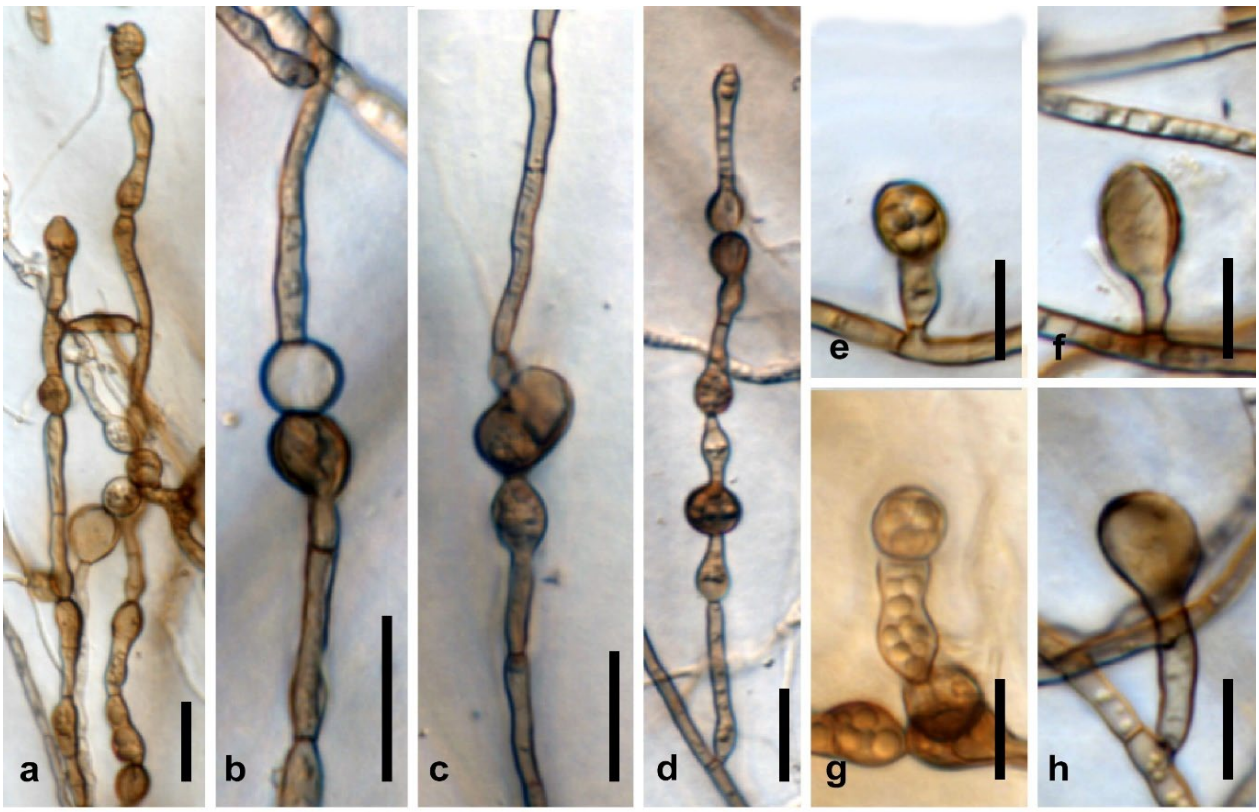


Figure 70 – Asexual morph of *Natipusillales*. a–d Swollen cells in the intercalary of hyphae. e–h Multicellular bodies. Scale bars: a–d = 20 µm, e–h = 10 µm.

Ascominuta is characterized by its globose asci containing four spores and broadly fusiform or ovoid, hyaline, 1-septate ascospores with a distinct sheath (Ranghoo & Hyde 2000). The type species, *A. lignicola*, was initially isolated from submerged wood in Hong Kong. Subsequently, Hu et al. (2010) described a second species, *A. ovalispora*, from submerged wood in Thailand. This species is distinguished from *A. lignicola* by its sac-like persistent sheath, compared to the irregular mucilaginous sheath of the latter. Due to the lack of molecular data at the time of its introduction, *Ascominuta* was initially classified as Ascomycetes *incertae sedis* (Ranghoo & Hyde 2000). Later, Lumbsch & Huhndorf (2007) placed it in *Dothideomycetes* genera *incertae sedis*, and followed by Wijayawardene et al. (2018, 2020).

General description

Sexual morph: *Ascomata* scattered or aggregated, erumpent to superficial, uniloculate, globose to subglobose, hyaline to brown, lacking ostioles, occasionally with minute papilla. *Peridium* thin, membranous, glabrous, forming a textura angularis in surface view. Pseudoparaphyses sparse or absent. *Asci* 4–8-spored, bitunicate, fissitunicate, globose to obclavate, lacking a pedicel, with or without an ocular chamber. *Ascospores* overlapping tri- to multi-seriate, arranged in a group, fusiform or clavate, straight, the upper cell often shorter and broader than the lower one, mostly 1-septate, hyaline, occasionally becoming 3-septate, pale brown at age, guttulate when young, smooth, thin-walled, with or without a gelatinous sheath (Ferrer et al. 2011). Asexual morph: Hyphomycetous. *Hyphae* septate, hyaline to lightly pigmented, mostly smooth, thick-walled, moniliform. *Swollen cells* globose to subglobose, smooth, initially hyaline then becoming light brown at maturity. *Multicellular bodies* mostly globose, ellipsoidal, or irregularly-

shaped, hyaline to lightly pigmented, smooth, thick-walled, arising from the mycelium, mostly formed intercalarily (Calabon et al. 2025) (Figs. 69, 70).

Families included in *Natipusillales*

Natipusillaceae Raja, Shearer & A.N. Mill.

Evolution and justification of order and problems

Natipusillales, estimated to have diverged approximately 180 MYA (stem age, Hongsanan et al. 2020b), is a sister group to the non-freshwater *Zeloasperisporiales*, which exhibits markedly distinct morphological features (Hongsanan et al. 2015a, Wijayawardene et al. 2022a).

Significance

Ecological and economic roles

Natipusillales taxa are saprobes that inhabit submerged woody substrates, facilitating the decomposition of lignocellulosic materials and thereby contributing to nutrient cycling in aquatic environments (Calabon et al. 2022, 2023a).

Chemical diversity

The chemical diversity of *Natipusillales* remains largely unexplored. Future investigations into the secondary metabolites produced by this fungus could offer significant insights into its ecological functions and potential applications in biotechnology or medicine.

***Neodactylariales* H. Zheng & Z.F. Yu, MycoKeys 73: 74 (2020)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Neodactylariales was introduced to accommodate a single family *Neodactylariaceae* and the genus *Neodactylaria* (Qiao et al. 2020).

History

Neodactylaria was established by Crous et al. (2017b) and typified by *Neodactylaria obpyriformis,* which was reported from human bronchoalveolar lavage in the USA. *Neodactylaria obpyriformis* showed similar morphological characteristics to *Dactylaria kumamotoensis* and *D. madrasensis* but differs from the former in having larger conidia which can have more than one septum whereas *D. kumamotoensis* has 12–40 × 4–8 μm with 1–3-septate conidia and *D. madresensis* has 9–19 × 4.5–6 μm conidia that are 1–2 septate. In addition, both species are reported from soil and plant debris in Japan and India, respectively and are only known from the type collection without living cultures. Thus, the molecular comparison between *Neodactylaria* and *Dactylaria* is impossible.

Neodactylaria also resembles *Pyricularia* species but differs in conidial morphology. Considering that, *Dactylaria sensu* is heterogenous genus and *Pyricularia* belongs to the *Magnaporthales* (*Sordariomycetes*) (Bussaban et al. 2005, Klaubauf et al. 2014), *Neodactylaria* was placed in the *Dothideomycetes* based on phylogenetic analyses, which recovered in the basal lineage of *Dothideomycetes* (Crous et al. 2017b). Qiao et al. (2020) found a second new species *N. simaoensis* from Southwest China which showed similar morphology to *Heliocephala proliferans* but differs in conidiogenous cells that were terminal or intercalary, with short-cylindrical denticles, and the conidia were 1- or 2-septate and constricted at the septum (Rao et al. 1984, Mel'nik et al. 2013). The BLAST search result showed the closest hits to *Neodactylaria* in the LSU gene region. The detailed morpho-molecular reinvestigation of the *N. obpyriformis* and *N. simaoensis* led to the establishment of a new order *Neodactylariales* and the family *Neodactylariaceae* which formed a sister clade to *Pleosporales* in the combined LSU, SSU, and TEF1 sequence data (Qiao et al. 2020).

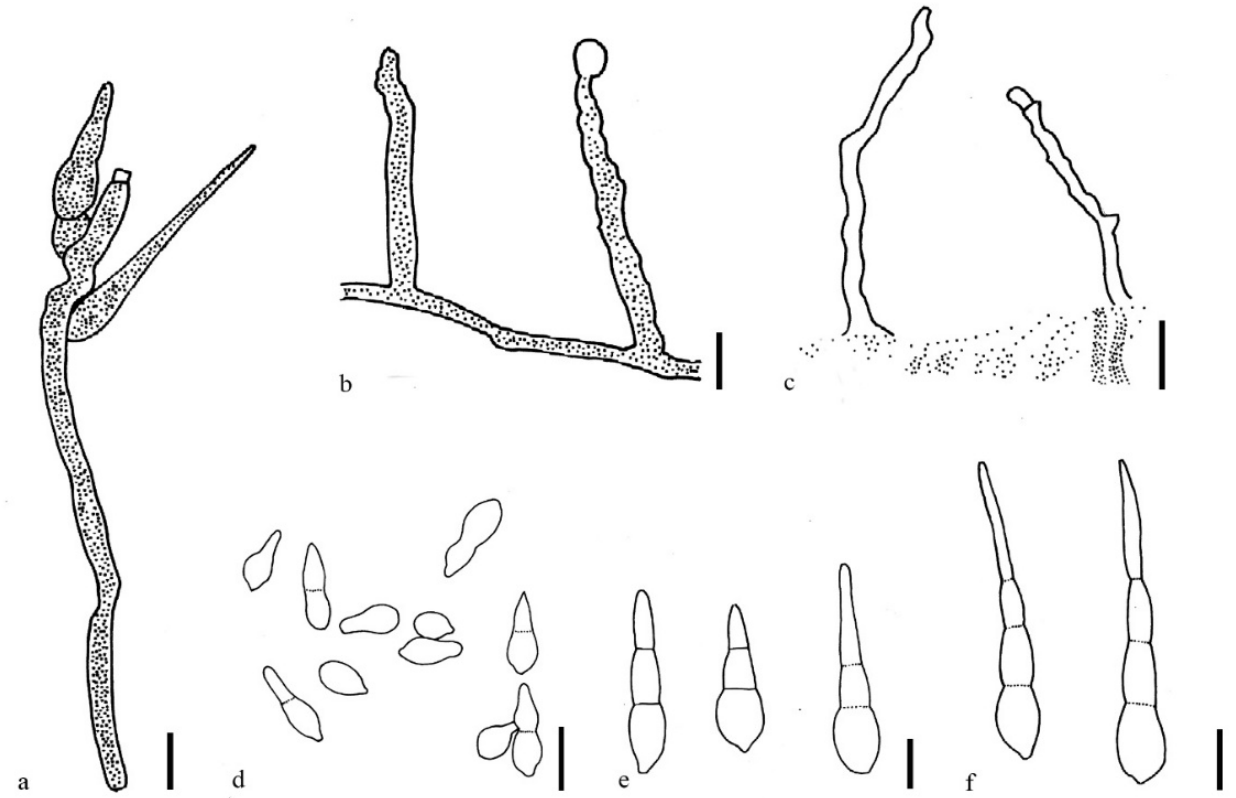


Figure 71 – Morphology of *Neodactylariales.* a, c Conidia and conidiophores (a *Neodactylaria simaoensis*, c *N. obpyriformis*). b Immature conidium and conidiogenous cells (*N. simaoensis*). d–f Conidia (d *N. obpyriformis*, e, f *N. obpyriformis*) (drawn from Crous et al. 2017b, Qiao et al. 2020). Scale bars: a–f = 10 μm.

General description

The taxa are reported only in their hyphomycetous asexual morph (Crous et al. 2017b, Qiao et al. 2020).

Sexual morph: Not observed. Asexual morph: *Mycelium* superficial or immersed, composed of branched, septate, hyaline to subhyaline hyphae. *Conidiophores* acroauxic, macronematous, mononematous, branched or unbranched. *Conidiogenous cells* mono- and polyblastic, sympodially extended. *Conidia* solitary, hyaline or pale pigmented, smooth, verrucous or echinulate (Fig. 71).

Families included in *Neodactylariales* H. Zheng & Z.F. Yu

Neodactylariaceae H. Zheng & Z.F. Yu

Significance

Ecological and economic roles

The taxa are reported on human-associated organs or saprobic on plant debris from China and the USA (Crous et al. 2017b, Qiao et al. 2020).

***Neophaeothecales* Abdollahz. & Crous, Studies in Mycology 95: 392 (2020)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Dothideomycetidae*

Introduction

Neophaeothecales comprises two genera (Abdollahzadeh et al. 2020, Crous et al. 2021b). Based on phylogenetic analysis of the LSU, TEF1-α, and RPB2 sequences, the order was determined to be

monophyletic (Abdollahzadeh et al. 2020). Based on morphological and molecular characteristics, this order consists only *Neophaeothecaceae* (Abdollahzadeh et al. 2020). Abdollahzadeh et al. (2020) described *Neophaeothecaceae*, which consists of two genera, *Neophaeotheca* and *Nothophaeotheca*, with the former considered the generic type (Abdollahzadeh et al. 2020, Crous et al. 2021b). Members of this order have been discovered on desert and coral plant leaves and twigs, plankton tows, coral, sponges, air-conditioning system humidifiers, and the remains of desert plants (Crous et al. 2016b, 2021b, Mitchison-Field et al. 2019).

History

Abdollahzadeh et al. (2020) proposed this order, which belongs to the class *Dothideomycetes*. The study of *Neophaeothecales* started with the discovery of *Phaeotheca triangularis* (de Hoog et al. 1997). The species is related to dothideaceous black yeasts and belongs to the family *Dothideaceae* because it is DNAse-positive and lacks woronin bodies at the septa. According to phylogenetic analyses of 5.8S and ITS2, *Mycosphaerella sensu lato* is probably the teleomorph of *P. triangularis* (De Hoog et al. 1999). Phylogenetic analysis of the ITS of *Mycosphaerella* species and related anamorphs and teleomorphs revealed that *Mycosphaerella* clustered with *P. triangularis*, which lacks a teleomorph (Goodwin et al. 2001). *Mycosphaerella sensu lato*, which had thousands of species and anamorphs in more than 30 genera and was assigned to the *Mycosphaerellaceae*, was re-examined, and phylogenetic analysis of LSU revealed that *P. triangularis* belongs to the same clade as *Capnodiaceae* members in *Capnodiales* (Crous et al. 2007a). Nonetheless, *Phaeotheca* species have been identified as *Capnodiales incertae sedis* in the phylogeny based on LSU (Crous et al. 2009c). Similar results were obtained when the phylogeny of *Dothideomycetes* was surveyed using LSU sequences. *Phaeotheca triangularis* and *P. salicorniae* were found to be placed in the same clade in the *Capnodiales*, but as *incertae sedis* taxa (Crous et al. 2016b). Finally, following the reconsideration of *Capnodiales sensu lato* based on the phylogeny of LSU, TEF1-α, and RPB2 sequences, as well as morphology and ecology, *Neophaeothecales* and *Neophaeothecaceae* were established to accommodate these two species, forming the new combinations *Neophaeotheca salicorniae* and *N. triangularis* (Abdollahzadeh et al. 2020).

General description

The term "dematiaceous fungi" refers to pigmented septate hyphae molds (Juravel et al. 2023). Endoconidia are conidia produced within a conidiogenous cell by protoplast cleavage (Tsuneda et al. 2004). *Nothophaeothecaceae* includes the genera *Nothophaeotheca* and *Neophaeotheca* (Hyde et al. 2024b), both of which have a dematiaceous hyphomycetous morph with endoconidia (Crous et al. 2021b). Both genera are morphologically similar (Crous et al. 2021b). No sexual morph is known for the species in this order. Conidial size and shape, as well as the size of swollen hyphal cells are used to distinguish *Neophaeotheca* species (Crous et al. 2016b).

Sexual morph: Undetermined. Asexual morph: *Mycelium* composed of branched, hyaline, septate, smooth hyphae that swell in terminal or intercalary cells, producing numerous endoconidia. *Endoconidia* globose to obovoid, brown, muriformly septate, verruculose, bursting open to release endoconidia that are ellipsoid to subglobose or irregular, red-brown, aseptate, and verruculose (adapted from Crous et al. 2021b) (Fig. 72).

Families included in *Neophaeothecales*

Neophaeothecaceae Abdollahz. & Crous

Evolution

Members of the *Neophaeothecales* were previously classified as *Capnodiales sensu lato*, but phylogenetic analysis of the LSU, TEF1-α, and RPB2 sequences revealed that they formed a strongly supported monophyletic clade and evolved into a distinct lineage (Abdollahzadeh et al. 2020). Whole-genome sequencing revealed that the ancestors of *Dothideomycetes* were saprobes (Haridas et al. 2020). The saprobic lifestyle of *Neophaeothecales* demonstrates that this order has maintained a primitive ancestral lifestyle throughout its evolution (Abdollahzadeh et al. 2020).

Justification of order and problems

To date, two genera (*Neophaeotheca, Nothophaeotheca*) have been identified within the order (Abdollahzadeh et al. 2020, Crous et al. 2021b). More specimens should be collected to determine the boundaries of the order.

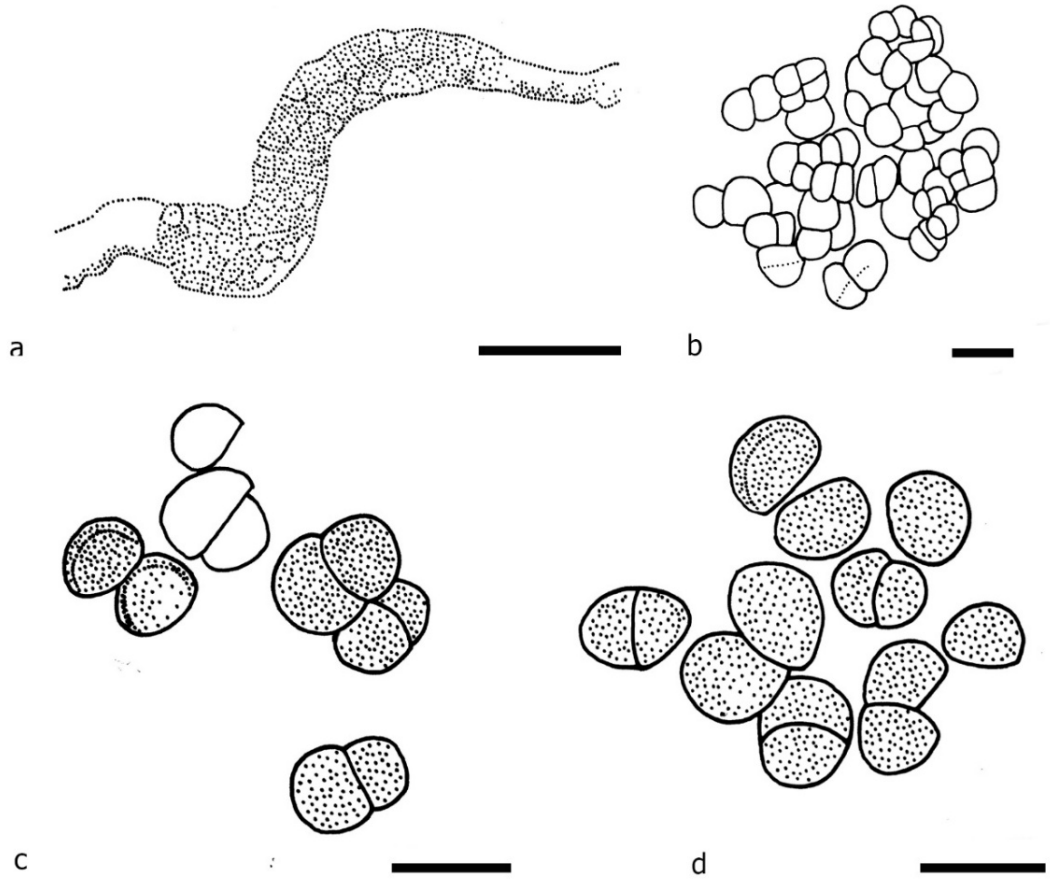


Figure 72 – Morphology of *Neophaeothecales*. a Hyphae with endoconidia. b–d Endoconidia (b *Neophaeotheca salicorniae*. c, d *Neophaeotheca salicorniae*) (drawn from Crous et al. 2016b, 2021b). Scale bars = 10 µm.

Significance

Ecological and economic roles

Taxa of this order were known as saprobes (Crous et al. 2016b). They were isolated from plankton tows, coral and sponges (Mitchison-Field et al. 2019). Additionally, *Neophaeotheca salicorniae* was isolated from leaves and twigs of a salt tolerant plant *Salicornia meyeriana* (*Amaranthaceae*) (Crous et al. 2016b). The halotolerance of *N. triangularis* in NaCl solutions has also been demonstrated. The fungus adaptation to salinity has biotechnological implications. Research could seek the identity of the related gene in order to produce halotolerant plants (Zajc et al. 2017). *Neophaeotheca triangularis* produces mycosporine that can absorb UV between 310–360 nm (Satyanarayana et al. 2019).

Chemical diversity

There is lack of literature on secondary metabolites from fungi in the *Neophaeothecales*. Mycosporine-glutamicol-glucoside was previously identified as a secondary metabolite of *N. triangularis*. It is also the primary mycosporine of this species (Satyanarayana et al. 2019). Mycosporine-like amino acids can dissipate UV radiation without producing toxic reactive oxygen species (ROS); as photoprotective agents, they absorb a wide range of the UV spectrum (Carreto and

Carignan 2011). Furthermore, under saline and non-saline growth conditions, this species can produce DHN-melanin as a secondary metabolite (Kogej et al. 2004). Melanin pigments and their subunits can be used to engineer high-performance, low-impact biocompatible optoelectronic devices, such as light-emitting diodes and memory devices, oras soft biocompatible functional materials with antioxidant properties (Ambrico 2016).

Other relevant data and future recommendations

Few studies have been conducted on the secondary metabolites of members of this order (Ambrico 2016, Satyanarayana et al. 2019). More research is needed in this area. Further collections should be made to identify new species in the genera *Neophaeotheca* and *Nothophaeotheca*. The isolation of the identified species of this order from coastal and desert areas (Crous et al. 2016b, 2021b) indirectly demonstrates their adaptation to salinity and dryness. Further tests are needed to confirm their adaptation and identify the genes involved in this adaptation. *Neophaeotheca* has potential applications for biotechnology.

Parmulariales **D.Q. Dai & K.D. Hyde, Phytotaxa 369(2): 73 (2018)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass **:** *Incertae sedis*

Introduction

Parmulariales are epifoliar taxa, and currently comprises 32 genera, with more than 1300 species (Marasinghe et al. 2023). *Parmulariales* was introduce by Dai et al. (2018) to accommodate a single family *Parmulariaceae*. Members of *Parmulariaceae* are distributed mostly in tropical to subtropical areas, and are reported with biotrophic and pathogenic lifestyles (Inácio & Cannon 2008, Dai et al. 2020). Most of the genera in *Parmulariaceae* are difficult to obtain in culture, due to their biotrophic properties (Guatimosim et al. 2015a). Only the type species *Parmularia styracis* has sequence data in GenBank. Due to the lack of molecular data, the generic definition of *Parmulariaceae* is mainly based on morphology, resulting in diversity of genera and morphological characters within the family (Inácio & Cannon 2008, Marasinghe et al. 2023).

History

Parmulariaceae was initially introduced by Müller & von Arx (1962), with *P. styracis* as the type species to accommodate epiphytic or parasitic taxa on living leaves, but was invalid as it lacked a Latin diagnosis. Müller & von Arx (1962) accepted several other taxa (e.g., *Aldona* spp.) in this family. Barr (1979a) validated *Parmulariaceae*, with a full family description. Inácio & Cannon (2008) provided a detailed monograph, and included 35 genera, however 34 genera were accepted by Lumbsch & Huhndorf (2010). Hyde et al. (2013) listed 30 genera, and excluded 4 genera (*viz*. *Coccodothis*, *Dothidasteroma*, *Englerodothis* and *Perischizon*) from *Parmulariaceae*. *Parmulariaceae* was previously placed in different orders, e.g., *Dothiorales*, *Microthyriales*, *Hemisphaeriales*, *Dothideales* and *Hysteriales* (Müller & von Arx 1962, Ainsworth 1971, Luttrell 1973, von Arx & Müller 1975, Barr 1979a, Hawksworth et al. 1983a, 1995). Guatimosim et al. (2015a) obtained sequences of *Parmularia styracis*, and established *Parmulariaceae* in *Asterinales*, as it was phylogenetically close with *Asterinaceae*. Dai et al. (2018) introduced *Parmulariales* based on multiple phylogenetic analyses. Hongsanan et al. (2020a) and Wijayawardene et al. (2022a) included 35 genera in *Parmulariaceae*. Marasinghe et al. (2023) accepted 32 genera, and provided the generic descriptions, illustrations and hand-drawings. Hyde et al. (2024b) accepted 38 genera.

General description

Parmulariaceae contains a range of ascomata types, asci and ascospores forms (Inácio & Cannon 2008), as numerous genera were placed in this family. *Parmulariaceae* typically have variable internal stromata, which is one of the main features to recognize this family from others in *Dothideomycetes* (Inácio & Cannon 2008).

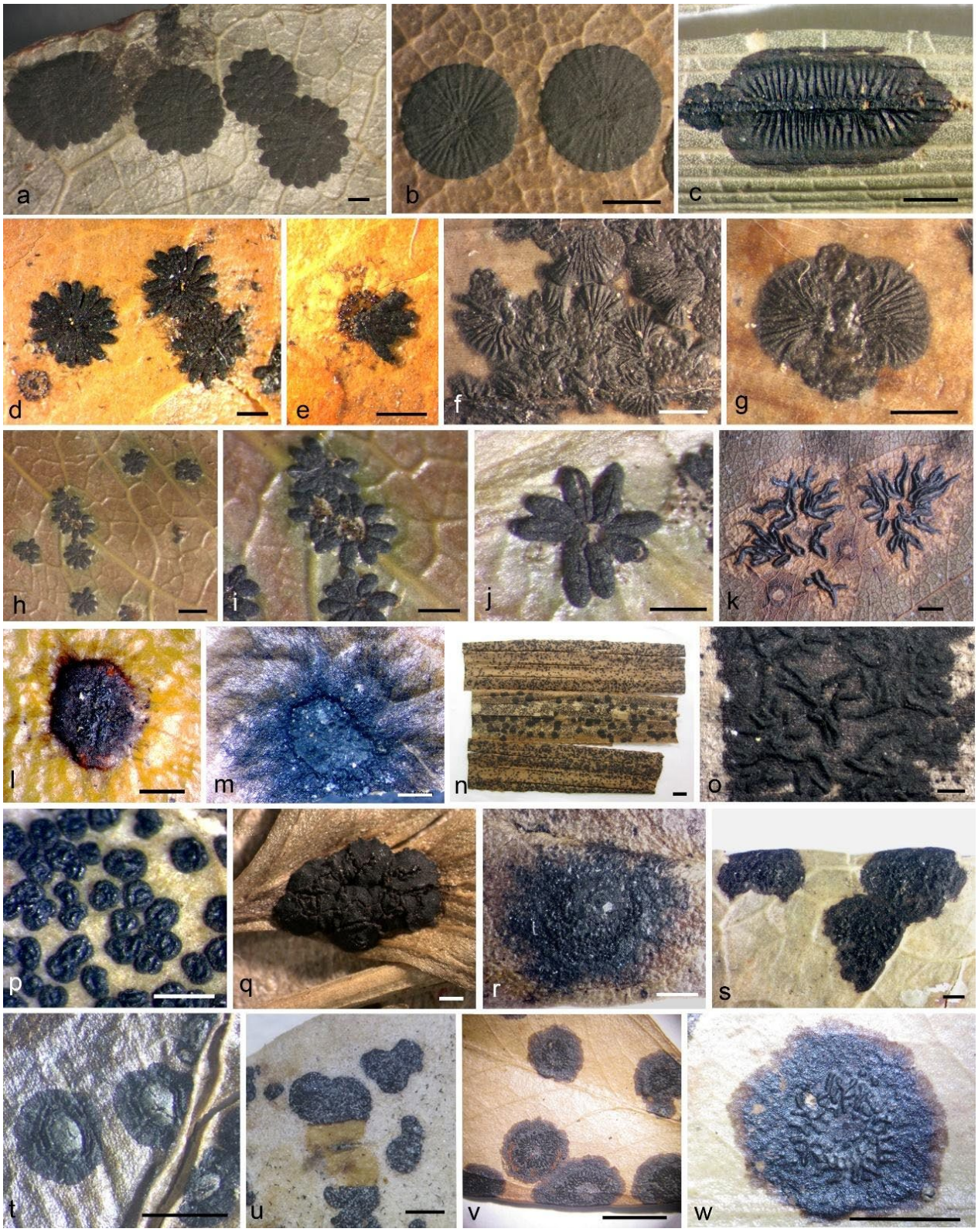


Figure 73 – Ascostromata of *Parmulariales.* a, b *Parmularia styracis*. c *Parmulariopsis pulchella*. d, e *Mintera reticulata*. f, g *Rhipidocarpon javanicum*. h, i, j *Viegasella pulchella*. k *Aldona stella-nigra*. l, m *Antoniomyces loranthicola*. n, o *Aulacostroma palawanense*. p *Cycloschizon brachylaenae*. q *Pachypatella alsophilae*. r *Palawaniella orbiculata*. s *Hysterostomella guaranitica*. t *Polycyclus andinus*. u *Protothyrium salvadorae*. v, w *Pseudolembosia geographica*. Scale bars: a, b, d, e, i, j, o–q, t–v = 500 µm, c, f–h, k, n, r–w = 1 mm.

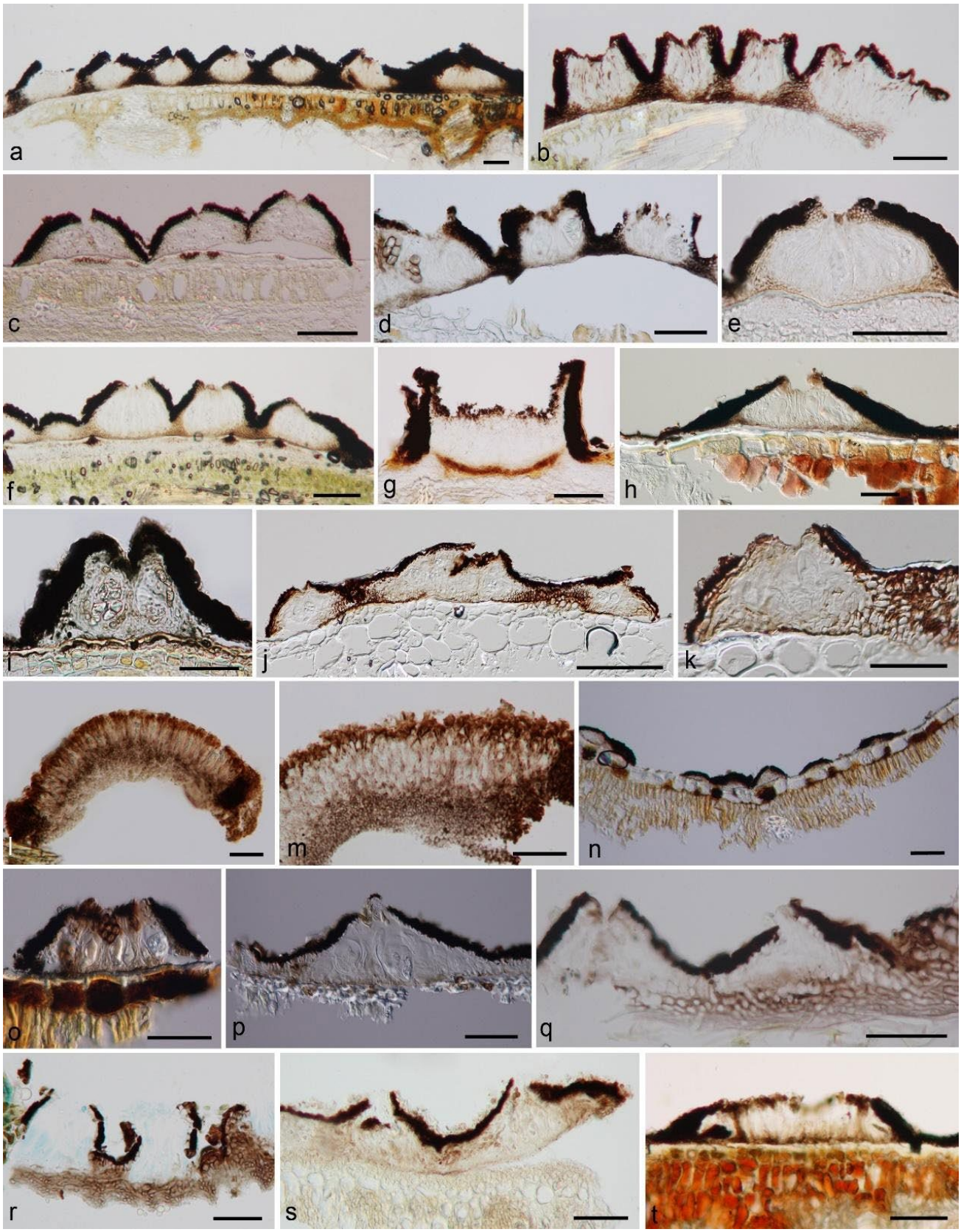


Figure 74 – Sections of ascostromata of *Parmulariales.* a *Parmularia styracis*. b *Parmulariopsis pulchella*. c *Mintera reticulata*. d *Rhipidocarpon javanicum*. e, f *Viegasella pulchella*. g *Aldona stella-nigra*. h *Antoniomyces loranthicola*. i *Aulacostroma palawanense*. j, k *Cycloschizon brachylaenae*. l, m *Pachypatella* alsophilae. n, o *Palawaniella orbiculata*. p *Hysterostomella guaranitica*. q *Polycyclus andinus*. r *Polycyclina rhytismoides*. s *Protothyrium salvadorae*. t *Pseudolembosia geographica*. Scale bars: a–h, j, l–n, s, t = 100 µm, i, k, o–r = 50 µm.

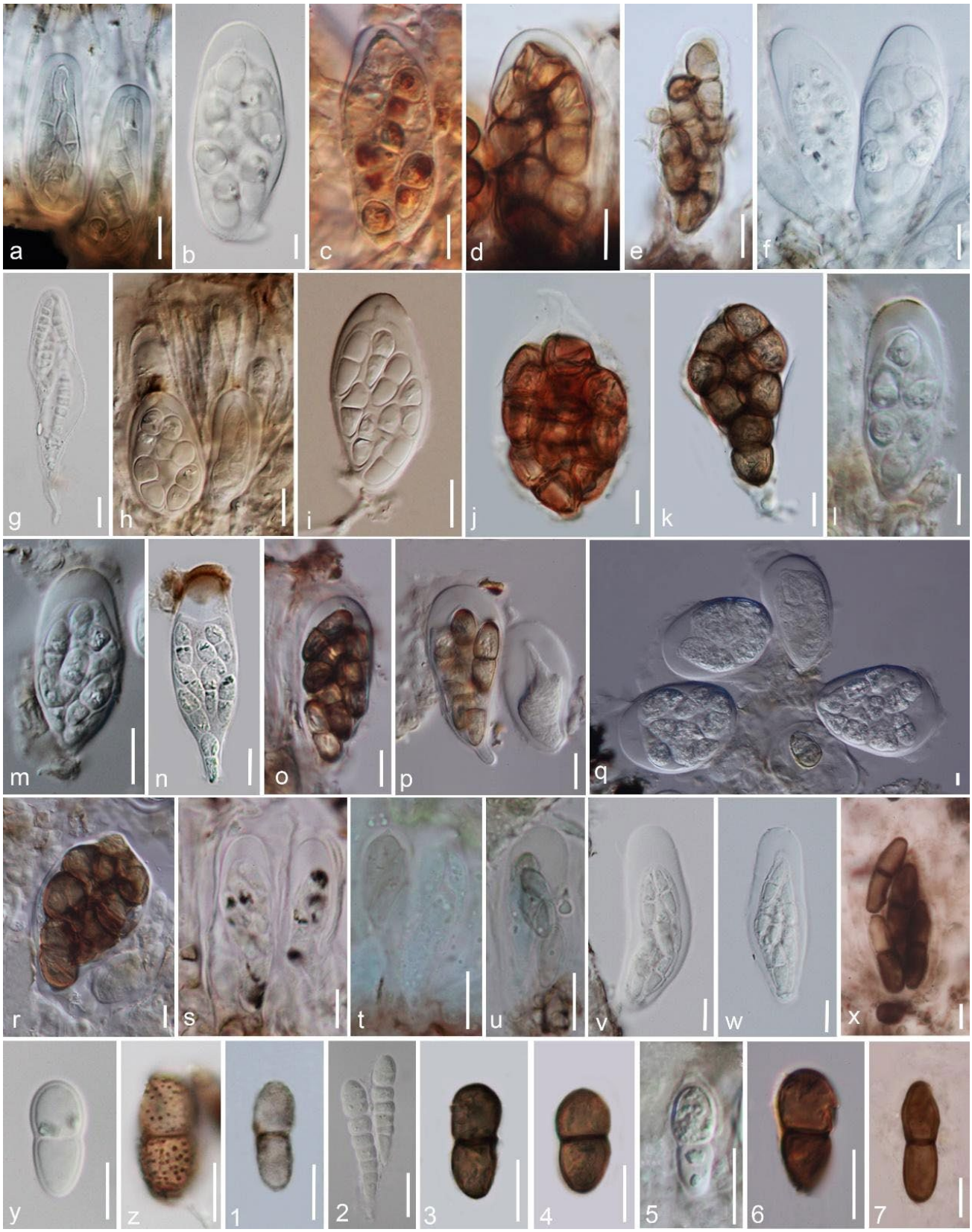


Figure 75 – Asci and ascospores morphology of *Parmulariales.* a *Parmularia styracis*. b, y *Parmulariopsis pulchella*. c *Mintera reticulata*. d, z *Rhipidocarpon javanicum*. e, f, 1 *Viegasella pulchella*. g, 2 *Aldona stella*-nigra. h, i *Antoniomyces loranthicola*. j, k, 3, 4 *Aulacostroma palawanense*. l, m, 5 *Cycloschizon brachylaenae*. n *Pachypatella alsophilae*. o, p, 6 *Palawaniella orbiculata*. q, r *Hysterostomella guaranitica*. s *Polycyclus andinus*. t, u *Polycyclina rhytismoides*. v, w *Protothyrium salvadorae*. x, 7 *Pseudolembosia geographica*. Scale bars: a–7 = 10 µm.

Mycelium is commonly present in members of *Parmulariaceae*. Haustoria occurs in several genera, e.g., *Aulacostroma*, *Parmularia*, *Mintera*, and *Viegasella*. Some genera, e.g., *Aulacostroma*, and *Mintera* have well-developed mycelium with appressoria. Most genera of *Parmulariaceae* lack asexual morphs.

Sexual morph: *Colonies* superficial, dark brown to black, rounded to irregular. *Hyphae* developing under ascomata, sometime spreading out from ascomata border. *Haustoria* absent or present, variable, irregular to lobate. *Internal stromata* absent or present. *Ascostromata* solitary, scattered, gregarious, or in groups, superficial to immersed, shield-like, elliptical, dark brown to black, carbonaceous to membranaceous, strongly flattened. *Locules* immersed in ascostromata or in longitudinal ridges radiating from the centre. *Peridium* composed of dark to hyaline, thick to thin cells of *textura prismatica* to *textura angularis*. *Hamathecium* of hyaline, septate pseudoparaphyses with brown apices, or pseudoparaphyses lacking. *Asci* bitunicate, broad cylindrical to subglobose, with an ocular chamber. *Ascospores* 2-seriate to irregular arranged, hyaline to dark brown, oblong to ellipsoid, septate, smooth- to verrucose-walled. Asexual morph: *Excipulariopsis*, *Placomelan* (Figs. 73, 74, 75).

Families included in *Parmulariales*

Parmulariaceae E. Müll. & Arx ex M.E. Barr

Evolution

Little has been reported about the evolution of *Parmulariales*. Guatimosim et al. (2015a) obtained ITS, LSU, and TEF1-α sequence data by directly extracting DNA from 30 fertile ascomata. According to Marasinghe et al. (2023) *Parmulariales* split from *Thyrinulaceae* at 109 (148–243) MYA. Hongsanan et al. (2020a) estimated *Parmulariales* originated at 115 MYA.

Justification of order and problems

Numerous epifoliar genera were placed in *Parmulariaceae*, however without molecular data, the generic delimitation is unclear (Marasinghe et al. 2023).

Significance

Ecological and economic roles

Parmulariaceae is widely distributed, and commonly occur from tropical to subtropical regions including African and South American continents (Inácio & Cannon 2008). Species of *Parmulariaceae* were found from over 50 hosts, of which angiosperms accounted for more than 90% (Inácio & Cannon 2008). Most genera were reported from more than five hosts, with *Hysterostomella* occurring on 25 hosts (Inácio & Cannon 2008). *Parmulariaceae* are epifoliar taxa, that occupy an important ecological niche (Marasinghe et al. 2023). Members of this family are epiphytic or parasitic on living leaves of plants and ferns or lichenicolous.

Chemical diversity

There is a lack of study on the industrial applications of *Parmulariaceae*, and further exploration of chemical compounds is needed.

Other relevant data and future recommendations

Epifoliar fungi usually play a crucial role in tropical forest systems. The study of the diversity of the genera in *Parmulariaceae* is of important significance for understanding the relationship between plants and fungi.

***Patellariales* D. Hawksw. & O.E. Erikss., Systema Ascomycetum 5(1): 181 (1986)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction & History

Patellariales was established based on morphological data to accommodate *Patellariaceae*, *Arthrorhaphidaceae* and *Phillipsiellaceae* (Hawksworth & Eriksson 1986). *Patellariaceae* was introduced to accommodate *Cryptodiscus*, *Mellitiosporium* and *Patellaria* (Corda 1838a) based on cup-shaped ascomata and septate ascospores. However, after the establishment, the family has gone through several changes and only *Patellaria* remains under this family whereas the other two genera are being treated in two different classes (*Lecanoromycetes* and *Leotiomycetes*) in *Ascomycota*. Rehm (1896) accepted 20 genera under two groups, *Pseudopatellariaceae* and *Eupatellariaceae* under *Discomycetes* and *Dermateaceae*. Saccardo & Sydow (1899) initially accepted 14 non-lichenized genera and later accepted 33 genera based on the number of spore septa for the saprobic taxa that grow on dead wood and parasites on lichen thalli and treated the family under *Discomyceteae*. Boudier (1907) accepted 30 genera. Clements & Shear (1931) accepted 35 genera including some lichenized genera based on having dark, waxy, ascomata with a carbonaceous peridium and they placed the family in the discomycetous order *Pezizales*.

Nannfeldt (1932) introduced two new groups which belong to eu-ascomycetes i.e. *Ascoloculares* and *Ascohymeniales*. However, Nannfeldt (1932) excluded *Patellaria* from both these groups by mentioning it is a discolichen with thick-walled asci embedded in a layer of gelatine along with paraphyses. His observation was re-examined by Luttrell (1951a) who stated that some taxa in *Hysteriaceae* and *Patellariaceae* might have a close relationship by their bitunicate ascal character. Later, Luttrell (1955) moved the family *Patellariaceae* to *Pleosporales*. Nannfeldt (1932) referred *Patellaria* and other related genera such as *Baggea*, *Rhytidhysteron* and *Holmiella* as discolichens similar to *Lecanorales*. Luttrell (1955) also treated the family under *Lecanorales* following Nannfeldt's (1932) treatment. However, Luttrell (1955) also noted a possible placement within *Hysteriales* or *Pleosporales*. The author further proposed the need for a separate order to accommodate *Patellariaceae* and other related families (Luttrell 1965). von Arx & Muller (1975) treated this family under *Dothiorales* by accepting 13 genera including some lichenized genera, *Buellia* and *Melaspilea*. However, Barr (1979a) again treated the family under *Hysteriales* along with *Parmulariaceae*, *Phillipsiellaceae*, *Roccellaceae*, *Opegraphaceae* and *Hysteriaceae* and accepted 16 genera. Eriksson (1982) proposed the name *Lecanidiales* and Hawksworth & Eriksson (1986) formally proposed *Patellariales* to accommodate *Patellariaceae*, *Arthrorhaphidaceae* and *Phillipsiellaceae* based on morphological data. However, Barr (1987b) accepted only *Patellariaceae* within *Patellariales* and accepted nine non-lichenized genera under this family. The author treated *Phillipsiellaceae* under *Arthoniales* based on myriangiaceous morphological features and did not accept *Arthrorhaphidaceae* without justification. However, the heterogeneous nature of this family has been questioned by many authors (Hafellner 1979, Eriksson & Hawksworth 1993a, Eriksson 1994b).

Eriksson & Hawksworth (1993a) accepted 12 genera under *Patellariaceae* by excluding several lichenized genera due to morphological variation and iodine reaction but treated the lichenized *Rhizocarpon* based on having similar ascomatal development. Kutorga & Hawksworth (1997) provided a monograph for *Patellariaceae* accepting 12 genera. Lumbsch & Huhndorf (2010) accepted 15 genera. Yacharoen (2015) provided the latest detailed investigation of this family and accepted 13 genera. However, the number of genera has increased in the past decade by accepting 18 genera (Ekanayaka et al. 2017a). Hongsanan et al. (2020b) and Wijayawardene et al. (2022a) accepted 21 and 19 genera respectively. The genera *Holmiella* and *Rhizodiscina* accepted in Hongsanan et al. (2020a) were not treated by Wijayawardene et al. (2022a). Pem et al. (2018) provided the latest taxonomic study for *Holmiella* by introducing two novel taxa and Yasin (2018) established a new genus *Rhizodiscina* without molecular data. However, Maharachchikumbura et al. (2021b) established a new family (*Holmiellaceae*) and the order to accommodate (*Holmiellales*) to accommodate the saprobic genus *Holmiella* based on morphology and phylogeny. Presently, 19 genera are accepted under *Patellariales* (Hyde et al. 2024b).

General description

The taxa are mostly characterized by strong cupulate ascomata that are rolled when dry, a hymenium with narrow anastomosing pseudoparaphyses and asci, and pseudoparaphyses initially attached to both the base and apex, but later become free at the apex (Kutorga & Hawksworth 1997). The asexual morph is not commonly reported. However, some species previously placed in *Rhytidhysteron* (von Arx & Müller 1975, Barr 1987b, Kutorga & Hawksworth 1997, Eriksson 2006, Lumbsch & Huhndorf 2010) have aposphaeria-like and diplodia-like asexual morphs (Yacharoen et al. 2015) but are presently placed in *Hysteriaceae*. *Holmiella sabina* shows a corniculariella-like asexual morph (Yacharoen et al. 2015). Pem et al. (2018) reported chlamydospores (asexual structures) from the cultures of *Holmiella junipericola*. However, *Holmiella* is presently placed in *Holmiellales* (Maharachchikumbura et al. 2021b).

Sexual morph: *Apothecia* mostly superficial, slightly immersed at beginning or rarely erumpent, solitary, scattered or in small aggregated groups, uniloculate, closed when young, opened at maturity, subglobose to globose, disc flattened or deeply cup-shaped, or convex, somewhat ellipsoid, with longitudinal or rounded opening, often folding at the rim, center, smooth, rough or zigzagged, thick or velvet in the middle, mostly black. *Anchoring hyphae* (vegetative hyphae) are branched, septate, brown to dark brown, connecting apothecia with host surface. *Exciple* (peridium) mostly comprising 2 layers, outer layer thicker than inner layer, pseudoparenchyma were formed, conjugated on host surface at the base, isodiametric cells or rarely of elongated and radiating cells, outer layer dense, compact with pigmented cells, usually binding with lighter inner layer which were, indistinct in some genera. *Hypothecium* (layer for which asci originate) or subhymenium, binding to exciple layer, inverted conically, merged with the host surface at the base, compressed, being pseudoparenchymatous, rarely prosenchymatous, slightly varied in thickness, hyaline. *Hamathecium* (sterilized tissue) always originating between asci, continuing growth in same direction as asci. *Pseudoparaphyses* present, erected or branched, septate or aseptate, slightly swollen on the apex, usually anastomosing, and forming a dark brown or black epithecium over the asci. *Asci* reproductive hyphae, originated on hypothecium layer, growth parallel with hamathecium, 8-spored, rarely for 4–6-spored, bitunicate, fissitunicate in some genera, cylindrical to oblong, clavate, broad in the middle, narrowed at the stipe with or without a pedicel. *Ascospores* obovoid or clavate or elliptic to oblong, mostly constricted at the septa, rounded at both ends, 1–3-septate, some muriform or euseptate, hyaline or brown to dark brown. Asexual morphs: Undetermined (Fig. 76).

Families included in *Patellariales*

Patellariaceae Corda

Evolution

The divergence time for *Patellariales* is estimated as 276 MYA (stem age, Hongsanan et al. 2020a).

Significance

Ecological and economic roles

The taxa are reported as saprobes on bark or wood, weak parasites, or rarely lichenized and mostly found on terrestrial habitats and occasionally in aquatic habitats (Kirk et al. 2008a, Jones et al. 2015) and are distributed worldwide (Kutorga & Hawksworth 1997). Notably, *Rhizodiscina lignyota* has been recorded on a basidiomycete (Yasin 2018).

Chemical diversity

The chemical diversity is not reported in the members of *Patellariales*.

Other relevant data and future recommendations

The order is mostly understudied and many taxa lack molecular data. The asexually reported species were transferred to different families, and no species have been reported in their asexual morph. Thus, further investigations are needed for the better taxonomic resolution of this group.

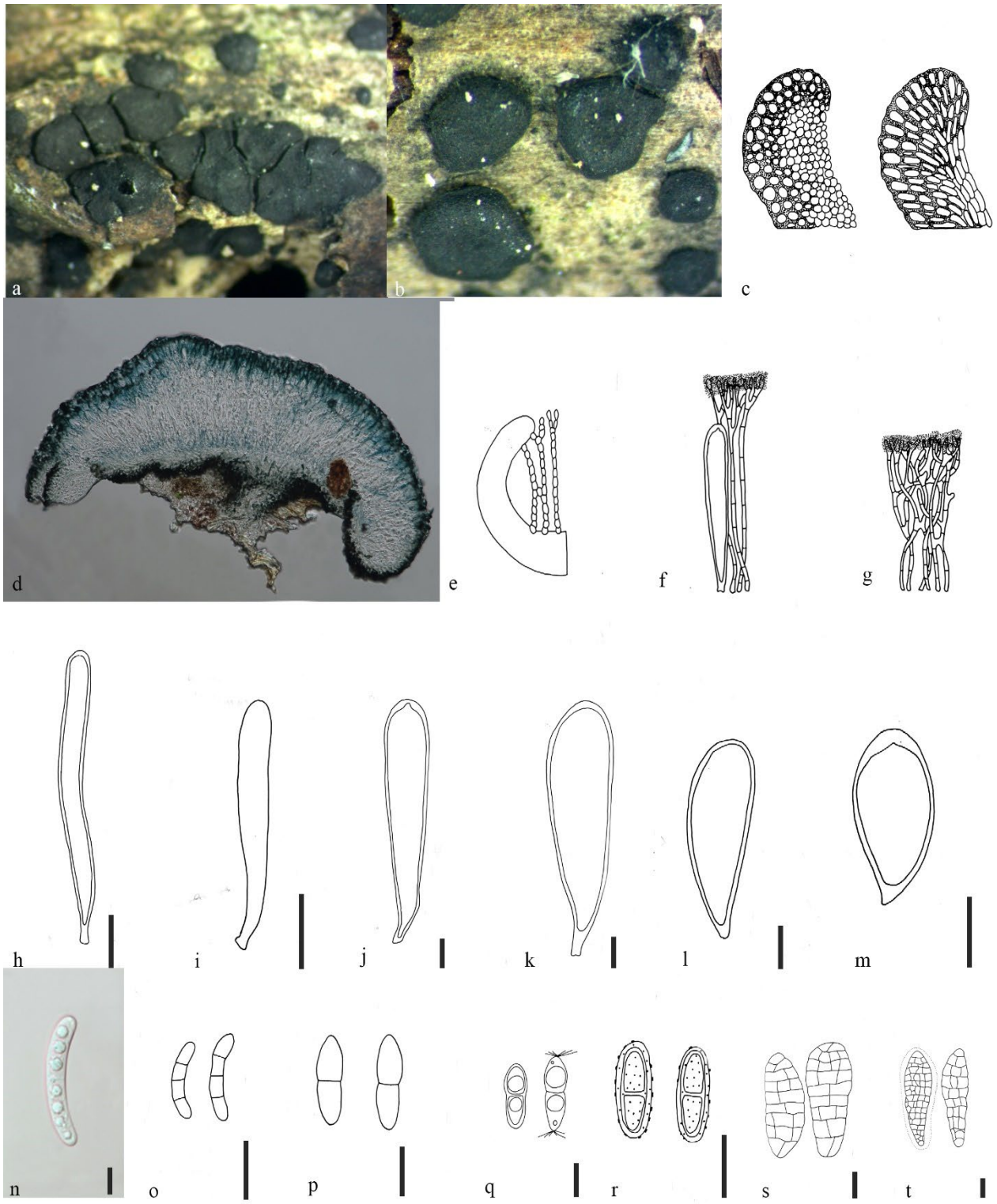


Figure 76 – Morphology of *Patellariales*. a, b Ascomata. c Exciple types. d Vertical section through ascoma. e Individual cells short and somewhat swollen to moniliform. f Individual cells elongated and branched towards the apices. g Individual cells elongated and branched and anastomosed (a–g *Patellaria* sp). h–m Ascus (h *Stratisporella episemoides*, i *Xylogramma mauriatra*, j *Tryblidaria fenestrate*, k *Haematomyxa vinosa*, l *Baggea pachyascus*, m *Banhegyia setispora*). n–t Ascospore (n *Patellaria* sp., o *Baggea pachyascus*, p *Xylogramma mauriatra*, q *Banhegyia setispora*, r *Stratisporella episemoides*, s *Haematomyxa vinosa*, t *Tryblidaria fenestrate*) (redrawn from Kutorga & Hawksworth 1997). Scale bars: a–m = 20 µm, n–t = 10 µm.

Phaeosclerales **G.G. Barreto, Souza-Motta, G.A. Silva, J.Z. Groenew., Crous & J.D.P. Bezerra, Fungal Systematics and Evolution 14: 85 (2024)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction & History

Phaeosclerales was introduced by Barreto et al. (2024) to accommodate a newly established family *Phaeoscleraceae* with the monotypic genus *Phaeosclera* that was introduced to accommodate *Phaeosclera dematioides*. The species was reported from the pith of *Pinus contorta* in Albert, Canada in its hyphomycetous asexual state that produced bulbil-like masses of cells (Sigler et al. 1981). *Phaeosclera* was accepted under *Dothideomycetes* genera *incertae sedis* (Wijayawardene et al. 2020, 2022a, Pem et al. 2024). The genus recovered as a basal clade to *Myriangiales*, *Endosporiales* and *Endophytiales* in the phylogenetic analyses conducted by Barreto et al. (2024). Thus, a new order *Phaeosclerales* was established based on the evidence from morphological, molecular and ecological variations (Barreto et al. 2024).

General description

The order has been established only on asexual morphology (Barreto et al. 2024).

Sexual morph: Not observed. Asexual morph: *Hyphae* dematiaceous and septate. *Bulbil-like masses* are smooth, dark brown, and with variable size, occasionally covered in a slimy coating. *Sclerotic cells* produced by the conversion of short strands of hyphae (adapted from Barreto et al. 2024) (Fig. 77).

Families included in *Phaeosclerales*

Phaeoscleraceae G.G. Barreto, Souza-Motta, G.A. Silva, J.Z. Groenew., Crous & J.D.P. Bezerra

Significance

Ecological and economic roles

Phaeosclera was originally reported as the pith of *Pinus contorta* (*Pinaceae*) in North America (Sigler 1981). McGinnis et al. (1985a) reported *Phaeosclera dematioides* as an etiologic agent of phaeohyphomycosis in cattle. Later studies reported that the same species also caused phaeohyphomycosis in humans (Matsumoto et al. 1987, Palencarova et al. 1995).

Chemical diversity

No relevant studies are available for the chemical diversity of *Phaeosclerales*.

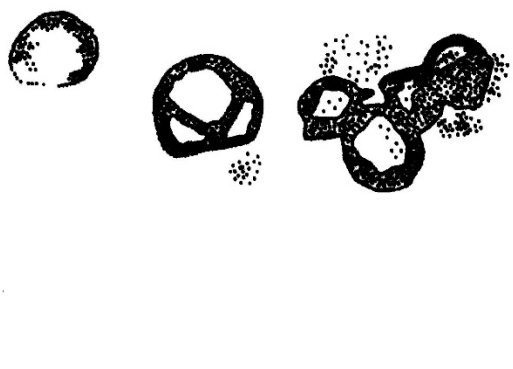


Figure 77 – Asexual morph of *Phaeosclerales* (*Paeosclera dematioides* in submucosal tissue of frontal nasal cavity of cattle) (redrawn from McGinnis et al. 1985a). Scale bar = 10 μm.

Phaeothecales **Abdollahz. & Crous, Studies in Mycology 95: 393 (2020)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Dothideomycetidae*

Introduction

In a multigene phylogenetic study, *Capnodiales* was recognized as polyphyletic and was split into seven orders, including *Phaeothecales* (Abdollahzadeh et al. 2020). In accordance with Crous et al. (2016b), *Phaeotheca* species were placed in two distinct clades introduced as two orders: *Phaeothecales* and *Neophaeothecales*. *Phaeothecales* was established based on the type species *Phaeotheca fissurella* (CBS 520.89), as a sister group of *Racodiales* (Abdollahzadeh et al. 2020).

History

Phaeotheca was introduced by Sigler et al. (1981) based on *P. fissurella* as a psychrophilic species producing endoconidia. DesRochers & Ouellette (1994) introduced the second species *Phaeotheca dimorphospora,* producing two types of endoconidia with optimum temperature 23 ℃ as compared to 15.5 ℃ for the type species *Phaeotheca fissurella*. *Phaeotheca triangularis* and *P. salicornia* (De Hoog et al. 1997, Crous et al. 2016b), differed from the other species by producing septate endoconidia. Phylogenetic studies based on LSU sequence data placed *Phaeotheca* in *Capnodiales* and recognized it as a polyphyletic genus and placed the type species *P. fissurella* in a distinct clade apart from *P. triangularis* and *P. salicornia* (Crous et al. 2007a, 2009c, 2016b). Crous et al. (2018a) introduced *Phaeotheca shathenatiana* and placed it together with *Phaeotheca fissurella* in the newly established family *Phaeothecaceae*. Finally, in a phylogenetic study by Abdollahzadeh et al. (2020), *Capnodiales* was split to seven orders and the species of *Phaeotheca* were placed in two newly established orders *Phaeothecales* (incl. the type species *P. fissurella*) and *Neophaeothecales* (incl. *P. triangularis* and *P. salicornia*). However, Hongsanan et al. (2020a) treated *Phaeothecaceae* as a member of *Capnodiales* but was accepted under the *Phaeothecales* (Hyde et al. 2024b, Pem et al. 2024).

General description

Sexual morph: Undetermined. Asexual morph: *Mycelium* consisting of hyaline to brown, smooth-walled, septate, branched hyphae, terminal or intercalary cells becoming swollen, developing numerous endoconidia. *Endoconidia* brown, smooth to verruculose, thin- to thick-walled, globose to obovoid, unicellular (adapted from Crous et al. 2018a) (Fig. 78).

Families included in *Phaeothecales*

Phaeothecaceae B.A. Darveauxoron.

Justification of order and problems

Phaeothecales forms a distinct clade recognized based on LSU and RPB2 sequence data which is also supported by ecology, lifestyle and morphology. There is no DNA sequence data available for *P. dimorphosa,* which is necessary to determine its taxonomic position but it is concurrently placed in *Phaeotheca* based on morphology.

Significance

Ecological and economic roles

Phaeothecales taxa are known as endoconidia producing fungi (Sigler et al. 1981, Abdollahzadeh et al. 2020). They are slow growing saprobic fungi which usually found in dry and extreme conditions and are reported on cankers, leaves and twigs.

Chemical diversity

Relevant studies are not available for the chemical diversity of *Phaeothecales*.

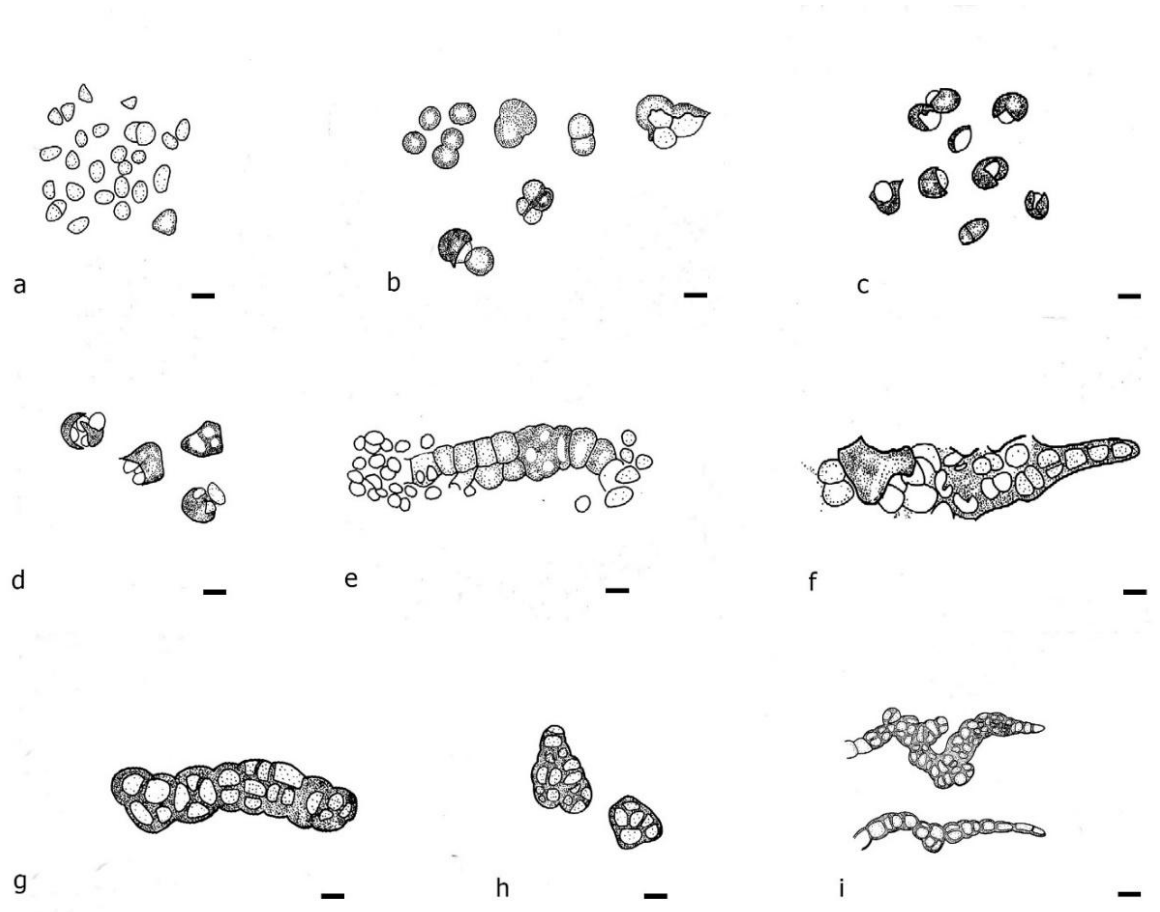


Figure 78 – Morphology of *Phaeothecales*. a Young endoconidia of *Phaeotheca fissurella*. b Swollen endoconidia *P. fissurella*. c, d Mother cells liberating endoconidia of *P. fissurella*. e, f Hyphae releasing endoconidia of *P. fissurella*. g, h Meristematic development of *P. fissurella* (redrawn from Zalar et al. 1999b). Scale bars: a–i = 10 μm.

Other relevant data and future recommendations

Three species have been discovered in a single genus *Phaeotheca,* within this order thus further sampling is needed to shed light on different aspects of evolution, ecology, physiology, chemistry and their potential roles in agriculture and industry.

***Phaeotrichales* Ariyaw. Jian K. Liu & K.D. Hyde, Fungal Diversity 63: 9 (2013)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Phaeotrichales comprised three genera, *viz*. *Echinoascotheca*, *Phaeotrichum* and *Trichodelitschia*, that are reported as coprophilous fungi (Hyde et al. 2013, Hongsanan et al. 2020a). The taxa are characterized by unilocular, stromatic, globose ascomata with a thin, carbonaceous peridium and dark brown to reddish-brown ascospores with terminal germ pores (Hyde et al. 2013). No asexual morph has been reported from these species (Hyde et al. 2013).

History

Phaeotrichales was introduced to accommodate a single family *Phaeotrichaceae* (Hyde et al. 2013). *Phaeotrichaceae* was introduced to accommodate the single genus *Phaeotrichum* (*P. circinufum* and the type *P. hystrioilaum*) and was characterized by dark brown, septate ascospores with terminal germ pores (Cain 1956a). The ordinal position of *Phaeotrichaceae* was not determined

by Cain (1956a). The family was placed in *Pleosporales* which was also accepted by Cannon & Kirk (2007). Barr (1987b) synonymized *Sporormiaceae* under *Phaeotrichaceae*. Later, Barr (1990a) treated them as separate families and placed *Phaeotrichaceae* under *Sordariales*, misinterpreting *Phaeotrichaceae* as having unitunicate asci. Barr (2000) finally restricted *Phaeotrichaceae* for the species with ascospores with germ pores and treated this family under *Pleosporales* based on bitunicate and fissitunicate asci with a well-developed refractive apical ring. However, the family contradicts the concept of *Pleosporales* in its lack of pseudoparaphyses, has cleistothecial ascomata with long setae, and conspicuous ascospores with germ pores at each end (Zhang et al. 2009b). A single unverified isolate of *Phaeotrichum benjaminii* recovered outside of *Pleosporales* in the phylogenetic study conducted by Schoch et al. (2009b). Zhang et al. (2012b) placed this family in *Dothideomycetes incertae sedis* and stated the need for broad molecular analysis. *Phaeotrichaceae* formed a strong monophyletic clade and sister to *Venturiaceae* in the SSU, LSU and mtSSU phylogenetic analyses (Kruys 2005). The family formed a distinct lineage and clustered in a clade with *Asterinales*, *Microthyriales* and *Venturiales* in the phylogenetic analyses conducted based on LSU, SSU, TEF1-α and RPB2 sequence data (Hyde et al. 2013). Thus, a new order *Phaeotrichales* was introduced. The order formed a sister clade to *Venturiales* in the ITS and LSU based phylogenetic analyses conducted by Hongsanan et al. (2020a).

General description

Phaeotrichum possesses untypical bitunicate asci. Its ascospore release mechanism was described as "simply breaking down and allowing the contents to become free in the cavity of the ascocarp". This type of release mechanism was considered as evolutionarily developed by Cain (1956a). Barr (1956) studied the development stage of *P. hystrioilaum* and defined it as *Phaeotrichum* developmental type based on the formation of ascostromata which remain completely closed, the development of thin-walled, unitunicate asci in fascicles scattered throughout the locule, and the deliquescence of asci at maturity that also occurs in *Eurotiales* (Hyde et al. 2013).

Sexual morph: *Ascomata* solitary, or in small groups, superficial, unilocular, stromatic, globose, black, perithecial or cleistothecial setose. *Peridium* thin, carbonaceous, membraneous. *Hamathecium* tissue absent or of evanescent cellular pseudoparaphyses *Asci* 8-spored, bitunicate, fissitunicate, in irregular or arranged in little groups or bundles and evanescent at maturity and sometimes with an apical ring, or without apical ring. *Ascospores* uniseriate or partially overlapping, dark brown to reddish-brown, sometimes fragmenting, composed of terminal germ pores, with or without a sheath. Asexual morph: Undetermined (Fig. 79).

Families included in *Phaeotrichales*

Phaeotrichaceae Cain

Evolution

The divergence time for *Phaeotrichales* is estimated as 229 MYA (Hongsanan et al. 2020a).

Justification of order and problems

Phaeotrichum accommodates five species, but molecular data are available for only two species. *Echinoascotheca* and *Trichodelitschia* both lack molecular data including the type species of *Phaeotrichum*.

Significance

Ecological and economic roles

The members of the order are reported as coprophilous from terrestrial habitats (Cain 1956a, Ebersohn & Eicker 1992, Matsushima 1995, Hyde et al. 2013, Hongsanan et al. 2020a). *Phaeotrichum* species have been reported on dung but *P. setosum* has been reported in soil (Hongsanan et al. 2020a).

Chemical diversity

No relevant studies are available for the chemical diversity of members of *Phaeotrichales*.

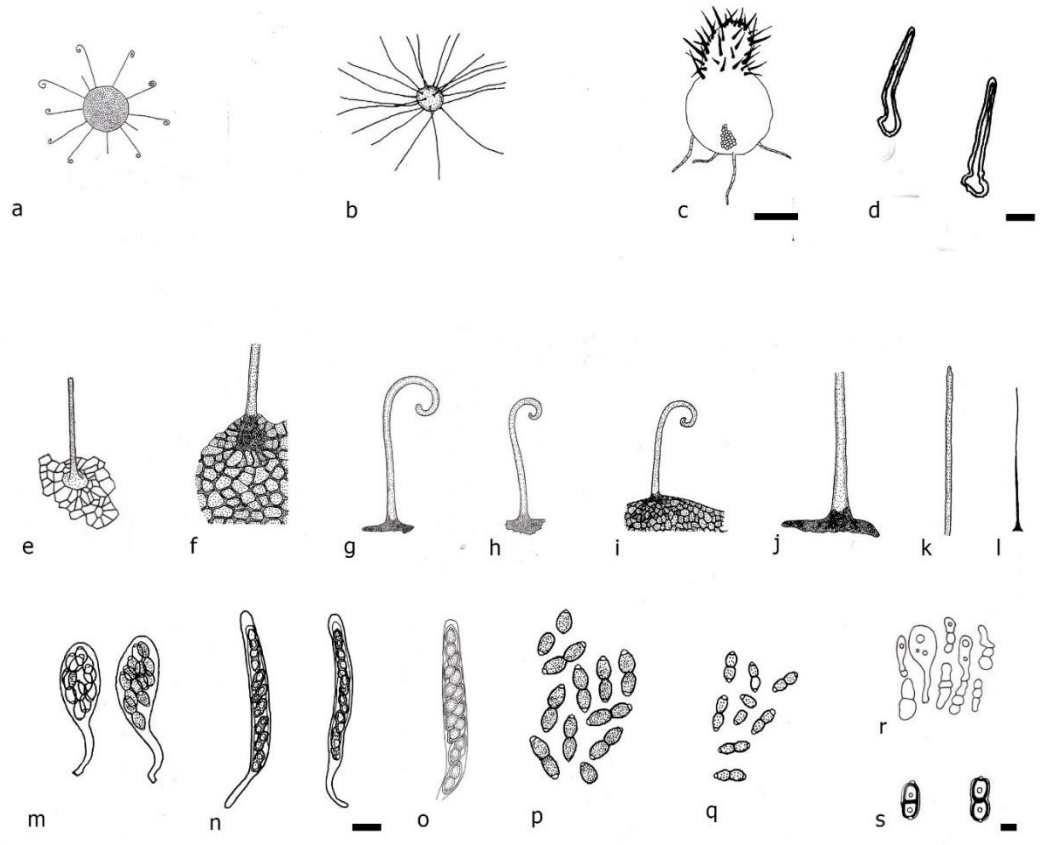


Figure 79 – Morphology of *Phaeotrichales*. a Ascomata with appendages of *Phaeotrichum circinatum*. b Ascomata with appendages of *Phaeotrichum hystricinum*. c Pseudothecium of *Trichodelitschia sweniensis*. d Spiny appendages of *Trichodelitschia sweniensis*. e Peridium surface showing attachment of appendage of *P. benjanlini*. f Part of peridium with basic of an appendage of *P. hystricinum*. g Appendages of *Phaeotrichum circinatum*. h Appendages of *P. circinatum*. i Partial cells of ascomata with appendage of *P. circinatum*. j Base of appendages of *P. hystricinum*. k Apex of appendage of *P. hystricinum*. l Appendages of *P. hystricinum*. m Ascospores of *P. hystricinum*. n Asci of *Trichodelitschia sweniensis*. o Asci of *T. bisporula*. p, q Ascospores of *P. hystricinum*. r Young asci and ascogenous cells of *P. circinatum*. s Ascospores of *Trichodelitschia sweniensis* (redrawn from Cain 1956a, Ebersohn & Eicker 1992). Scale bars: c = 100 µm, d–n = 10 µm.

Pleosporales **Luttr. ex M.E. Barr, Prodromus to class Loculoascomycetes: 67 (1987)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Pleosporomycetidae*

Introduction

Pleosporales, are a diverse group of Ascomycetes, characterized by a cosmopolitan distribution. Presently, *Pleosporales* stands as the largest order within *Dothideomycetes*, encompassing ~11,100 species. This number represents about 34%, of all species classified under this class (Bánki et al. in 2023). The order is diverse in its family and genus composition, with 95 families and 690 genera (this study). Of these genera, 44 are currently placed in the ‘genera *incertae sedis*', indicating a level of uncertainty in their precise classification. *Pleosporales* is systematically divided into two distinct suborders *viz*. *Massarineae* and *Pleosporineae*. Within this order, approximately 50%, of the species are members of three families: *Didymellaceae*,

Phaeosphaeriaceae and *Pleosporaceae*. This highlights the dominance of these families within the order. Species belonging to *Alternaria*, *Ascochyta sensu lato*, *Leptosphaeria sensu lato* and *Phoma sensu lato* are particularly noteworthy, each containing more than 500 species. The evolutionary timeline of the *Pleosporales* is estimated to date back to 205 MYA (stem age), a testament to their long-standing presence and adaptation through geological eras. The species within this order have adapted to a wide range of ecological niches and life modes. These include functioning as epiphytes, saprobes, endophytes, and parasites. They also play roles as pathogens, which is significant from an ecological and economic perspective, particularly as they can be hyperparasites affecting fungi or insects and may exist as lichenized fungi (Zhang et al. 2012b, Hyde et al. 2013, Wanasinghe et al. 2018, Hongsanan et al. 2020a, Pem et al. 2024). A notable aspect of *Pleosporales* is their impact on economically important crops, as numerous species within this order are pathogens causing various plant diseases. The structural characteristics of *Pleosporales* are distinctive. They have perithecioid ascomata, often accompanied by a papilla. The asci are bitunicate and typically fissitunicate, containing mostly septate ascospores. These ascospores exhibit a range of colors and shapes and may be enveloped by a gelatinous sheath (Zhang et al. 2012b, Hyde et al. 2013, Jaklitsch & Voglmayr 2016, Jaklitsch et al. 2018). The morphological classifications of the order are determined by the structure of their ascomata, shape and arrangement of asci within locules, presence and type of hamathecium, configuration of papillae or ostioles, form of ascospores and their natural habitats. Different species in *Pleosporales* exhibit varied ecological or morphological traits. For example, *Leptosphaeriaceae* species can be either saprobic or parasitic, featuring lightly colored ascospores with multiple septa. *Lophiostomataceae* typically lead a saprobic existence, distinguished by ascomata with a flattened apex. *Sporormiaceae*, being coprophilous, have heavily pigmented ascospores with multiple septa and germ slits and may have ostioles that are either aperiphysate or periphysate. As for their asexual forms, *Pleosporales* primarily appear as coelomycetes, although some may appear as hyphomycetes (Zhang et al. 2012b, Hyde et al. 2013, Liu et al. 2024).

History

Pleosporaceae (type of *Pleosporales*) was earlier placed in *Sphaeriales*, based on morphological characteristics such as immersed ascomata and the presence of pseudoparaphyses (Ellis & Everhart 1892, Lindau 1897c, Winter 1887, Wehmeyer 1975). However, the family underwent a reassignment when Theissen & Sydow (1918), followed by Wehmeyer (1975), placed it within the *Pseudosphaeriaceae*. This shift coincided with the introduction of the *Pseudosphaeriales* by Theissen & Sydow (1918). *Pseudosphaeriales*, primarily represented by *Pseudosphaeriaceae*, was distinguished from *Dothideales* due to its characteristic uniloculate, perithecioid ascostromata. This classification, however, faced challenges. Luttrell (1955) argued that the character of uni- or pluri-loculate ascostromata was insufficient for differentiating orders within *Dothideomycetes*. Consequently, the familial type of *Pseudosphaeriales*, along with its type genus, *Pseudosphaeria*, was transferred to *Dothideales*. This transfer effectively rendered *Pseudosphaeriales* a synonym of *Dothideales*. Amidst this taxonomic reshuffling, the term "*Pseudosphaeriales*" had been applied in various contexts, leading to confusion. To address this, Luttrell (1955) proposed the name "*Pleosporales*" (though initially invalid due to the absence of a Latin diagnosis) as a replacement for the confusing term *Pseudosphaeriales*. This new order, *Pleosporales*, initially included seven families *viz*. *Botryosphaeriaceae*, *Didymosphaeriaceae*, *Herpotrichiellaceae*, *Lophiostomataceae*, *Mesnieraceae*, *Pleosporaceae* and *Venturiaceae*. Müller & von Arx (1962) reused the term *Pseudosphaeriales* but expanded its scope to include 12 families: *Capnodiaceae*, *Chaetothyriaceae*, *Dimeriaceae*, *Lophiostomataceae, Mesnieraceae*, *Micropeltaceae*, *Microthyriaceae*, *Mycosphaerellaceae*, *Pleosporaceae*, *Sporormiaceae*, *Trichothyriaceae* and *Venturiaceae*.

Luttrell (1973), made significant contributions to the classification of the *Pleosporales*, based on a range of morphological characteristics. These included the structure of ascomata, the morphology of asci and their arrangement in locules, the presence and type of hamathecium, the shape of papillae or ostioles, the morphology of ascospores, and the type of habitats. Based on these

criteria, he included eight families within *Pleosporales*: *Botryosphaeriaceae*, *Dimeriaceae*, *Lophiostomataceae*, *Mesnieraceae*, *Mycoporaceae*, *Pleosporaceae*, *Sporormiaceae* and *Venturiaceae*. Von Arx & Müller (1975) proposed a reclassification, accepting only a single order, *Dothideales*, which they divided into two suborders. The first, *Dothideineae*, included *Atichiales*, *Dothiorales*, *Hysteriales* and *Myriangiales*, while the second, *Pseudosphaeriineae*, comprised *Capnodiales*, *Chaetothyriales*, *Hemisphaeriales*, *Lophiostomatales*, *Microthyriales*, *Perisporiales*, *Pleosporales*, *Pseudosphaeriales* and *Trichothyriales*. However, this proposal was not widely adopted in the mycological community. Barr (1979b) accepted three existing families: *Lophiostomataceae*, *Pleosporaceae* and *Venturiaceae*; and added 11 others into *Pleosporales*, organizing these families into six suborders. In this classification, the morphology of pseudoparaphyses was given significant emphasis at the order level. Barr (1983a) further refined the taxonomy by introducing *Melanommatales* to accommodate taxa with trabeculate pseudoparaphyses, characterized by sporormia-like centrum development. This was distinct from the cellular pseudoparaphyses (pleospora-like centrum development) found in members of *Pleosporales*. *Melanommatales*, as defined by Barr (1990a), included *Didymosphaeriaceae*, *Fenestellaceae*, *Massariaceae*, *Melanommataceae*, *Microthyriaceae*, *Mytilinidiaceae*, *Platystomaceae* and *Requienellaceae*.

Pleosporales was formally recognized by Barr (1987b). This order was described with perithecioid ascomata usually with a papillate apex, ostioles that may or may not contain periphyses, the presence of cellular pseudoparaphyses, bitunicate asci, and ascospores with varying shapes, pigmentation, and septation. Initially, 18 families were included: *Arthopyreniaceae*, *Botryosphaeriaceae*, *Cucurbitariaceae*, *Dacampiaceae*, *Dimeriaceae*, *Hysteriaceae*, *Leptosphaeriaceae*, *Lophiostomataceae*, *Parodiellaceae*, *Phaeosphaeriaceae*, *Phaeotrichaceae*, *Pleomassariaceae*, *Pleosporaceae*, *Polystomellaceae*, *Pyrenophoraceae*, *Micropeltidaceae*, *Tubeufiaceae* and *Venturiaceae*. Subsequent phylogenetic analyses, particularly those based on DNA sequence comparisons, brought significant insights into the natural groupings within these orders. Studies by Reynolds (1991), Liew et al. (2000) and Lumbsch & Lindemuth (2001), indicated that the separation of orders (*Pleosporales* and *Melanommatales*) based on the *Pleospora* or *Sporormia* centrum type did not reflect a natural grouping. As a result, *Melanommatales* was merged into *Pleosporales*. Further refinement of the *Pleosporales* taxonomy continued with the addition of six more families: *Cucurbitariaceae*, *Diademaceae*, *Didymosphaeriaceae*, *Mytilinidiaceae*, *Testudinaceae* and *Zopfiaceae* (Lumbsch & Huhndorf 2007). Intensive sampling and multigene phylogenetic studies led to the acceptance of 20 families within *Pleosporales*. These included *Aigialaceae*, *Amniculicolaceae*, *Delitschiaceae*, *Didymellaceae*, *Didymosphaeriaceae*, *Hypsostromataceae*, *Lentitheciaceae*, *Leptosphaeriaceae*, *Lindgomycetaceae*, *Lophiostomataceae*, *Massarinaceae*, *Melanommataceae*, *Montagnulaceae*, *Morosphaeriaceae*, *Phaeosphaeriaceae*, *Pleosporaceae*, *Pleomassariaceae*, *Sporormiaceae*, *Tetraplosphaeriaceae* and *Trematosphaeriaceae* (Boehm et al. 2009b, c, Mugambi & Huhndorf 2009, Schoch et al. 2009b, Shearer et al. 2009, Suetrong et al. 2009, Tanaka et al. 2009, Zhang et al. 2009a). Additionally, five other families *viz*. *Arthopyreniaceae*, *Cucurbitariaceae*, *Diademaceae*, *Teichosporaceae* and *Zopfiaceae* were tentatively included in the order (Kruys et al. 2006). However, in Zhang et al. (2011b), the *Venturiaceae* was excluded from *Pleosporales* and placed in a new order, *Venturiales*.

The study of the *Pleosporales* reached a significant milestone with the monograph provided by Zhang et al. (2012b). This work offered detailed descriptions for 174 genera and recognized 25 families within the order, marking it as a key resource for mycologists and taxonomists studying this group. In addition to providing a broad overview of the order, Zhang et al. (2012b) specifically addressed the suborder *Massarineae* within *Pleosporales*. They included five families in this suborder: *Lentitheciaceae*, *Massarinaceae*, *Montagnulaceae*, *Morosphaeriaceae* and *Trematosphaeriaceae*. Further expanding the knowledge on *Pleosporales*, Hyde et al. (2013) work "Families of *Dothideomycetes*" placed 41 families within the order. Notably, they introduced *Anteagloniaceae*, *Bambusicolaceae*, *Biatriosporaceae*, *Salsugineaceae* and *Thyridariaceae* as new families within the order.

Following a series of studies that incorporated both morphological and phylogenetic evidence, a significant expansion of the *Pleosporales* occurred with the introduction of 48 new families. This began in 2014 with the introduction of *Acrocalymmaceae* by Trakunyingcharoen et al. (2014) and *Roussoellaceae* by Liu et al. (2014a). The following year, 2015, was particularly notable for its additions of *Amorosiaceae* by Thambugala et al. (2015), *Ascocylindricaceae* by Ariyawansa et al. (2015) *Astrosphaeriellaceae* by Phookamsak et al. (2015), *Latoruaceae* and *Macrodiplodiopsidaceae* by Crous et al. (2014b), *Neophaeosphaeriaceae* by Ariyawansa et al. (2015), *Parabambusicolaceae* by Tanaka et al. (2015), *Paradictyoarthriniaceae* by Liu et al. 2015a), *Pseudoastrosphaeriellaceae* by Phookamsak et al. (2015), *Sulcatisporaceae* by Tanaka et al. (2015) and *Wicklowiaceae* by Ariyawansa et al. (2015). In 2016, new families *Cyclothyriellaceae* by Jaklitsch & Voglmayr (2016), *Dictyosporiaceae* by Boonmee et al. (2016), *Ligninsphaeriaceae* by Zhang et al. (2016a), *Longipedicellataceae* by Phukhamsakda et al. (2016), *Nigrogranaceae* and *Ohleriaceae* by Jaklitsch & Voglmayr (2016) were added. In 2017 *Aquasubmersaceae* by Hashimoto et al. (2017), *Camarosporiaceae* and *Camarosporidiellaceae* by Wanasinghe et al. (2017b), *Cryptocoryneaceae* by Hashimoto et al. (2017), *Fuscostagonosporaceae* by Hyde et al. (2017b), *Libertasomycetaceae* by Crous & Groenewald (2017), *Lizoniaceae* by Boonmee et al. (2017), *Neocamarosporiaceae* by Wanasinghe et al. (2017a), *Neohendersoniaceae* by Tanaka et al. (2017), *Occultibambusaceae* by Dai et al. (2017), *Pleomonodictydaceae* by Hernández-Restrepo et al. (2017) and *Pseudocoleodictyosporaceae* by Doilom et al. (2017) were introduced. In 2018, *Fusculinaceae* by Crous et al. (2018a), *Lentimurisporaceae* by Liu et al. (2018a), *Neomassariaceae* by Ariyawansa et al. (2018), *Neopyrenochaetaceae* and *Parapyrenochaetaceae* by Valenzuela-Lopez et al. (2018), *Phaeoseptaceae* by Hyde et al. (2018b), *Pseudolophiotremataceae* by Hongsanan et al. (2018), *Pseudopyrenochaetaceae* and *Pyrenochaetopsidaceae* by Valenzuela-Lopez et al. (2018), and *Tzeananiaceae* by Ariyawansa et al. (2018) were introduced. The expansion continued in 2019 with the addition of *Pseudoberkleasmiaceae* by Hyde et al. (2019) and *Striatiguttulaceae* by Zhang et al. (2019a). In 2020 and 2021, families such as *Longiostiolaceae*, *Neomassarinaceae*, *Paralophiostomataceae*, *Pseudomassarinaceae* by Hongsanan et al. (2020b), Mapook et al. (2020a), Phukhamsakda et al. (2020), and *Anastomitrabeculiaceae* by Bhunjun et al. (2021) were introduced, further illustrating the dynamic and evolving taxonomy within *Pleosporales*. In 2023, *Ageratinicolaceae*, *Leptosphaerioidaceae* and *Profundisphaeriaceae* were introduced by Senanayake et al. (2023) and Zhang et al. (2023c). Finally, 95 families are accepted under *Pleosporales*.

General description

Pleosporales typically possess bitunicate and fissitunicate asci, as well as perithecioid-like ascostromata, a common characteristic of *Dothideomycetes*. Most pleosporalean taxa have pseudoparaphyses among their well-arranged asci (Zhang et al. 2009c). The current approach to classifying *Pleosporales* at the family level primarily relies on morphological characteristics of the ascomata, such as size and the shape of the ostiole or papilla. The presence or absence of periphyses and the features of the centrum (including pseudoparaphyses, asci and ascospores) are also critical for classification, as outlined by several mycologists (Barr 1990a, Shearer et al. 2009, Suetrong et al. 2009, Tanaka et al. 2009, Zhang et al. 2009a). Most *Pleosporales* species have uni-loculate ascomata. However, certain families i.e. *Astrosphaeriellaceae*, *Didymosphaeriaceae* and *Parabambusicolaceae* possess ascostromata with multiple locules (Hongsanan et al. 2020a). The presence, absence, and forms of the papilla and ostiole serving as important criteria for classification at the generic level or higher, as initially suggested by Clements & Shear (1931). Later studies, such as those by Zhang et al. (2009b), have demonstrated that the vertically flattened papilla is an effective criterion for familial-level classification, exemplified in families i.e. *Amniculicolaceae* and *Lophiostomataceae*. Papillae and ostioles are present in most *Pleosporales* species. However, *Diademaceae* members are characterized by apothecial ascomata, while certain genera within *Corynesporascaceae*, *Sporormiaceae*, *Testudinaceae* and *Zopfiaceae* possess cleistothecioid ascomata (Zhang et al. 2012b, Hongsanan et al. 2020a). The presence of an ostiolar neck covered by

dark setae is a distinguishing feature used in segregating some genera, such as *Dematiopleospora* in the *Phaeosphaeriaceae* and *Keissleriella* in the *Lentitheciaceae* (Wanasinghe et al. 2018).

The presence of pseudoparaphyses is a distinctive feature of the *Pleosporales*. This characteristic has been documented and discussed in various mycological studies, including those by Liew et al. (2000), Kirk et al. (2008a), Zhang et al. (2012b) and more recently by Hongsanan et al. (2020a). In some *Pleosporales* families, pseudoparaphyses may deliquesce or dissolve as the ascomata mature, but in most members of this order, they are persistent. There is a significant variation in the structure of pseudoparaphyses among different *Pleosporales* species, leading to their tentative division into two types: trabeculate and cellular. Trabeculate pseudoparaphyses, as described by Hongsanan et al. (2020a), are characterized by a diameter of around 1 μm, clear anastomosis between asci, and are embedded in a gelatinous matrix. On the other hand, cellular pseudoparaphyses encompass all other types. The taxonomic significance of these structural differences in pseudoparaphyses has been a subject of re-evaluation (Liew et al. 2000, Zhang et al. 2012b). The majority of species in certain *Pleosporales* families, such as *Aigialaceae*, *Ascocylindricaceae*, *Astrosphaeriellaceae*, *Biatriosporaceae*, *Cyclothyriellaceae*, *Fuscostagonosporaceae*, *Hypsostromataceae*, *Ohleriaceae*, *Pseudoastrosphaeriellaceae*, *Pseudomassarinaceae*, *Salsugineaceae* and *Striatiguttulaceae*, do not produce cellular pseudoparaphyses. This absence marks an important morphological distinction within the order and contributes to the ongoing discussion and study of *Pleosporales* taxonomy and phylogeny.

The asci of *Pleosporales* are primarily bitunicate and usually exhibit a fissitunicate nature. These are mostly cylindrical, clavate, or cylindro-clavate, although they can occasionally be somewhat obclavate or spherical, as observed in the *Corynesporascaceae*. Some genera, such as *Amniculicola* and *Asteromassaria*, feature ocular chambers, while others, like those in the *Astrosphaeriellaceae* and *Massaria*, may possess a large apical ring that reacts to iodine (J-). The ascospores of *Pleosporales* exhibit a range of characteristics. They can be hyaline or variously pigmented. In terms of structure, they can be amerosporous, as seen in species of *Semidelitschia*; phragmosporous, as in *Phaeosphaeria* and *Massariosphaeria*; dictyosporous or muriform, as found in *Camarosporidiella*, *Halojulellaceae*, and *Pleospora*; or scolecosporous, as in species of *Cochliobolus*, *Entodesmium* and *Lophionema*. Although ascospore morphology has traditionally been a key factor in differentiating genera within some families, such as *Arthopyreniaceae* (Watson 1929) and *Testudinaceae* (Hawksworth 1979), its variability even within a single species has been demonstrated. For example, *Mamillisphaeria dimorphospora* produces two types of ascospores: one type is large and hyaline, while the other is comparatively smaller and brown. This variability has led to numerous studies questioning the reliability of ascospore characteristics for classification above the genus level (Zhang et al. 2012b).

Pleosporales exhibits a variety of anamorphic features that are predominantly coelomycetous, although hyphomycetous forms are also common (Wijayawardene et al. 2017b). Anamorphs that resemble *Phoma*, *Pyrenochaeta*, or *Camarosporium* along with their relatives, are among the most common. Most families within the *Pleosporales* are reported to have both coelomycetous and hyphomycetous anamorphic features. For example, families such as *Amniculicolaceae*, *Astrosphaeriellaceae*, *Leptosphaeriaceae*, *Massarinaceae*, *Parabambusicolaceae* and *Phaeosphaeriaceae* exhibit both forms. On the other hand, certain families are known only for their coelomycetous anamorphs, i.e. *Camarosporidiellaceae*, *Didymellaceae*, *Roussoellaceae* and *Sporormiaceae*, while families i.e. *Dictyosporiaceae*, *Hermatomycetaceae* and *Periconiaceae* are reported only with hyphomycetous anamorphs. The presence and characteristics of anamorphs are significant for taxonomic classification within the *Pleosporales*. Anamorphs can be critical for distinguishing higher-rank taxa. For instance, the specific traits of the anamorph of *Neocamarosporiaceae* were crucial in differentiating it from *Pleosporaceae*. This highlights the importance of understanding both the teleomorphic and anamorphic stages of fungi in the study of *Pleosporales*, particularly for accurate identification and classification.

Sexual morph: *Ascomata* stromatic, uni- or multi-loculate, pseudothecial, cleistothecial or apothecial, solitary or in groups, immersed to superficial or erumpent through host tissue, globose to

subglobose, pyriform or vary in shape, coriaceous, with or without ostioles, setae and periphyses, glabrous or setose brown to black. *Peridium* single or multi-layered, composed of angular to globose, black to hyaline cells. *Hamathecium* comprising or lacking trabeculate or cellular pseudoparaphyses. *Asci* cylindrical to clavate or ellipsoidal or occasionally obclavate or spherical, bitunicate, fissitunicate, with or without an ocular chamber, sessile to subsessile, or usually with a short pedicel. *Ascospores* filiform or ellipsoidal to fusiform, aseptate or septate, hyaline or colored, smooth- or rough-walled, with or without guttules, thin- or thick-walled, with or without various types of appendages and/or sheaths. Asexual morph: coelomycetous or hyphomycetous. *Coelomycetes: Conidiomata* acervular or pycnidial, solitary or gregarious, immersed to erumpent, uni- or multi-loculate, with or without an ostiole. *Conidiomatal wall* composed of angular to globose hyaline to brown cells. *Conidiophores* cylindrical to ampulliform, sometimes reduced to conidiogenous cells. *Conidiogenous cells* holoblastic, enteroblastic, phialidic, annellidic, integrated to discrete, doliiform, lageniform or cylindrical, sympodial or percurrent proliferations, hyaline to brown. *Conidia* vary in shape, hyaline to brown, aseptate or septate, walls smooth or rough, echinulate, punctuate or verrucose, some with appendage or mucilaginous sheath. *Hyphomycetes: Conidiomata* sporodochial or synnematal, solitary to gregarious. *Conidiophores* macronematous to micronematous, mononematous or synnematous, straight or flexuous, aseptate or septate, unbranched or branched, hyaline to brown. *Conidiogenous cells* blastic, phialidic, integrated or discrete, determinate or proliferating sympodially or percurrently, mostly cylindrical or oblong. *Conidia* solitary or in chains, acrogenous, pleurogenous or acropleurogenous, vary in shape, straight to curved, rounded or obtuse to truncate at apex, truncate at base, aseptate or septate, hyaline to dark brown, echinulate, punctuate or verrucose (Figs. 80, 81, 82, 83, 84).

Families included in *Pleosporales*

Acrocalymmaceae Crous & Trakun.
Ageratinicolaceae Li Lu, K.D. Hyde & Tibpromma
Aigialaceae Suetrong, Sakay., E.B.G. Jones, Kohlm., Volkm.-Kohlm. & C.L. Schoch
Amniculicolaceae Y. Zhang ter, C.L. Schoch, J. Fourn., Crous & K.D. Hyde
Amorosiaceae Thambug. & K.D. Hyde
Anastomitrabeculiaceae Bhunjun, Phukhams. & K.D. Hyde
Anteagloniaceae K.D. Hyde, Jian K. Liu & A. Mapook
Aquasubmersaceae A. Hashim. & Kaz. Tanaka
Ascocylindricaceae Abdel-Wahab, Bahkali, E.B.G. Jones, Ariyaw. & K.D. Hyde
Astrosphaeriellaceae Phook. & K.D. Hyde (= *Caryosporaceae* Huang Zhang, K.D. Hyde & Ariyaw.)
Bambusicolaceae D.Q. Dai & K.D. Hyde
Biatriosporaceae K.D. Hyde
Camarosporiaceae Wanas., Wijayaw., K.D. Hyde & Crous
Camarosporidiellaceae Wanas., Wijayaw., Crous & K.D. Hyde
Coniothyriaceae W.B. Cooke
Corynesporascaceae Sivan.
Cryptocoryneaceae A. Hashim. & Kaz. Tanaka
Cucurbitariaceae G. Winter (= *Fenestellaceae* M.E. Barr)
Cyclothyriellaceae Jaklitsch & Voglmayr
Didymosphaeriaceae Munk
Dothidotthiaceae Crous & A.J.L. Phillips
Fuscostagonosporaceae Jayasiri, Camporesi & K.D. Hyde
Fusculinaceae Crous
Halojulellaceae Suetrong, K.D. Hyde & E.B.G. Jones
Halotthiaceae Ying Zhang, J. Fourn. & K.D. Hyde
Hermatomycetaceae Locq.
Hypsostromataceae Huhndorf

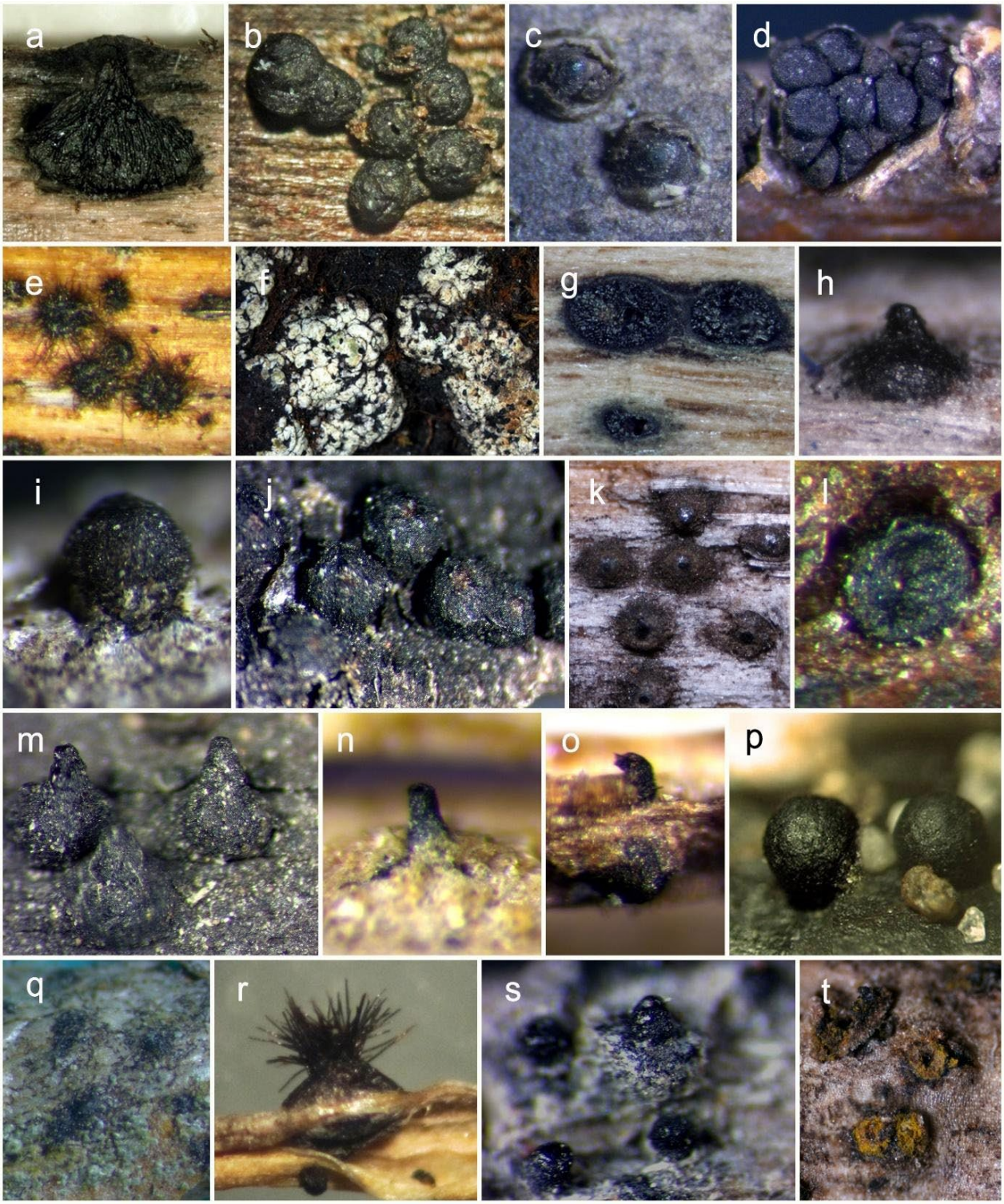


Figure 80 – Morphology of ascomata of *Pleosporales*. a *Aigialus grandis*. b *Amniculicola lignicola*. c *Astragalicola vasilyevae*. d *Camarosporidiella caraganicola*. e *Comoclathris sedi*. f *Dacampia hookeri*. g *Halojulella avicenniae*. h *Lophiomurispora hongheensis*. i *Marjia tianschanica*. j *Monoseptella rosae*. k *Montagnula donacina*. l *Neocamarosporium lamiacearum*. m *Neopaucispora* rosaecae. n *Paramassariosphaeria clematidicola*. o *Parathyridaria rosae*. p *Pontoporeia biturbinata*. q *Pseudosplanchnonema phorcioides*. r *Pyrenophora phaeocomes*. s *Sporormurispora atraphaxidis*. t *Thyridaria jonahhulmei*.

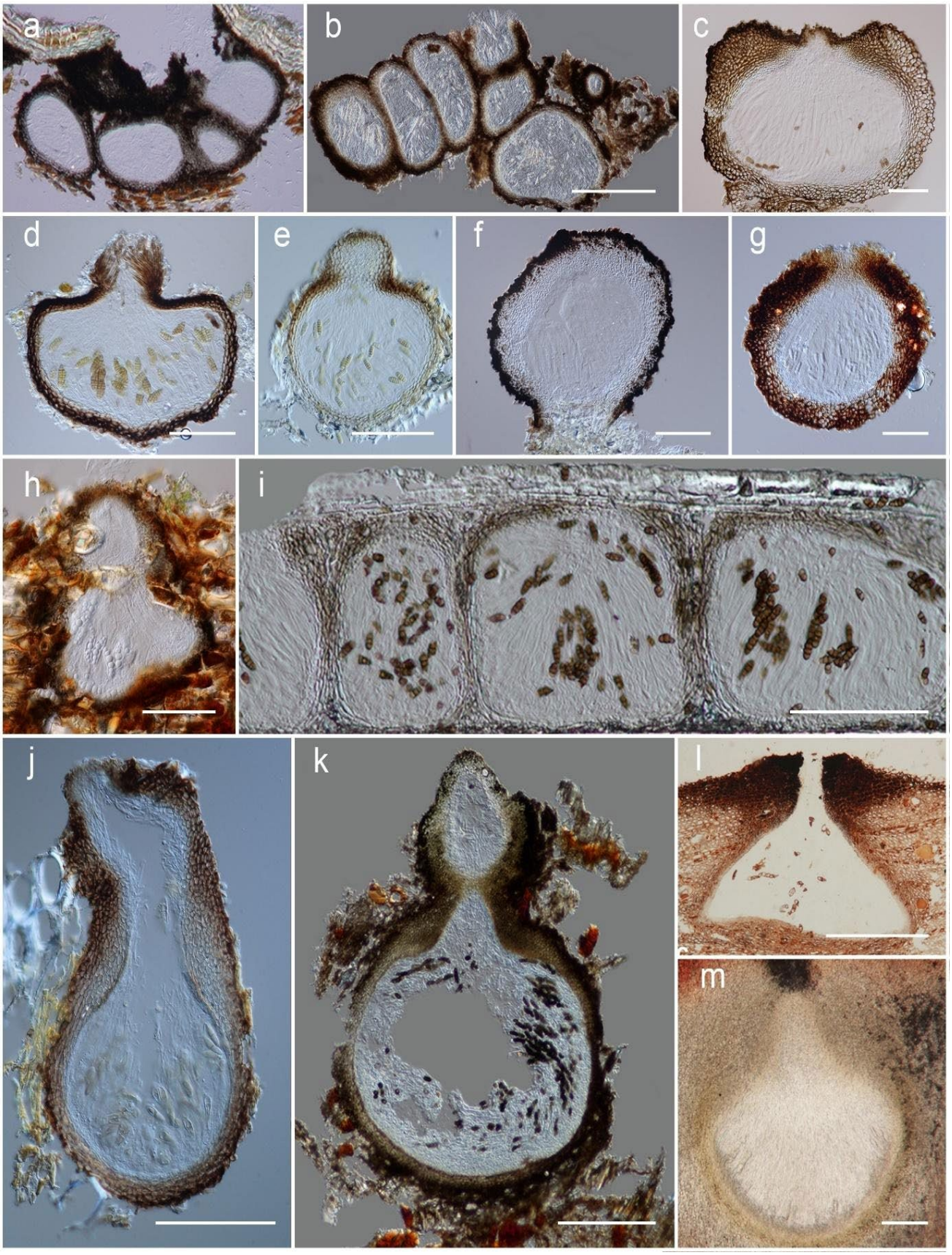


Figure 81 – Different shapes of ascomata of *Pleosporales*. a *Angustimassarina coryli*. b *Brunneofusispora sinensis*. c *Camarosporidiella laburni*. d *Dematiopleospora salsolae*. e Italica *achilleae*. f *Marjia uzbekistanica*. g *Monoseptella rosae*. h *Neoaquastroma guttulatum*. i *Neokalmusia jonahhulmei*. j *Parathyridaria rosae*. k *Thyridaria jonahhulmei*. l *Salsuginea ramicola*. m *Shiraia bambusicola*. Scale bars: a–m = 100 µm.

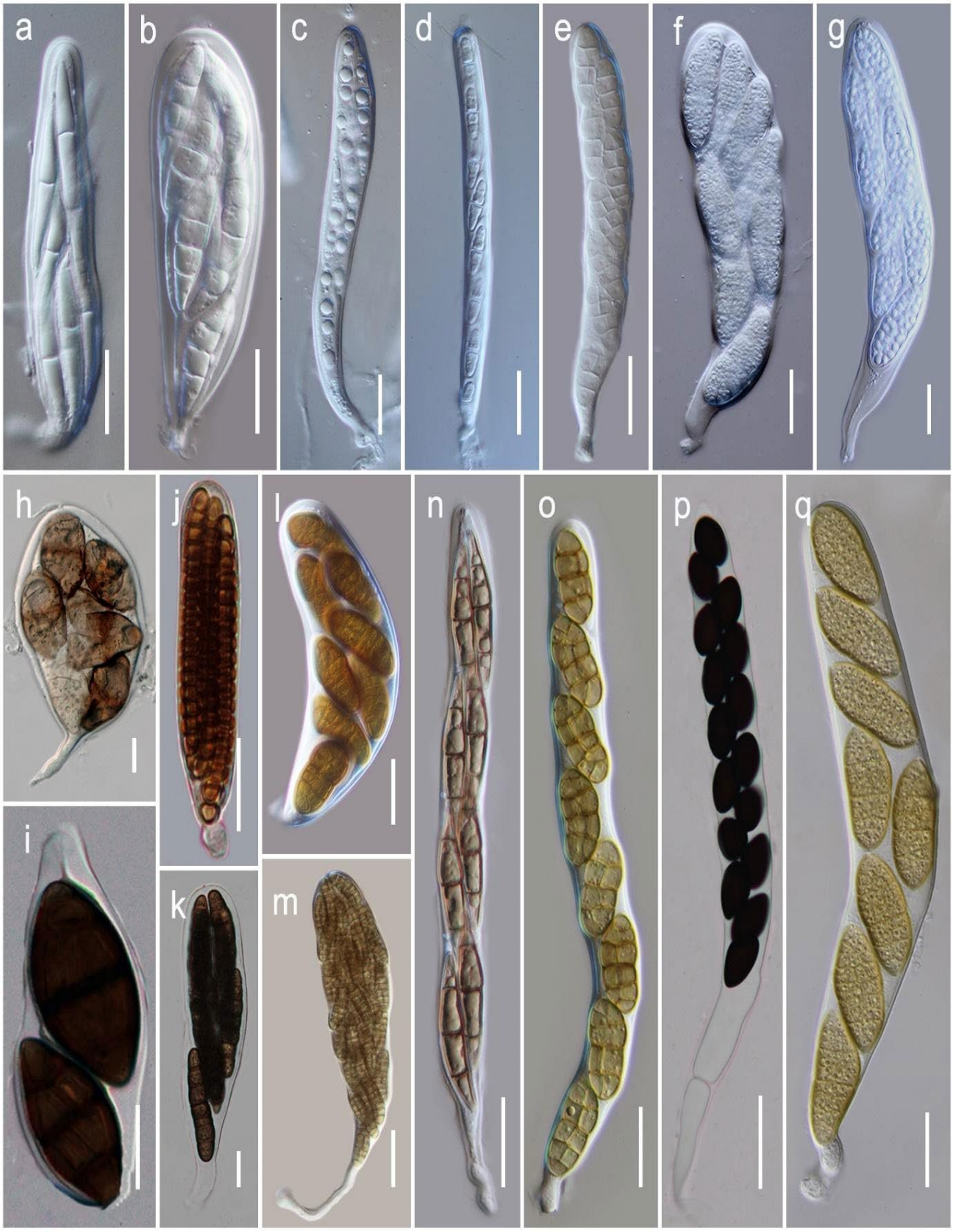


Figure 82 – Morphology of asci of *Pleosporales*. a *Neoastrosphaeriella sribooniensis*. b *Neoaquastroma guttulatum*. c *Keissleriella phragmiticola*. d *Monoseptella* rosae. e *Muriformistrickeria rosae*. f *Shearia formosa*. g *Muritestudina chiangraiensis*. h *Zopfia rhizophila*. i *Bimuria* novae-*zelandiae*. j *Sporormia fimetaria*. k *Pleomassaria* siparia. l *Comoclathris italica*. m *Phaeoseptum hydei*. n *Pithomyces caryotae*. o *Camarosporidiella eufemiana*. p *Delitschia didyma*. q *Parafenestella ostryae*. Scale bars: a–q = 20 µm.

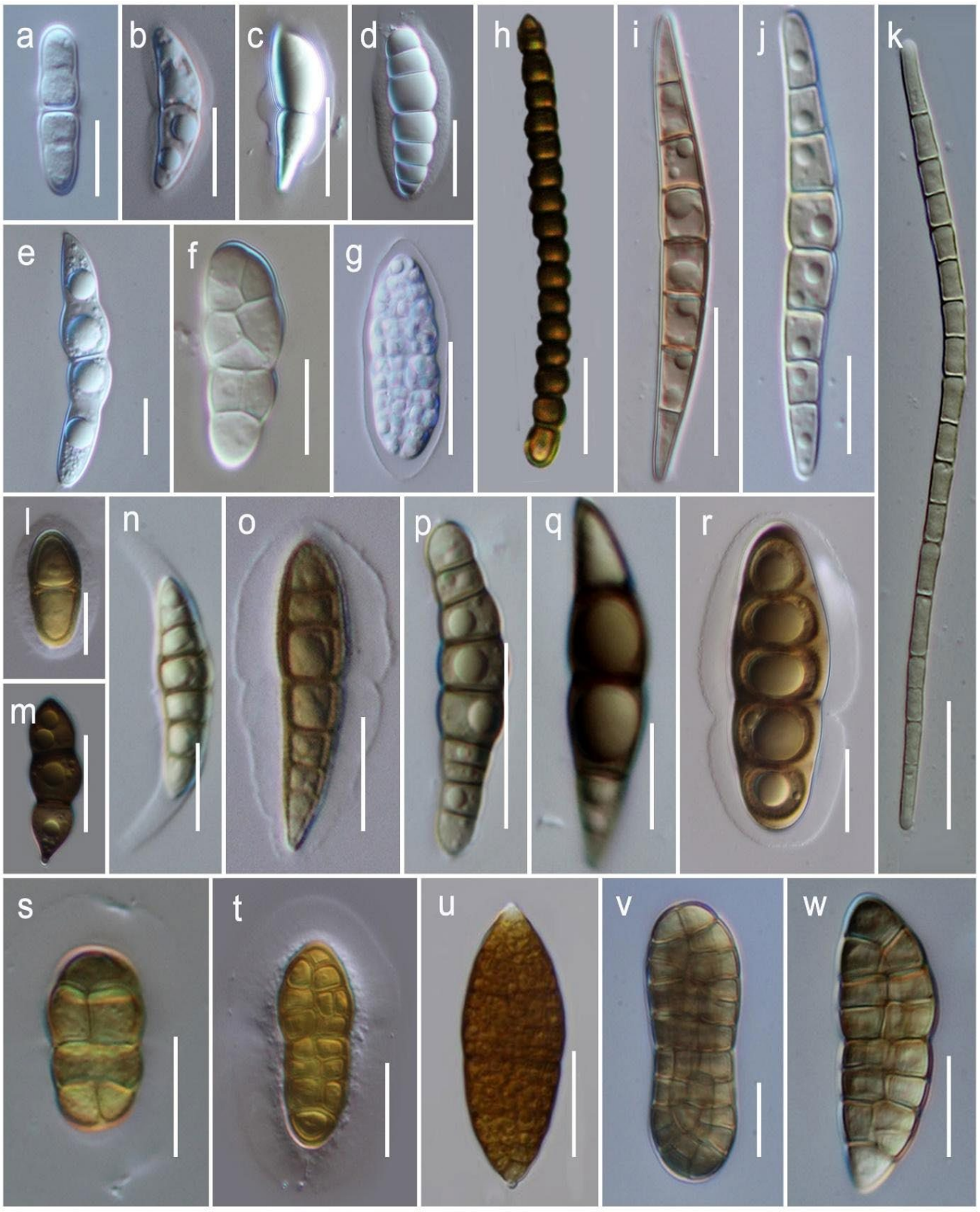


Figure 83 – Morphology of ascospores of *Pleosporales*. a *Monoseptella rosae*. b *Brunneofusispora* sinensis. c *Loculosulcatispora hongheensis*. d *Neoaquastroma guttulatum*. e *Keissleriella phragmiticola*. f *Muriformistrickeria rosae*. g *Muritestudina chiangraiensis*. h *Sporormia fimetaria*. i *Pithomyces licualae*. j *Ophiobolus artemisiicola*. k *Ophiobolus artemisiae*. l *Pseudodidymosphaeria* phlei. m *Thyridaria jonahhulmei*. n *Sigarispora medicaginicola*. o *S. junci*. p *S. caryophyllacearum*. q *Neopaucispora rosaecae*. r *Pseudosplanchnonema phorcioides*. s *Neocamarosporium lamiacearum*. t *Comoclathris italica*. u *Parafenestella ostryae*. v *Camarosporidiella premilcurensis*. w *Dematiopleospora salsolae*. Scale bars: a–w = 10 µm.



Figure 84 – Morphology of asexual morphs of *Pleosporales* (a–d pycnidial conidiomata, e an acervulus conidioma, a–p coelomycetes, q–w hyphomycetes). a *Camarosporidiella schulzeri*. b *Versicolorisporium triseptatum*. c *Acrocalymma medicaginis*. d *Chaetosphaeronema hispidulum*. e *Thyrostroma tiliae*. f *Alloneottiosporina thailandica*. g *Aquasubmersa mircensis*. h *Sulcatispora acerina*. i *Tetraploa sasicola*. j *Roussoellopsis macrospora*. k *Versicolorisporium triseptatum*. l *Staurosphaeria lycii*. m *Prosthemium stellare*. n *Thyrostroma tiliae*. o *Amarenographium ammophilae*. p *Murilentithecium clematidis*. q *Bhatiellae rosae*. r *Stemphylium vesicarium*. s *Alternaria baoshanensis*. t *Curvularia lunata*. u *Bipolaris luttrellii*. v *Bhatiellae rosae*. w *Pithomyces caryotae*. Scale bars: a–w = 10 µm.

Dacampiaceae Körb.
Delitschiaceae M.E. Barr
Diademaceae Shoemaker & C.E. Babc.
Dictyosporiaceae Boonmee & K.D. Hyde
Didymellaceae Gruyter, Aveskamp & Verkley (= *Microsphaeropsidaceae* Qian Chen et al.)

Latoruaceae Crous
Lentimurisporaceae N.G. Liu, J.K Liu & K.D. Hyde
Lentitheciaceae Y. Zhang ter, C.L. Schoch, J. Fourn., Crous & K.D. Hyde
Leptosphaeriaceae M.E. Barr
Leptosphaerioidaceae J.F. Zhang, Jian K. Liu & K.D. Hyde
Libertasomycetaceae Crous
Ligninsphaeriaceae K.D. Hyde & Ariyaw.
Lindgomycetaceae K. Hiray., Kaz. Tanaka & Shearer
Lizoniaceae Boonmee & K.D. Hyde
Longiostiolaceae Phukhams., Doilom & K.D. Hyde
Longipedicellataceae Phukhams., Bhat & K.D. Hyde
Lophiostomataceae Sacc.
Lophiotremataceae K. Hiray. & Kaz.
Macrodiplodiopsidaceae Voglmayr, Jaklitsch & Crous
Massariaceae Nitschke
Massarinaceae Munk
Megacapitulaceae Rajeshk., Sruthi OP, Hongsanan, Jeewon, Karuna, Harik
Melanommataceae G. Winter (= *Pseudodidymellaceae* A. Hashim. & Kaz. Tanaka)
Morosphaeriaceae Suetrong, Sakay., E.B.G. Jones & C.L. Schoch
Mycoporaceae Zahlbr.
Neocamarosporiaceae Wanas., Wijayaw., Crous & K.D. Hyde
Neohendersoniaceae Giraldo & Crous
Neomassariaceae H.A. Ariyaw., Jaklitsch & Voglmayr
Neomassarinaceae Mapook & K.D. Hyde
Neophaeosphaeriaceae Ariyaw. & K.D. Hyde
Neopyrenochaetaceae Valenz.-Lopez, Crous, Cano, Guarro & Stchigel
Nigrogranaceae Jaklitsch & Voglmayr
Occultibambusaceae D.Q. Dai & K.D. Hyde
Ohleriaceae Jaklitsch & Voglmayr
Parabambusicolaceae Kaz. Tanaka & K. Hiray.
Paradictyoarthriniaceae Doilom, Ariyaw., Bhat & K.D. Hyde
Paralophiostomataceae V.V. Sarma & M. Niranjan.
Parapyrenochaetaceae Valenz.-Lopez, Crous, Stchigel, Guarro & Cano
Periconiaceae Nann.
Phaeoseptaceae S. Boonmee, Thambugala & K.D. Hyde
Phaeosphaeriaceae M.E. Barr
Pleomassariaceae M.E. Barr
Pleomonodictydaceae Hern.-Restr., J. Mena & Gené
Pleosporaceae Nitschke
Profundisphaeriaceae J.F. Zhang, Jian K. Liu & K.D. Hyde
Pseudoastrosphaeriellaceae Phook. & K.D. Hyde
Pseudoberkleasmiaceae Phukhams. & K.D. Hyde
Pseudocoleodictyosporaceae Doilom & K.D. Hyde
Pseudolophiotremataceae K.D. Hyde & Hongsanan
Pseudomassarinaceae Phukhams & K.D. Hyde
Pseudopyrenochaetaceae Valenz.-López, Crous, Stchigel, Guarro & J.F. Cano
Pyrenochaetopsidaceae Valenz.-López, Crous, Cano, Guarro & Stchigel
Roussoellaceae Jian K. Liu, Phook., D.Q. Dai & K.D. Hyde
Salsugineaceae K.D. Hyde & Tibpromma
Shiraiaceae Y.X. Liu, Zi Y. Liu & K.D. Hyde
Sporormiaceae Munk
Striatiguttulaceae S.N. Zhang, K.D. Hyde & J.K. Liu

Sublophiostomataceae
Sulcatisporaceae Kaz. Tanaka & K. Hiray.
Teichosporaceae M.E. Barr
Testudinaceae Arx
Tetraplosphaeriaceae Kaz. Tanaka & K. Hiray
Thyridariaceae Q. Tian & K.D. Hyde
Torulaceae Corda
Trematosphaeriaceae K.D. Hyde, Y. Zhang ter, Suetrong & E.B.G. Jones
Tzeananiaceae H.A. Ariyaw., A.J.L. Phillips & Chuang
Wicklowiaceae Ariyaw. & K.D. Hyde
Zopfiaceae G. Arnaud ex D. Hawksw.

Pleosporales genera *Incertae sedis*
Aegeanispora E.B.G. Jones & Abdel-Wahab
Antealophiotrema A. Hashim. & Kaz. Tanaka
Ascorhombispora L. Cai & K.D. Hyde
Briansuttonia R.F. Castañeda, Minter & Saikawa
Chaetodiplodia P. Karst.
Chaetophoma Cooke
Cheiromoniliophora Tzean & J.L. Chen
Cyclothyrium Petr.
Dangeardiella Sacc. & P. Syd.
Daruvedia Dennis
Dokmaia Promp.
Farasanispora Abdel-Wahab, Bahkali & E.B.G. Jones
Fusiformiseptata W. Dong, H. Zhang & K.D. Hyde
Glaxoa P.F. Cannon
Hobus Jaklitsch & Voglmayr
Homostegia Fuckel
Inflatispora Y. Zhang ter, J. Fourn. & K.D. Hyde
Isthmosporella Shearer & J.L. Crane
Lorrainsmithia Y.P. Tan, Minns & E. Lacey
Mangifericomes E.F. Yang & Tibpromma
Megacapitula J.L. Chen & Tzean
Megatomentella D.A.C. Almeida, Gusmão & A.N. Mill.
Neocamarographium Crous
Neochrosporium R.P. Liu, Meng Zhang & Y.H. Geng
Neocurreya Thambug. & K.D. Hyde
Ostropella (Sacc.) Höhn.
Paraepicoccum Matsush.
Paraliomyces Kohlm.
Parameliola Hongsanan, Peršoh & K.D. Hyde
Parastenospora Crous
Perthomyces Crous
Phialophorophoma Linder
Pleosphaerellula Naumov & Czerepan.
Pseudohendersonia Crous & M.E. Palm
Pseudomultiseptospora Phookamsak, Rajeshk., Karun. & Wijayaw.
Pyrenochaeta De Not.
Rebentischia P. Karst.
Repetophragma Subram.
Scleroramularia Batzer & Crous

Setophaeosphaeria Crous & Y. Zhang ter
Sirodesmium De Not.
Spiroplana Voglmayr, M.J. Park & H.D. Shin
Stuartella Fabre
Xenolophium Syd

Evolution

Pleosporales originated from a common ancestral lineage within *Ascomycota*, which exhibits a faster evolutionary rate than *Basidiomycota*. This may be evidenced by the large number of species found in *Pleosporales*. It is estimated that the earliest members of this order diverged between 282 and 161 MYA, with a crown age of 260–148 MYA (Liu et al. 2017b, Samarakoon et al. 2019), during the late Paleozoic to early Mesozoic era (Taylor et al. 2009b). The diversification of *Pleosporales* is closely linked to the evolution of their host organisms, including plants, as well as environmental changes. As terrestrial ecosystems developed and diversified, *Pleosporales* adapted to various ecological niches i.e. saprobic, pathogenic, and symbiotic lifestyles. A key factor in the success of *Pleosporales* has been their morphological adaptations. This order is characterized by its ascomata, which are typically perithecioid with a frequently papillate apex. The asci are bitunicate, a feature that enables them to discharge spores with considerable force, an adaptation that likely evolved for effective spore dispersal. The ascospores of *Pleosporales* are varied in shape, color, septation, and possess gelatinous appendages or sheaths, reflecting their adaptation to various environmental conditions and dispersal strategies. For instance, ascospores with a gelatinous sheath or appendages may aid in attachment to plant substrates in aquatic or marine habitats (Mortimer et al. 2021). The subapical appendages might be an adaptation for marine-based habitats, and the loss of appendaged ascospores could be potentially advantageous for adaptation to non-aquatic habitats.

Advancements in molecular phylogenetics have significantly deepened our understanding of *Pleosporales* evolution. Studies focusing on DNA sequences have revealed the complex relationships within the order, highlighting the convergence of morphological traits and the importance of genetic adaptations (Liu et al. 2017b). These studies have also challenged traditional classifications based solely on morphology, leading to the reclassification and introduction of new families within the order. The ecological roles of *Pleosporales* are diverse. Many species are saprobes, playing a crucial role in nutrient cycling by decomposing organic matter. Others have evolved as plant pathogens, significantly impacting agriculture and forestry. There are also species that have formed symbiotic relationships with plants, algae, or animals. The co-evolution of *Pleosporales* with their hosts and environments has been a driving force in their diversification. Recent phylogenetic studies have led to the discovery of new families and genera within *Pleosporales*, indicating that the diversity of the order is greater than previously thought. Ongoing research continues to uncover the evolutionary history of this group, including the study of fossilized fungi and advanced genomic analyses (Samarakoon et al. 2019).

Justification of order and problems

The current challenge in understanding the relationships within *Pleosporales*, particularly among its numerous families, is compounded by the lack of comprehensive DNA sequence data for many of its representatives. This gap in genetic information presents a considerable obstacle in elucidating the phylogenetic relationships and evolutionary history of various genera and species within *Pleosporales*. Traditionally, the classification of *Pleosporales* species has largely been based on morphological characteristics. This approach, while valuable in the initial identification and categorization of these fungi, has inherent limitations. Morphological features can vary significantly depending on environmental conditions and developmental stages, potentially leading to classifications that do not accurately reflect true genetic relationships. As a result, without supporting genetic data, many genera, and species within *Pleosporales* may be placed in artificial groupings based on their observable physical traits rather than their genetic lineage. The absence of DNA sequence data in *Pleosporales* taxonomy highlights a critical gap in the understanding of this diverse

and ecologically significant group of fungi. Relying solely on morphological classification can lead to a misunderstanding of the complex evolutionary relationships and ecological roles. DNA sequencing offers a more robust and reliable method for determining phylogenetic relationships, as it provides direct insights into the genetic makeup of organisms, unaffected by external environmental factors. Incorporating molecular data into the taxonomy of *Pleosporales* is essential for a more precise understanding of the biodiversity and evolutionary patterns.

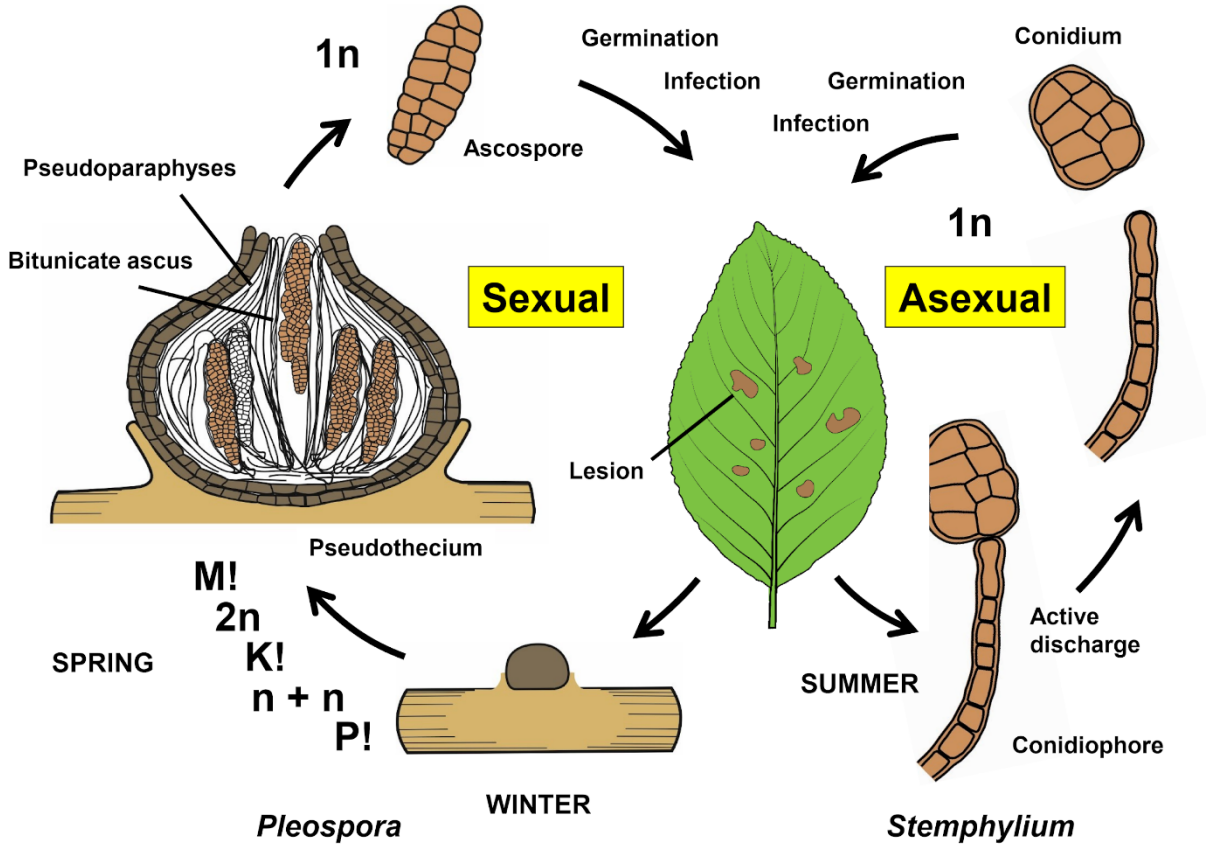


Figure 85 – Life cycle of *Pleospora herbarum* (current name *Stemphylium vesicarium*) (*Pleosporales*) on leaves of *Pyrus communis* (*Rosaceae*). 1n = haploid, n+n = dikaryotic, 2n = diploid, K! = karyogamy, M! = meiosis, P! = plasmogamy. **the conidiogenous cell is always swollen in *Stemphylium* - very characteristic.

Species within the *Pleosporales* are facing considerable conservation pressures due to a range of unfavorable conditions such as intensification of land use, which often accompanies growing human populations, environmental exploitation and pollution, the spread of invasive species, and the challenges posed by climate change (Wanasinghe et al. 2021). These fungi are particularly sensitive to environmental changes and global warming. This sensitivity may be leading to the extinction of a large number of species that are unable to adapt quickly enough to the pace of environmental change. This situation has instilled a sense of urgency within the research community, as there is a growing concern that future opportunities for study and conservation of these species might soon be lost. Addressing these challenges and working to mitigate species loss requires a concerted effort. A crucial step in this direction would be the development of a robust, updated fungal classification system (Hyde et al. 2024b). This system should facilitate clear taxonomic communication and be based on extensive fungal sampling from different geographic regions. Such an approach would not only enhance our understanding of fungal diversity but also aid in the development of strategies to conserve these ecologically and scientifically valuable species. The task is significant, but it is vital for preserving the biological diversity and ecological balance of our planet.

Significance

Ecological and economic roles

Didymellaceae encompasses numerous important plant pathogen species, with some being of concern to quarantine (Aveskamp et al. 2008, 2010, Chen et al. 2015b). *Ascochyta*, *Nothophoma*, and *Stagonosporopsis* species are considered serious quarantine organisms in various countries and regions (Vaghefi et al. 2012). Notably, species of *Ascochyta* are the causal agents of blackspot disease in peas, a significant issue in major pea-growing areas globally (Bretag et al. 2006, Liu et al. 2016c). Many taxa within *Didymellaceae*, typically reported as saprobes and soil microbes, are suggested to have the potential to become pathogenic under suitable host conditions (Aveskamp et al. 2008). *Pleosporaceae* species typically exhibit saprobic, endophytic, opportunistic human, and plant pathogenic characteristics. Certain genera, such as *Alternaria*, produce toxic compounds including alternariols, altenuene, tentoxin, and tenuazonic acid, which cause infections in fruits, vegetables, and grains (Bullerman 2003). Other genera such as *Bipolaris* are commonly associated with leaf spots, leaf blights, root and foot rots, and other disease symptoms on high-value field crops in the *Poaceae*, including rice, maize, wheat, and sorghum (Manamgoda et al. 2014). *Camarosporium* species are recognized as plant pathogens with a global distribution (Wanasinghe et al. 2017a). For instance, *Camarosporium pistaciae* is a prevalent pathogen causing blight in pistachio production in Greece (Assimakopoulou & Elena 2010, Wanasinghe et al. 2017a). In Europe, Smith et al. (1988) have identified *Camarosporium dalmaticum*, *C. flaccidum*, *C. pistaciae* and *C. strobilinum* as plant pathogens. *Coniothyrium* species are known for their pathogenic effects on *Eucalyptus* sp. worldwide, causing lesions (*Coniothyrium eucalypticola*), necrotic leaf spots (*C. parvum*), and leaf spots in young leaves (*C. ovatum*). Members of the *Dothidotthiaceae*, prevalent in both tropical and temperate regions, are known to cause a variety of plant diseases including canker, dieback, leaf spots, and root rot (Hyde et al. 2013, Marin-Felix et al. 2017, Hongsanan et al. 2020a). In *Leptosphaeriaceae*, several asexual morphs have been identified as economically important plant pathogens. *Neoleptosphaeria rubefaciens* is associated with skin necrosis on apple fruits, a serious concern for apple production (Boerema et al. 1994). *Plenodomus lingam* (= *Leptosphaeria maculans*) is a well-known pathogen causing blackleg disease in canola, a major issue for brassica crops worldwide (Van de Wouw et al. 2016). *Plenodomus biglobosa*, another species in this family, causes black rot disease in *Wasabia japonica*, highlighting their diverse pathogenic impact on various crops (de Gruyter et al. 2013). *Helminthosporium solani*, a member of *Massarinaceae*, is an economically significant pathogen of potatoes, responsible for the silver scurf disease that affects tubers (Errampalli et al. 2001). This disease can lead to substantial yield losses, emphasizing the economic impact of this pathogen. *Neottiosporina paspali*, associated with the leaves of *Paspalum*, has a wide host range (Sutton 1980). Members of the *Pseudopyrenochaetaceae*, notably soil-borne, also pose threats to agriculture. *Pseudopyrenochaeta lycopersici*, causing corky root disease in tomato crops, leads to considerable yield losses (Shimono et al. 2021). This pathogen also affects other crops like pepper, eggplant, tobacco, melon, cucumber, spinach, and safflower, demonstrating its wide host range and potential for extensive agricultural damage.

Pithomyces is a notable example, acting both as a human and plant pathogen (Litz & Cavagnolo 2010). This dual pathogenicity highlights the potential impact of this genus on agricultural productivity and human health. *Biatriospora sensu lato* is another economically important genus within *Pleosporales*. Its species have diverse ecological roles, being pathogenic to humans, endophytic, and saprobic. This diversity, as noted in studies, underscores its significance in both economic and ecological contexts (Hyde & Borse 1986, Kolařík et al. 2017, Ahmed et al. 2018). Some species within *Phoma sensu lato* are pathogens, not only affecting humans (Balis et al. 2006) but also cattle (Costa et al. 1993) and fish (Ross et al. 1975, Hatai et al. 1986, Voronin 1989, Faisal et al. 2007). This broad host range demonstrates the potential of *Phoma sensu lato* species to impact various aspects of health and agriculture. Members of the *Pyrenochaetopsidaceae* are found in clinical human specimens, including blood, dermatitis, ear lesions, skin, sputum, and toenails, as well as in river environments associated with leaf spots (Boerema et al. 2004, Crous et al. 2011a,

Valenzuela-Lopez et al. 2018). Their presence in such diverse habitats and conditions highlights their adaptability and potential health implications.

Aigialaceae is reported to consist entirely of saprobic fungi. These taxa are commonly found on wood in mangroves and various plant hosts across marine and terrestrial habitats (Hyde & Lee 1998). Their role is crucial in the recycling of nutrients, contributing to the ecological balance in these environments (Hyde & Jones 1988). Similarly, *Halotthiaceae* comprises saprobes found in both marine and terrestrial environments. However, some species within this family, such as *Halotthia posidoniae*, exhibit pathogenic behavior, particularly in marine settings where it is known to affect *Posidonia oceanica*. Another species, *Sulcosporium thailandicum*, is noted for causing necrotic leaf spots on grass blades, indicating its potential impact on plant health (Purahong & Hyde 2011). Members of the *Lindgomycetaceae* and many other *Pleosporales* families are found in freshwater habitats, in their sexual and asexual states, often collected from submerged wood. This habitat preference indicates their role in the decomposition and nutrient cycling within these freshwater ecosystems (Bucher et al. 2004a).

Dacampiaceae taxa are lichenized, lichenicolous, or non-lichenized fungi. These groups contribute to their respective ecosystems, but their specific interactions, particularly with lichen hosts, are not fully understood and require further research. This gap in knowledge points to the complexity and diversity of interactions within fungal communities and their environments. In *Cyclothyriellaceae*, species are typically found on bark, decayed twigs, or submerged dead twigs of specific tree species such as *Acer* spp. *Aesculus hippocastanum*, and *Ulmus* spp. They are often found in association with other fungi, including *Nitschkia parasitans*.

The relationship between *Pleosporales* species and entomogenous fungi, particularly within the *Tzeananiaceae*, presents an intriguing area for future research. Currently, there are not many *Pleosporales* species known to be associated with entomogenous fungi. A notable example is *Tzeananiaceae*, which has been found on the fruiting body of *Ophiocordyceps macroacicularis*. The study conducted by Ariyawansa et al. (2018) highlights the need for further investigation into this association. Specifically, the nutritional mode of *Tzeanania taiwanensis* and its interaction with *Ophiocordyceps macroacicularis* remains unclear. Given the complexity and relatively unexplored nature of these interactions, future research in this area is not only essential but could also lead to fascinating discoveries about the life cycles, survival strategies, and ecological significance of both *Pleosporales* and entomogenous fungi.

Chemical diversity

Pleosporales show a capacity for producing bioactive compounds with potential in pharmaceutical and agricultural applications. *Aigialus parvus*, a member of the *Aigialaceae*, is noted for producing aigialomycins A and hypothemycin. These compounds exhibit antimalarial activity, highlighting their potential in medical applications (Isaka et al. 2002). Similarly, the *Anteagloniaceae* members produce unique red-orange to pink pigments. These pigments are involved in the synthesis of anteaglonialides and palmarumycins, extracted from *Anteaglonium* sp. cultures. These compounds demonstrate strong cytotoxic effects against Ewing's sarcoma cell line CHP-100, indicating their potential in cancer therapy (Xu et al. 2015). *Biatriospora* species are known for their diverse metabolic profiles, including the production of potent antibiotics (Shaw et al. 2015, Stodůlková et al. 2015). The *Lindgomycetaceae* family produces lindgomycin, an unusual antibiotic polyketide with activity against human and plant pathogenic microorganisms (Wu et al. 2015). The genus *Periconia* also demonstrates potential in bioactive compound production, with species capable of synthesizing valuable metabolites (Kim et al. 2004, Harnpicharnchai et al. 2009, Zhang et al. 2015a, 2016a). *Phaeosphaeriaceae* species contribute to this trend, having the ability to produce secondary metabolites with antimicrobial activities (Mapook et al. 2020a). In *Sporormiaceae*, *Westerdykella reniformis* produces the antibiotic metabolites melinacidin IV and chetracin B (Ebead et al. 2012). *Wicklowia aquatica* has yielded novel compounds, including three new nonadride derivatives and two new C-9 compounds, which have shown promising properties as precursors of nonadrides, along with other known compounds with potential applications (source not specified). Beyond

pharmaceutical uses, *Epicoccum layuense* is studied as a potential biocontrol agent against grapevine trunk pathogens, demonstrating the agricultural applications of *Pleosporales* (Del Frari et al. 2019). *Acrocalymma pterocarpi*, reported from pods of *Pterocarpus indicus*, an important plant in forestry and indigenous medicine in South-East Asia (Jayasiri et al. 2019).

Other relevant data and future recommendations

Future studies are needed to delve deeper into genomic aspects, with an emphasis on whole-genome sequencing to unravel evolutionary history, pathogenicity mechanisms and ecological adaptations. Molecular phylogenetic studies will continue to play a crucial role in resolving taxonomic complexities, particularly in distinguishing closely related species and elucidating their evolutionary relationships. Ecological and environmental studies are essential to comprehend the roles and interactions of *Pleosporales* within various ecosystems. Investigating the impact of climate change on their diversity and distribution can provide valuable insights into ecosystem resilience. In addition, understanding host-pathogen dynamics is crucial, especially given that many *Pleosporales* species are known plant pathogens. This knowledge can lead to improved management of crop diseases and the development of resistant plant varieties. The exploration of *Pleosporales* as potential biocontrol agents offers a sustainable alternative to chemical pesticides. The research related secondary metabolites with potential applications such as in medicine, agriculture, and industry are poorly documented in this order. Systematic screening and characterization of potential compounds could lead to significant breakthroughs in drug discovery and the development of industrial enzymes. The biotechnological potential of *Pleosporales*, including enzyme production, bioremediation, and biofuel generation, is an area ripe for exploration. Conservation and biodiversity assessment of *Pleosporales*, particularly in lesser-explored regions, are crucial for preserving these fungi. Understanding the impact of human activities on their habitats can guide effective conservation policies and habitat preservation. Public awareness and education about the ecological importance of fungi, including *Pleosporales*, are key to fostering conservation efforts. Engaging the public in citizen science projects can enhance data collection and foster community interest in fungal ecology. International collaboration and data sharing are vital for accelerating our understanding of *Pleosporales*. An interdisciplinary approach, integrating various scientific disciplines, is essential for a comprehensive understanding of these fungi. As research continues, we can expect to gain further insights into the evolutionary mechanisms, ecological roles, and potential applications of this diverse and ecologically significant group of fungi.

***Racodiales* Abdollahz. & Crous, Studies in Mycology 95: 393 (2020)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Dothideomycetidae*

Introduction

Racodiales was introduced based on *Racodiaceae* Link, in a phylogenetic study on *Capnodiales* evolution through a polyphasic approach based on ecology, lifestyle, morphology and DNA sequence data (Abdollahzadeh et al. 2020). It is based on *Racodium*, a lichen fungus which has previously been assigned to *Capnodiales sensu lato* (Muggia et al. 2008, Nelsen et al. 2009, Ruibal et al. 2009). *Racodium rupestre,* is the only representative with available DNA sequence data, of the order *Racodiales,* is a widespread rock inhabitant lichen fungus associated with the green algae *Trentepohlia* (Muggia et al. 2008). It grows in cool recesses of rocks with high humidity and no direct rain (Hawksworth et al. 2011). The nomenclature history of *Racodium*, as a lichen fungus based on *R. rupestre*, has been discussed in detail by Hawksworth et al. (2011).

General description

Thallus filamentous, of elongated, straight hyphae, longitudinally arranged, in close association with photobiont, not corticate, dark brown to black, forming wefts or circular patches, margin not

delimited; hyphae 4–7 per photobiont filament, straight and parallel, unbranched, non-nodulose. Ascomata and conidiomata not known (adapted from Smith et al. 2009) (Fig. 86).

Families included in *Racodiales*

Racodiaceae Link

Evolution

According to ribosomal DNA phylogenetic study, *Racodium rupestre* along with *Cystocoleus ebeneus*, are true rock inhabitant dothideomycetous lichens most likely evolved from a rock inhabitant ancestor but more data is necessary to test this hypothesis (Ruibal et al. 2009).

Justification of order and problems

Racodiales was recognized based on LSU sequence data and supported by ecology and lifestyle.

Significance

Ecological and economic roles

The taxa are reported from Europe, North America, South America, Africa, Asia and Australia and commonly reported as rock-inhabiting taxa and some are pathogenic (Abdollahzadeh et al. 2020).

Chemical diversity

Relevant studies are not available chemical diversity of *Racodiales*.

Other relevant data and future recommendations

Ribosomal DNA sequence data are available for *R. rupestre*, the only species of *Racodiales*, thus additional taxa and genes are needed to understand the evolution, ecology, physiology, chemistry, and potential applications.

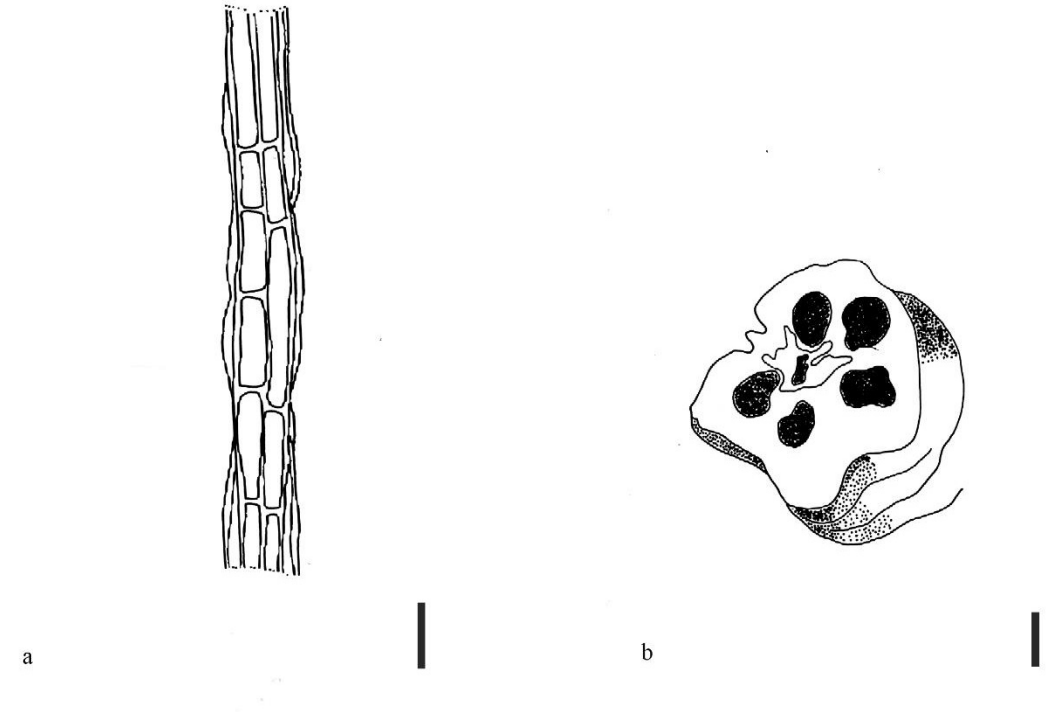


Figure 86 – Ascomata morphology of *Racodiales*. a Filament of *Racodium rupestre*. b SEM micrograph of *Racodium rupestre* (redrawn from Hawksworth et al. 2011). Scale bars: a = 10 μm, b = 2 μm.

Sporidesmiales **Crous, Persoonia 40: 377 (2018)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Sporidesmiales was introduced by Crous et al. (2018a) and presently contains only *Sporidesmiaceae* with a single genus *Sporidesmium*. *Sporidesmium* was only known as an asexual genus until Zhang et al. (2017a) introduced a sexual morph species *Sporidesmium thailandense* which was collected from a freshwater habitat in Thailand.

History

Sporidesmiaceae was introduced by Fries (1849b) and has received very little usage. Presently, there is only one genus accepted in this family. Shenoy et al. (2006) found that *Sporidesmium* and some morphologically similar genera are not monophyletic, as they are distributed among different families and orders in *Dothideomycetes* and *Sordariomycetes*. Su et al. (2016a) reported similar results. A monophyletic clade with species resembling the type species of *Sporidesmium* was designated as *Sporidesmiaceae sensu stricto*, and a new family *Distoseptisporaceae* was introduced to accommodate a new sporidesmium-like genus *Distoseptispora* (Su et al. 2016a). Crous et al. (2018a) raised *Sporidesmiaceae* to *Sporidesmiales* based on the morphology and phylogenetic analysis.

General description

Sexual morph: *Ascomata* perithecial, scattered or solitary, immersed with neck erumpent through host surface, uniloculate, subglobose or ellipsoidal. *Neck* cylindrical, central or lateral. *Ostiole* periphysate. *Peridium* three-layered. *Paraphyses* numerous, hypha-like, hyaline, septate, unbranched. *Asci* unitunicate, 8-spored, apically rounded, with a distinct, relatively small, refractive, J-, wedge-shaped, apical ring. *Ascospores* obliquely uni-seriate, hyaline. Asexual morph: *Colonies* black, effuse. *Mycelium* comprising hyaline to pale brown, branched, septate, thin-walled hyphae. *Conidiophores* solitary or in clusters, single, or sometimes aggregated in groups, straight or curved, septate. *Conidiogenous cells* monoblastic, holoblastic, terminal. *Conidia* dry, solitary, obclavate to cylindrical or fusoid, straight to flexuous, apex obtuse, base obconically truncate, smooth-walled (Fig. 87).

Families included in *Sporidesmiales*

Sporidesmiaceae Fr.

Evolution

The divergence time for *Sporidesmiales* has been estimated as 81 MYA, which falls in the range of family status (Hyde et al. 2020d). Hyde et al. (2021a) re-estimated divergence time for *Sporidesmiales* as 133 MYA which falls in the range of order status.

Justification of order and problems

Sporidesmium is a large and heterogeneous genus. To date, 500 species epithets are referred to the genus (Index Fungorum 2025). However, many previously described species were revised and transferred to over 30 genera. Studies based on phylogenetic analysis have been carried out to further re-examine the classification of sporidesmium-like taxa, given that the generic delimitations based on morphology data appear to be questionable. *Sporidesmium* and morphologically similar genera are clearly not monophyletic, as they are distributed among different families and orders in *Dothideomycetes* and *Sordariomycetes* (Shenoy et al. 2006, Su et al. 2016a). Molecular sequence data are lacking for many sporodesmium-like genera except for *Distoseptispora* (Dong et al. 2020). Further study based on collections, especially the sexual morph of this group is needed.

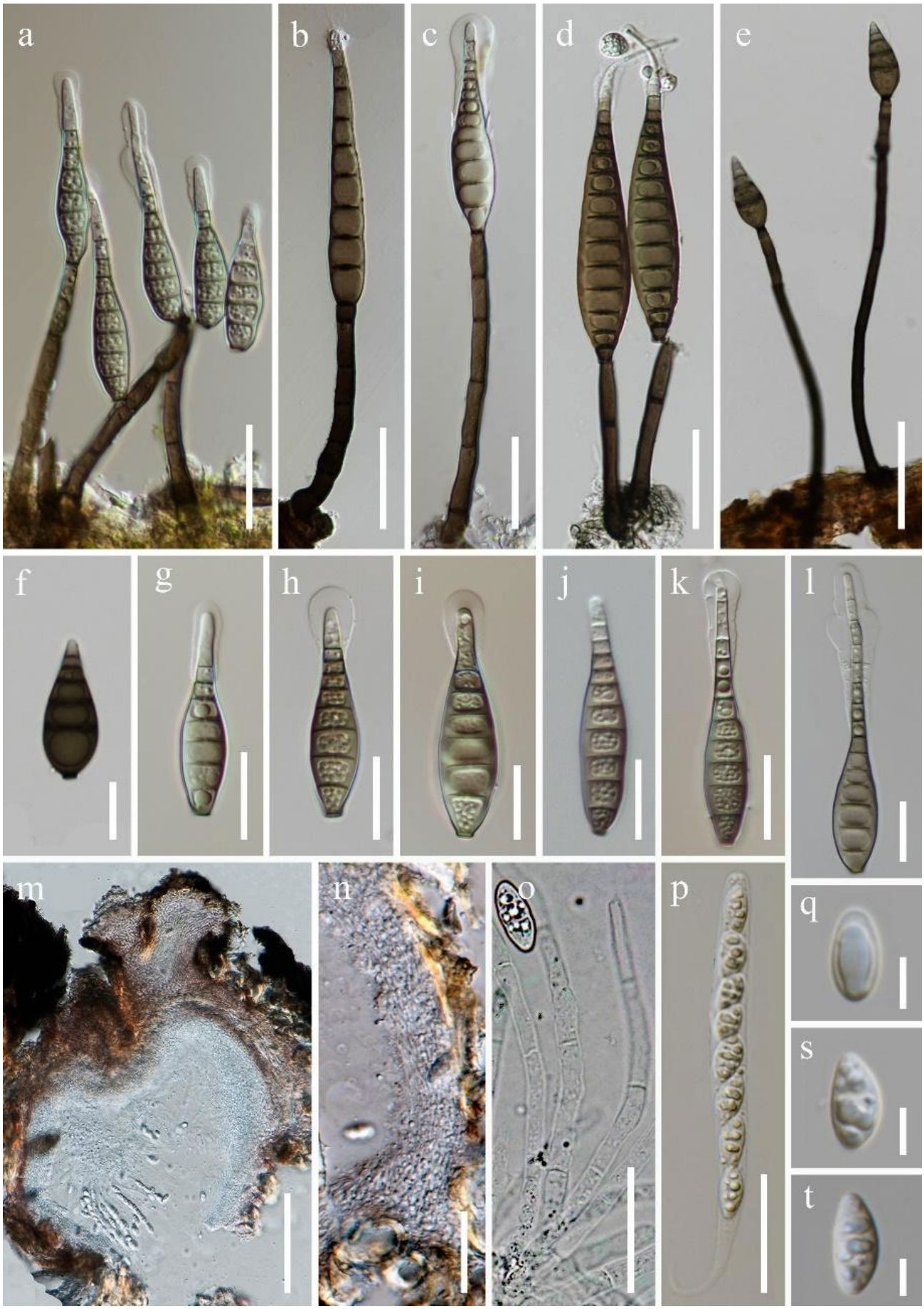

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Figure 87 – Morphology of *Sporidesmiales*. a–l Asexual morph of *Sporidesmium* spp. m–t *Sporidesmium lignicola*. Scale bars: m = 100 μm, e, n = 50 μm, b–d, o, p = 30 μm, a = 20 μm, f–l = 15 μm, q–t = 5 μm.

Significance

Ecological and economic roles

Taxa are saprobic on woody debris in terrestrial and aquatic habitats or mycoparasites of fungi. Saprobes can decompose lignocellulose in woody litter, resulting in the softening of the wood and release of nutrients in the form of simple molecules that are reused by plants and other organisms (Yuen et al. 1998). Thus, they play an important role in nutrient and carbon cycling, biological diversity, and ecosystem functioning (Palmer et al. 1997, Wong et al. 1998a).

Chemical diversity

No relevant studies are available for the chemical diversity of *Sporidesmiales*.

***Stigmatodiscales* Voglmayr & Jaklitsch, Fungal Diversity 80: 275 (2016)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction & History

Stigmatodiscales was introduced by Voglmayr et al. (2016). Phylogenetic analyses placed *Stigmatodiscales* within *Dothideomycetes*, with the closest relatives being unclear (Voglmayr et al. 2016, Poncet et al. 2022). The two new genera: *Asterodiscus* and *Stigmatodiscus* are similar in terms of morphology. They have saccate, fissitunicate asci, large, 3-septate ascospores with an eccentric euseptum and two additional distosepta and are encased in a thick gelatinous sheath.

They have saccate, fissitunicate asci, large, 3-septate ascospores with an eccentric euseptum and two additional distosepta and are encased in a thick gelatinous sheath. They also have apothecial ascomata embedded in host tissue that lack an excipulum. Ascospores of *Stigmatodiscus* resemble those of *Stigmatomassaria* and are not found in other *Dothideomycetes*. *Arthopyreniaceae*, have ascospores comparable to those of *Asterodiscus*, however the ascomata of members of this family do not expand to become apothecial (Hyde et al. 2013). *Architrypethelium* and *Ornatopyrenis*, two members of the *Trypetheliaceae*, have ascospores that are comparable in size to those found in the *Stigmatodiscales* but are pyrenocarpous and lichenized (Aptroot 1991a). Even though the ascospores of *Asteromassaria* and *Stigmatomassaria* are very similar to those of the *Stigmatodiscales*, they are phylogenetically distinct. *Stigmatodiscales* species constitute a clade with strong support within *Dothideomycetes*, *Asteromassaria* and *Stigmatomassaria* are contained within *Pleomassariaceae*, *Pleosporales*.

The ascomatal characteristics of the genera *Asterodiscus* and *Stigmatodiscus* are comparable. *Stigmatodiscus* features dark brown, asymmetric ascospores with the distal part being noticeably larger than the proximal part, in contrast to *Asterodiscus* which has hyaline, barely asymmetric ascospores that turn brownish only after ejection. However, *Asterodiscus* was synonymized under *Stigmatodiscus* in recent studies (Voglmayr & Amengual 2018, Calabon et al. 2023b) and consequently only a single genus *Stigmatodiscus* is accepted under *Stigmatodiscales* (Hyde et al. 2024b).

General description

Sexual morph: *Ascomata* apothecioid, embedded in cortex of dead twigs, without distinct margin nor excipulum. *Hamathecium* paraphysate; paraphyses septate, unbranched or rarely branched and anastomosing above, with free apical ends, covered by an epithecium. *Asci* bitunicate, fissitunicate, I-, without a ring. *Ascospores* large, slightly to strongly asymmetric, hyaline to brown, multiseptate with one euseptum and several distosepta, wall surrounded by gel coating. Asexual

morph: *Conidiomata* in nature immersed, peridermal, pycnidial. *Conidiogenous cells* phialidic. *Conidia* hyaline, falcate to semicircular (adapted from Voglmayr et al. 2016) (Fig. 88).

Families included in *Stigmatodiscales*

Stigmatodiscaceae Voglmayr & Jaklitsch

Justification of order and problems

Voglmayr et al. (2016) collected a dothideomycetous species from dead corticated twigs of *Carpinus orientalis* during a survey on corticolous ascomycetes in Istria, Croatia. The ascospores resembled those of *Stigmatomassaria pupula* (*Pleomassariaceae*, *Pleosporales*; see Barr 1982, under *Splanchnonema pupula*). Detailed morphological analysis revealed that the ascomata were apothecial, with ascomata opening at maturity and possessing septate paraphyses with apical swellings at their free ends. Initially, they were thought to represent poorly formed, aberrant ascomata of *Stigmatomassaria*. Sequence data proved beyond doubt that it did not belong to *Stigmatomassaria* or even *Pleosporales*. Dothideomycetous affinities were confirmed by NCBI Blast searches, however there was closer related taxa. Later, they discovered another Dothideomycetous species on corticated dead twigs of *Tamarix* sp. but this time with apothecial ascomata that had apically enlarged paraphyses and ascospores that matched the genus *Asteromassaria* (*Pleomassariaceae*, *Pleosporales*; see Barr 1982). Sequence data from pure cultures showed a phylogenetic link to the apothecial *Dothideomycetes* that were similar to *Stigmatomassaria*. After consulting the taxonomic literature, these taxa could not be identified, and no genera or families offered themselves were available for a taxonomic placement. Therefore, in accordance with the findings of multigene phylogenetic analyses and thorough morphological examinations, they classified the new genera *Asterodiscus* and *Stigmatodiscus*, which were positioned in a new family and order within *Dothideomycetes*. These taxa are distributed in Central and Southern Europe (Voglmayr et al. 2016, 2017b, Voglmayr & Amengual 2018).

Significance

Ecological and economic roles

Ecologically, all species are corticolous on freshly dead branches of various shrubs and trees. Species of *Asterodiscus* and *Stigmatodiscus* are described by development on recently dead corticated twigs attached to the trees. While *Stigmatodiscus* has predominantly been found on different *Acer* species (*A. campestre*, *A. monspessulanum*, and *A. sempervirens*), it has also been found on the unrelated *Carpinus orientalis*. *Asterodiscus* appears to be restricted to *Tamarix* spp. During the current investigation on several *Tamarix* spp. and *Acer monspessulanum*, respectively, *Asterodiscus tamaricis* and *Stigmatodiscus enigmatic*us, which are widely widespread in Central and Southern Europe, have frequently been observed. A high level of drought tolerance is shown by the fact that it mostly occurs on exposed twigs in a submediterranean climate. They have not yet been discovered on these widely dispersed hosts, highlighting once more the necessity of thorough biodiversity research on corticolous ascomycetes (Voglmayr & Jaklitsch 2008, 2011, 2014, Jaklitsch & Voglmayr 2011, 2014, Voglmayr et al. 2012, Jaklitsch et al. 2013, 2014, 2015, Checa et al. 2015, Galán et al. 2015).

Chemical diversity

No chemical diversity is reported in the order *Stigmatodiscales*.

***Strigulales* Lücking, M.P. Nelsen & K.D. Hyde, Fungal Diversity 63: 10 (2013)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

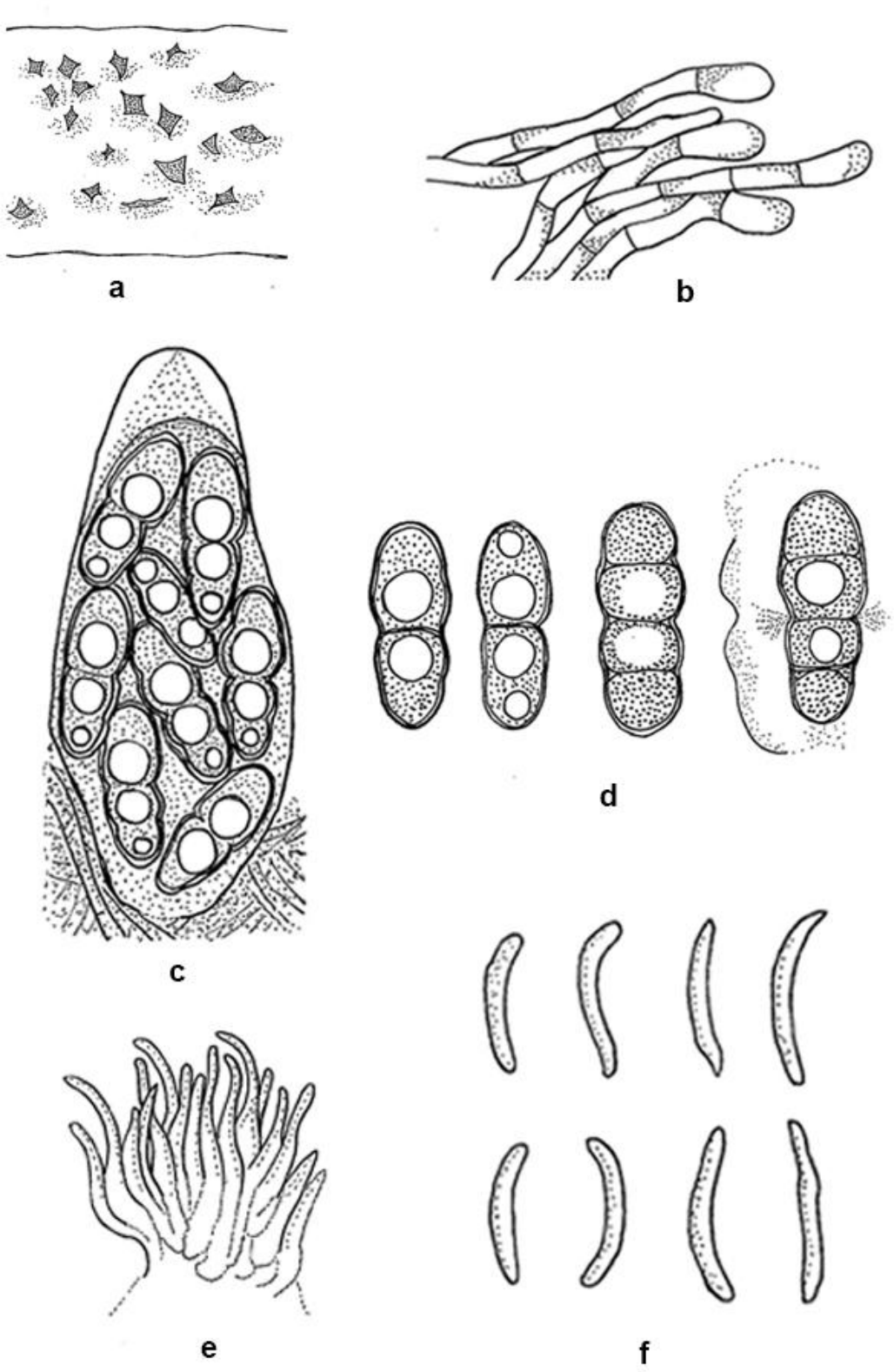


Figure 88 – Sexual and asexual morph of *Stigmatodiscales.* a Ascomata of *Stigmatodiscus enigmaticus* erumpent from bark in face view. b Septate, apically inflated paraphyses of *Stigmatodiscus enigmaticus*. c Ascus of *Asterodiscus tamaricis*. d Mature ascospores of *Stigmatodiscus enigmaticus* showing the gel sheath. e Phialides of *Asterodiscus tamaricis* producing conidia. f Falcate conidia of *Asterodiscus tamaricis* (drawn from Voglmayr et al. 2016). Scale bars: d–f = 200 µm, g–i = 50 µm, j–n = 10 µm.

Introduction

Strigulales is a lichenized order in *Dothideomycetes*. Two families, *Strigulaceae* and *Tenuitholiascaceae*, are accepted in this order, which can be separated based on multigene phylogenetic analyses as well as phenotypic characters (Hongsanan et al. 2020a). *Strigulales* comprises 115 species assigned to 14 genera. The order represents *Strigula*, one of the most important foliicolous genera (Lücking 2008). Members of *Strigulales* differ from most *Trypetheliales* in having euseptate ascospores with few septa and the lack of secondary chemistry (Hongsanan et al. 2020a). It also differs from *Monoblastiales* in having unbranched physes and the macroconidia producing gelatinous appendages (Hongsanan et al. 2020a).

History

Strigulales was established by Lücking et al. in Hyde et al. (2013) to accommodate the lichenized family *Strigulaceae*. For a general discussion of the family *Strigulaceae* see Lücking & Nelsen in Hyde et al. (2013; *Strigulaceae*). *Strigulaceae* was originally introduced to include all pyrenocarpus lichens growing on leaves (Zahlbruckner 1898). Notably, in doing so, Zahlbruckner separated foliicolous species of *Porina* as *Phylloporina* in *Strigulaceae*, whereas non-foliicolous species were kept by him as *Porina sensu stricto* in *Pyrenulaceae*, emphasizing the highly artificial nature of this classification. The systematic placement of *Strigulaceae* has been much discussed in the literature. It had been variously included in *Pyrenulales* and *Melanommatales* (= *Pleosporales*; Lumbsch & Huhndorf 2010), the first molecular approach (Schmitt et al. 2005) seemed to suggest placement of *Strigula stigmatella* in *Chaetothyriomycetidae*, more precisely in the *Verrucariaceae*. However, this was based on a misidentification of the sequenced specimen, which turned out to be a species of *Verrucaria sensu lato* close to *V. aquatilis* (Hyde et al. 2013). The image of ascus and ascospores of *Strigula stigmatella* presented in Schmitt et al. (2005) is actually not based on the sequenced specimen. A broader approach including specimens of *Strigula*, *Phyllobathelium*, and *Flavobathelium* showed that *Strigulaceae* is monophyletic and belongs in *Dothideomycetes* (Nelsen et al. 2009).

Recently, molecular phylogenetic analysis focusing on a broad set of foliicolous species hitherto assigned to the genus *Strigula* demonstrated that the latter is heterogeneous and can be divided into six genera, all characterized by a combination of morphological and anatomical features (Jiang et al. 2020b). Based on characters of the ascospores and macro- and microconidia, three further genera are recognized: *Phyllocharis*, *Dichoporis*, and the newly established genus *Swinscowia* (Hongsanan et al. 2020a). Currently, 115 species assigned to 14 genera are included in *Strigulaceae*.

Simultaneously, a new family, *Tenuitholiascaceae* was established to accommodate a novel lineage sister to *Strigulaceae* (Jiang et al. 2020a). To assess placement of the new lineage within *Dothideomycetes*, a dataset consisting of three loci (SSU, LSU, and TEF1-α) was analysed. Even if superficially similar to *Porina* in *Lecanoromycetes*, it was evident that the new lineage was a member of class *Dothideomycetes*, forming a clade supported sister to *Strigulaceae*. Since the asci of the novel lineage differed from those of *Strigulaceae* in lacking a thickened tholus and ocular chamber, it was considered prudent to introduce the monospecific family *Tenuitholiascaceae* and genus *Tenuitholiascus* for the new species *T. porinoides* (Jiang et al. 2020a).

General description

The order is characterized by crustose, mostly epiphytic habit on leaves, tree bark, and rocks; sub or supracucicular (leaves); trentepohlioid photobiont (including *Cephaleuros*, *Phycopelti*s and *Trentepohlia*). Sexual morph: *Ascomata* perithecioid, distinct or rarely reduced involucrellum, prosoplectenchymatous excipulum, unbranched to more rarely branched and sometimes anastomosing, but not net-like physes. *Asci* fissitunicate, with or without ocular chamber. *Ascospores* mostly fusiform to oblong, 1-septate (sometimes 3–7-septate to muriform), euseptate, hyaline. Asexual morph: *Conidia* produced in pycnidia, with the macroconidia typically being septate to muriform, terminal, gelatinous appendages, lack of secondary substances (crystalline anthraquinone pigments are found in *Flavobathelium*) (Figs. 89, 90).

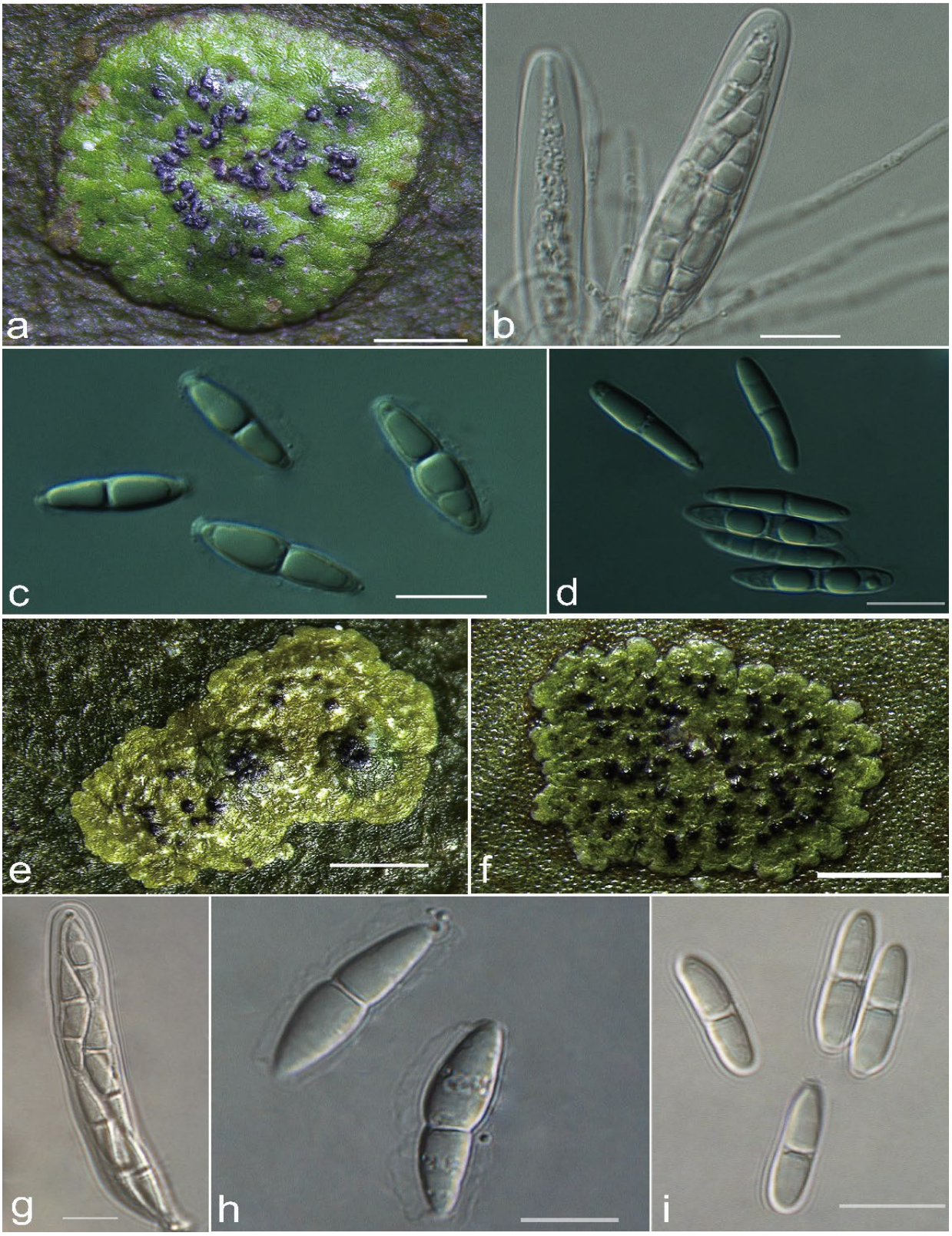


Figure 89 – Morphology of *Strigulales. Strigula acuticonidiarum* (holotype, HMAS–L 0138045). a Thallus with perithecia and pycnidia. b Asci, with eight biseriate ascospores. c Ascospores, with constriction at septum. d Macroconidia. *Strigula smaragdula* e Thallus with perithecia (HMAS–L 06211). f Thallus with pycnidia (HMAS–L 0138067). g Ascus, with eight biseriate ascospores (HMAS–L 0138066). h Ascospores, with 1-septate (HMAS–L0138066). i Macroconidia (HMAS–L 0138066). Scale bars: a, e, f = 300 µm, b, d, h = 10 µm (adapted from Jiang et al. 2017a; see that reference for further details).

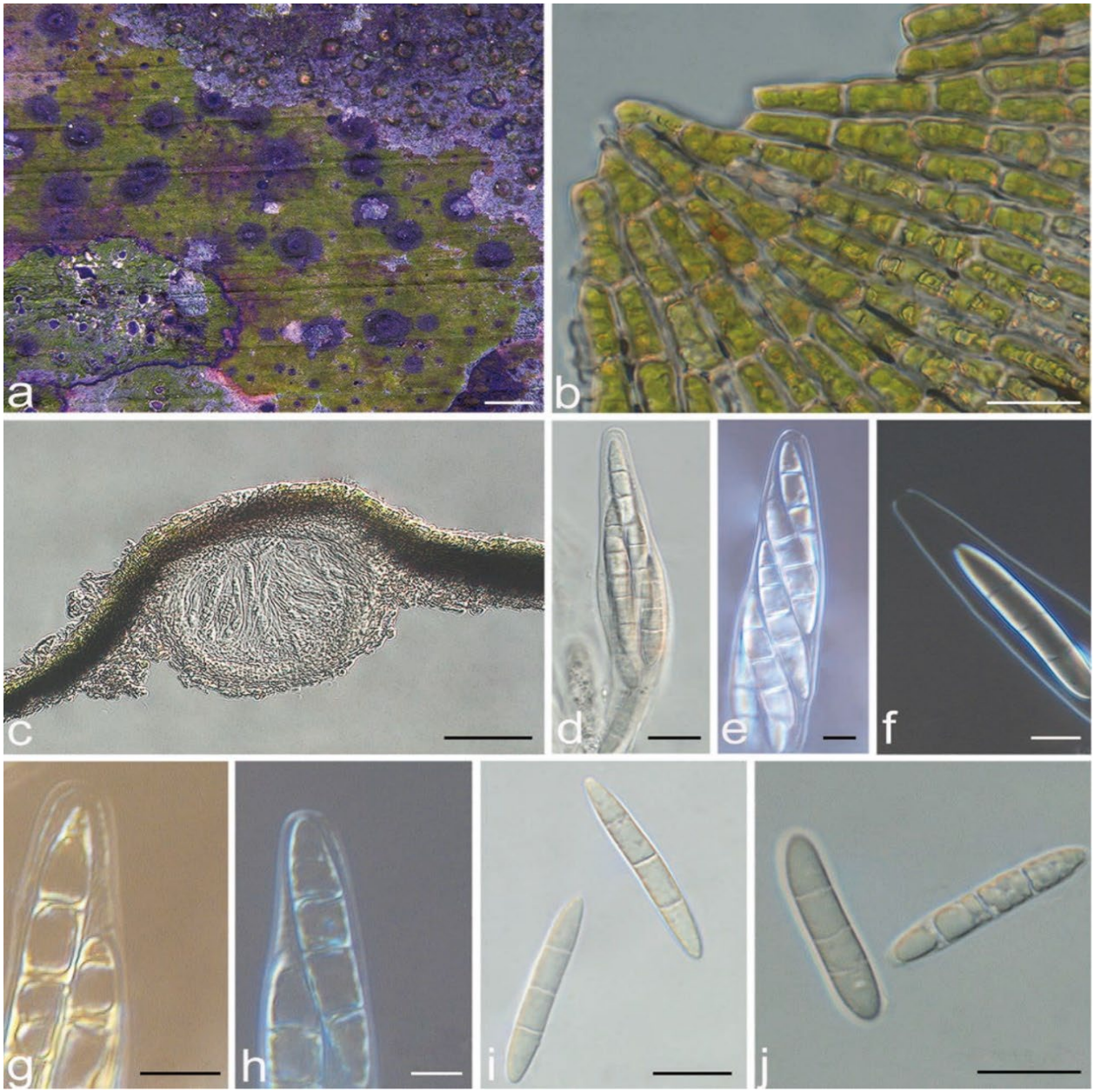


Figure 90 – Morphology of *Strigulales. Tenuitholiascus porinoides* (HMAS–L0139638). a Thallus. b The *Phycopeltis* algal partner. c Perithecia in vertical section. d Ascus (HMAS–L0139639). e Ascus (HMAS–L0139640). f Ascus apex (HMAS–L0141346). g Ascus with iodine reaction (HMAS–L0139638). h Ascus with iodine reaction (HMAS–L0141348). i Ascospores (HMAS–L0139639). j Ascospores (HMAS–L0139638) (adapted from Jiang et al. 2020c). Scale bars: a = 300 μm, b = 10 μm, c = 20 μm, d, i, j = 10 μm, e–h = 5 μm.

Families included in *Strigulales*

Strigulaceae Zahlbr.

Tenuitholiascaceae S.H. Jiang, Lücking & J.C. Wei

Evolution

The divergence time for *Strigulales* is estimated as 201 MYA (stem age, Hongsanan et al. 2020b).

Justification of order and problems

The genus *Swinscowia* in *Strigulaceae*, was introduced for non-foliicolous species centered around *Strigula jamesii* (Hongsanan et al. 2020a). Since the latter is the only species sequenced so far, it is unclear whether the taxa included here all form a monophyletic group. Given the phylogenetic and morpho-anatomical differentiation in the foliicolous lineages, likely more than one genus may be recognized for the non-foliicolous species here placed in *Swinscowia*. In addition, the small, exclusively foliicolous genus *Phyllocraterina*, currently containing two species (Lücking & Sérusiaux 2013), largely corresponds to non-foliicolous species of *Swinscowia* with muriform ascospores. *Phyllocraterina* was maintained as a separate genus because of the different substrate and photobiont and because of the unbranched paraphyses (Hongsanan et al. 2020a). Whereas the separation of *Dichoporis* from *Swinscowia* is straightforward, it is currently unclear how both genera relate to the foliicolous *Phylloporis* and *Phyllocraterina*, respectively. Thus, broad taxon sampling with multigenes is important to clarify the phylogenetic relationship between these genera.

Morphologically similar species have shown an independent phylogenetic evolution. This indicates a considerable degree of cryptic diversification in foliicolous representatives of *Strigula sensu lato*, particularly in the presumably widespread taxa *Strigula antillarum*, *S. concreta*, *S. nitidula*, and *S. smaragdula* (Jiang et al. 2017b, 2022). Thus, broad sampling is also needed for species delimitation.

Significance

Ecological and economic roles

Indicator values of foliicolous *Strigulales* have been published that allow applications in monitoring the conservation status of forest ecosystems (Lücking 1997). Some species of *Strigula sensu lato* are now placed in *Phylloporis*, *Puiggariella*, *Raciborskiella*, *Racoplaca*, and *Strigula sensu stricto* and allow a rather precise monitoring, as their scores are highly specific to individual genera and species (Lücking 1997, Hongsanan et al. 2020a). In a recent study, the population genetics of a new species segregated from *Strigula smaragdula*, *S. multiformis*, and its correlation with modeled habitat preferences was studied (Oh et al. 2019).

Chemical diversity

Crystalline anthraquinone pigments are found in *Flavobathelium*. However, these chemical substances are not exclusive for *Strigulales*.

***Superstratomycetales* van Nieuwenh., Miądl., Houbraken, Adan, Lutzoni & Samson, Fungal Systematics and Evolution 7: 332 (2021)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Superstratomycetales was proposed by van Nieuwenhuijzen et al. (2016b) and was placed in *Dothideomycetes* and related to *Trypetheliales*. This order comprises only one genus (*Superstatomyces*), with four species that are confirmed through phylogenetic analyses of ITS, LSU, EF-1a sequence data (van Nieuwenhuijzen et al. 2016b, Wijayawardene et al. 2017a, 2017b).

History

The history of *Superstratomycetales* started in 2016, when several taxa were studied on oil-treated timber that was exposed to the outdoors in Australia and Netherlands (Van Nieuwenhuijzen et al. 2016b). Those taxa formed a sister clade to *Trypetheliales* in the multigene phylogenetic analyses conducted based on ITS, SSU, LSU, mtSSU, RPB1, RPB2, and EF-1α sequence data. The taxa were identified as three species, *Superstratomyces flavomucosus*, S. *atroviridis*, and *S. albomucosus* in the new genus *Superstratomyces*, a new family *Superstratomycetaceae* and the new order *Superstratomycetales* in *Dothideomycetes* (Van Nieuwenhuijzen et al. 2016b). Later

Superstratomyces tardicrescens was introduced from USA and Spain to this order, that showed distinct features from known *Superstratomyces* in having small conidia that are produced on well-developed conidiophores, whereas larger conidia are produced on single phialides in others (Crous et al. 2018a). However, the ordinal, familial and generic classifications were not formally validated as the generic description was not provided to distinguish the genus from other known groups. Consequently, Crous et al. (2021c) validated the genus, family and order by providing a description which was also supported by a single gene (LSU) phylogeny and the order formed a sister clade to *Eremomycetales*.

General description

The taxa are only reported in the asexual morph that are mainly available on colonies.

Sexual morph: Undermined. Asexual morph: *Coelomycetous. Conidiomata* pycnidial, superficial, solitary or confluent, glabrous, globose, brown to black, exuding a white mass of slimy conidia. *Pycnidial wall* pseudoparenchymatous, of *textura angularis*, composed of 3–5 layers of pale brown to brown cells. *Setae* present or absent, verrucose to tuberculate, erect to recurved, septate, hyaline to subhyaline at apex and turning brown towards base. *Conidiophores* reduced to conidiogenous cells or branched, smooth-walled, with terminal and intercalary conidiogenous cells, hyaline. *Conidiogenous cells* cylindrical to doliiform or ampulliform, phialidic, smooth-walled, hyaline. *Conidia* cylindrical to navicular or ovoid, aseptate, smooth- and thin-walled, guttulate, hyaline (adapted from Hongsanan et al. 2020b, Crous et al. 2021c, Fig. 91).

Families included in *Superstratomycetales*

Superstratomycetaceae van Nieuwenh.

Justification of order and problems

The ordinal placement of *Superstratomycetales* has been subjected to change. The order formed a sister clade to *Trypetheliales* when it was published (on ITS, SSU, LSU, mtSSU, RPB1, RPB2, and EF-1α sequences data) (Van Nieuwenhuijzen et al. 2016b).

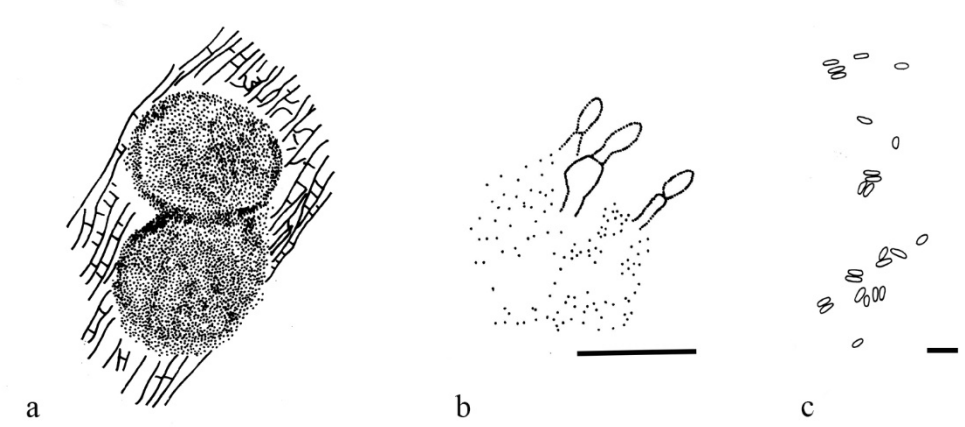


Figure 91 – Morphology of *Superstratomycetales* (*Superstratomyces atroviridis*). a Pycnidia. b Conidiogenous cells. c Conidia (drawn from Van Nieuwenhuijzen et al. 2016, redrawn from Hongsanan et al. 2020). Scale bars: b, c = 10 μm.

Later, the order recovered as sister clade to *Acrospermales* (based on LSU, RPB2, SSU and TEF1 sequence data) (Hongsanan et al. 2020b) and *Eremomycetales* (based on LSU sequence data) (Crous et al. 2021c). In addition, the ordinal or familial placement was established mainly based on molecular data (Van Nieuwenhuijzen et al. 2016b).

Significance

Ecological and economic roles

The taxa are reported from exposed, oil-treated wood (*Pycnanthus angolensis* and *Pinus sylvestris*), leaves of *Hakea multilinearis* and hymen eye specimen from Australia, Netherlands and USA (Crous et al. 2018a, 2021c).

Chemical diversity

There are no chemical diversity reports available for *Superstratomycetales*.

Trypetheliales Lücking, Aptroot & Sipman, Bibliotheca Lichenologica 97: 13 (2008)

Subphylum *: Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Trypetheliales was established by Aptroot et al. (2008a) to accommodate the single family *Trypetheliaceae*. Ertz et al. (2015) added the second family *Polycoccaceae* based on morpho-molecular analyses. *Trypetheliaceae* primarily comprises lichenized fungi, although a few members are non-lichenized, while *Polycoccaceae* consists entirely of lichenicolous fungi. The taxa within *Trypetheliales* are characterized by perithecioid ascomata that may appear solitary or aggregated in pseudostromata, branched and anastomosing paraphysoids forming a distinct network, and hyaline or occasionally brown ascospores. The ascospores are typically transversely septate to muriform, often with diamond-shaped lumina and angular wall thickenings. However, these characteristics may vary among members, including the degree of anastomosis of the hamathecium and the morphology of the ascospores (Hongsanan et al. 2020a).

History

The exploration of *Trypetheliaceae* dates to the early days of lichenology. Acharius (1817b, c) documented ten *Trypethelium* species, laying the foundation for subsequent studies. Eschweiler (1824) formally established the family *Trypetheliaceae*, with Fée (1831) subsequently presenting a comprehensive monograph detailing 19 *Trypethelium* species. Over time, additional species have been described from various regions such as Australia, Brazil, and Borneo by different authors including Eschweiler (1824, 1833), Krempelhuber (1875), Montagne (1851, 1856), and Müller (1884, 1885). Trevisan (1861) provided an initial synopsis of the family, further solidifying its recognition. Throughout the years, *Trypetheliaceae* has been studied by numerous lichenologists, including Tuckerman (1872), Zahlbruckner (1903-1907, 1926), Smith (1921), Malme (1924), Fink (1935), and Keissler (1937). The generic concept within the family has evolved over time, with genera initially included such as *Arthonia*, *Chiodecton* and *Glyphis* and now classified in different families or classes (Johnson 1940).

Traditionally, *Trypetheliaceae* encompassed seven primary genera: *Pseudopyrenula* (ecorticate, featuring astrothelioid ascospores), *Polymeridium* (ecorticate, with euseptate ascospores), *Trypethelium* (corticate, characterized by ascomata with apical ostiole and astrothelioid, transversely septate ascospores), *Laurera* (corticate, with ascomata bearing apical ostiole and astrothelioid, muriform ascospores), *Astrothelium* (corticate, ascomata with lateral or shared ostiole and astrothelioid, transversely septate ascospores), *Campylothelium* (corticate, with ascomata having lateral ostiole and astrothelioid, muriform ascospores), and *Cryptothelium* (corticate, with ascomata bearing shared ostiole and astrothelioid, muriform ascospores) (Hyde et al. 2013, Hongsanan et al. 2020a). Subsequently, additional genera were incorporated into this family, such as *Exiliseptum* (corticate, with ascomata featuring shared ostiole and euseptate ascospores), *Bathelium* (corticate, characterized by pseudostromatic ascomata composed of brown, jigsaw-puzzle-shaped hyphal cells), *Architrypethelium* (corticate, with ascomata having apical or lateral ostiole and transversely septate, very large, hyaline or brown ascospores) (Aptroot 1991a), and *Aptrootia* (corticate, with ascomata

bearing apical ostiole and muriform, dark brown ascospores) (Lücking et al. 2007). A comprehensive revision of *Trypetheliaceae* by Aptroot et al. (2016) recognized 418 species, with an estimated total of about 800 species globally (Aptroot et al. 2019). Thiyagaraja et al. (2021a) merged *Arthopyreniaceae* into *Trypetheliaceae* based on sequence data from the type material of *Arthopyrenia cerasi*. The order presently accommodates two families including *Polycoccaceae* and *Trypetheliaceae*.

General description

Trypetheliaceae is characterized by the aggregation of separate perithecia, forming a stroma with its own apical pore. Within these structures, the asci are borne enclosed in a flask-shaped fruiting body. The members of this family typically have a crustose thallus with *Trentepohlia* as the photobiont. However, the microscopic structures that are fundamental to the characterization of this family were not considered in earlier studies (Hongsanan et al. 2020a). While *Trypetheliaceae* and *Polycoccaceae* share similarities in morphology, such as perithecioid ascomata and branched, anastomosing paraphysoids within a hymenial gel matrix, as well as bitunicate asci, *Polycoccaceae* differs in its non-lichenized, lichenicolous habit and the presence of 1-septate, brown, typically smaller ascospores (adapted from Ertz et al. 2015).

Sexual morph: *Thallus* reduced and ecorticate, white, to distinctly corticate, yellow-brown to olive-green, sometimes partly or completely bright yellow, orange or red due to superficial anthraquinone pigments. *Photobiont Trentepohlia* (lichenized species). *Ascomata* scattered, clustered, often becoming grouped, sometimes united by a clypeus or enclosed in galls, aggregated in pseudostromata, or fused with common ostiole, immersed to sessile, immersed with only the ostiole visible to erumpent and the upper half exposed when mature, brown-black but usually covered by thallus, globose to pear-shaped or conical, subglobose to obpyriform, coriaceous to carbonaceous, ostiolate, ostiole round, neck not extended and scarcely distinguishable from the ascomatal wall; wall even in thickness or somewhat broader near the ostiole, composed of 3–6 layers of polyhedral pseudoparenchymatous cells, radially compressed in vertical section and roughly isodiametric in surface view, forming a *textura angularis*; outer layers of cells with ± evenly thickened walls, brown to dark brown and continuing below the centrum; inner layers less intensely pigmented to hyaline with thin-walled cells. *Excipulum* dense, consisting of compressed hyphae, appearing prosoplectenchymatous in thin, bleached sections but structure usually difficult to observe due to heavy carbonization, generally dark brown to brown-black. *Hamathecium* composed of a branched and anastomosing net of thin and regularly septate to remotely septate narrow hyphal filaments, probably trabeculate pseudoparaphyses (referred as paraphysoids in some species), rarely fexuose, periphyses absent; hymenial gel I+ blue to violet or unchanged, gelatinous matrix, occasionally with hyaline or yellow oil inspersion. *Asci* 1–8-spored, bitunicate, fssitunicate, obclavate, subclavate or cylindrical, short pedicellate, with refractive ring and wide, inamyloid ocular chamber comprising more than half of the width of the ascus, wall thicker in the upper part of mature asci, with a small internal apical beak. *Ascospores* irregularly arranged to biseriate, fusiform-ellipsoid to oblong, 1-septate (euseptate); cells ± equal in size or the upper cell larger and broader, apices generally rounded or rarely attenuated, somewhat or not constricted at the septum, with distosepta and sometimes additional eusepta and rectangular to diamond-shaped (generally six-angled) lumina, muriform, hyaline to dark brown, smooth or delicately verruculose, sometimes with a gelatinous sheath, either as polar pads or irregular median pads or a complete sheath enveloping the whole ascospore. Asexual morph: *Pycnidia* immersed, immersed to erumpent, crowded and intermixed with the ascomata. visible as black dots in specific, often pseudostromatic areas on fertile thalli, or whole thalli only producing pycnidia; rarely old ascospores within asci transforming into pycnidia. *Conidiogenous cells* holoblastic, arising from the pycnidial wall, subcylindrical to elongate-ampulliform and strongly tapered towards the apex, with 1–2 annelations. *Conidia* (narrowly) oblong to elliptic, acrogenous, hyaline, aseptate, bacillar (adapted from Hongsanan et al. 2020a, Figs. 92, 93).

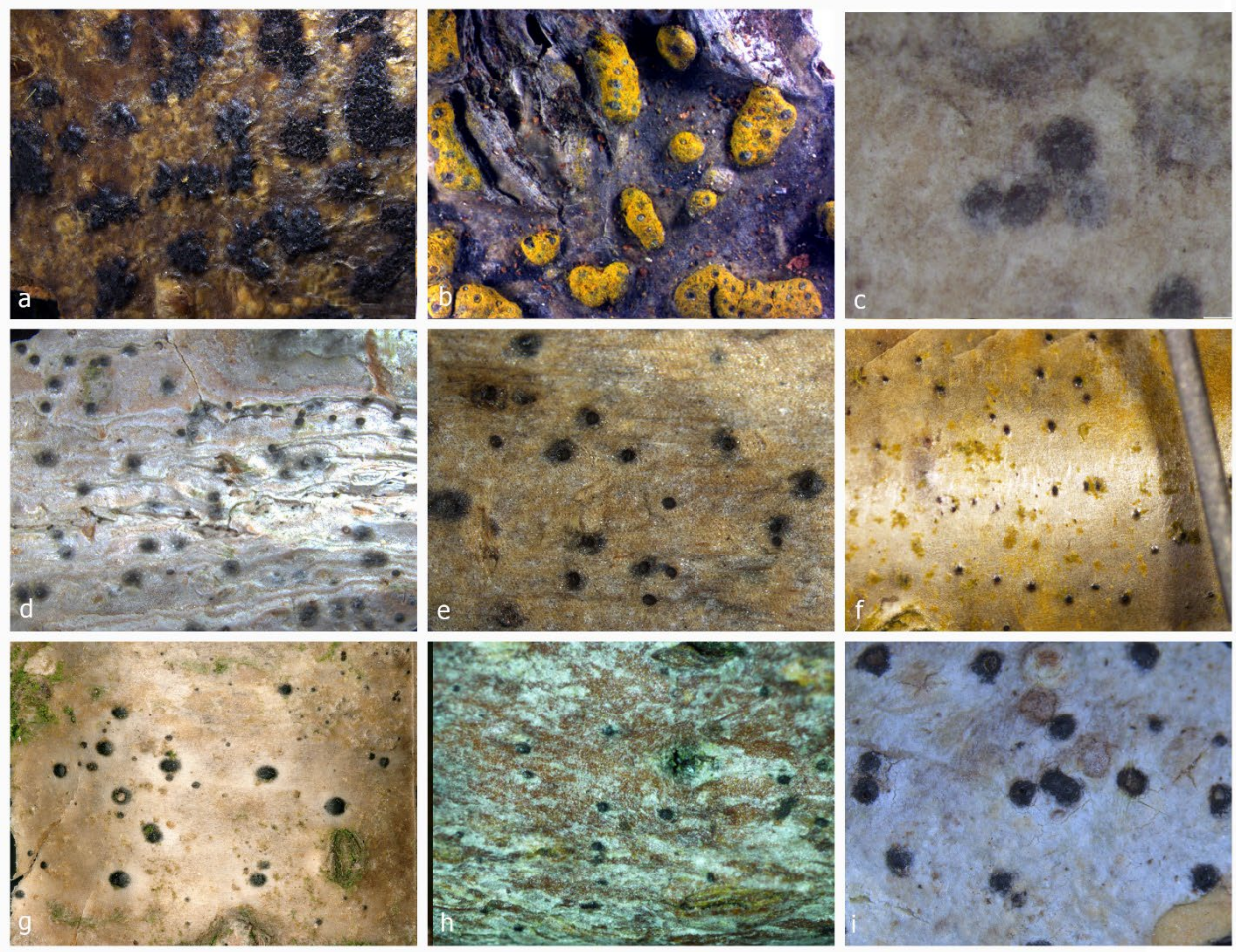


Figure 92 – Ascomata of *Trypetheliales*. a, b, d *Trypetheliaceae* species. c *Alloarthopyrenia italica*, e *Bogoriella pandanicola*. f *Arthopyrenia viridescens*. g *A. cerasi*. h *A. callunae*. i *Pseudopyrenula endoxanthoides.*

Families included in *Trypetheliales*

Polycoccaceae Ertz, Hafellner & Diederich

Trypetheliaceae Zenker

Evolution

Based on the divergence time estimates in *Dothideomycetes* (Liu et al. 2017b), the order was diversified by approximately 215 (140–298) MYA (crown age) and 309 (231–388) MYA (stem age).

Justification of order and problems

In the phylogenetic analyses, *Trypetheliales* formed a distinct and strongly supported clade based on LSU sequence data (Ertz et al. 2015). While in analyses of SSU, RPB2, SSU, and TEF1-α sequence data, the order was found to be sister to *Mytilinidiales*, although with relatively low statistical support (Hongsanan et al. 2020a). Thus, broad taxon sampling for *Trypetheliales* and its adjacent orders are important to study its phylogenetic relationship.

Significance

Ecological and economic roles

Trypetheliaceae taxa are predominantly lichenized, although some are reported as less or non-lichenized, mainly inhabiting corticolous habitats and rarely saxicolous habitats. They are primarily distributed in tropical to subtropical regions (Aptroot et al. 2016), often found in tropical lowland to lower montane rainforests, dry forests, and savannas (Hongsanan et al. 2020a). *Polycoccaceae*, on the other hand, consists entirely of lichenicolous fungi (Ertz et al. 2015).

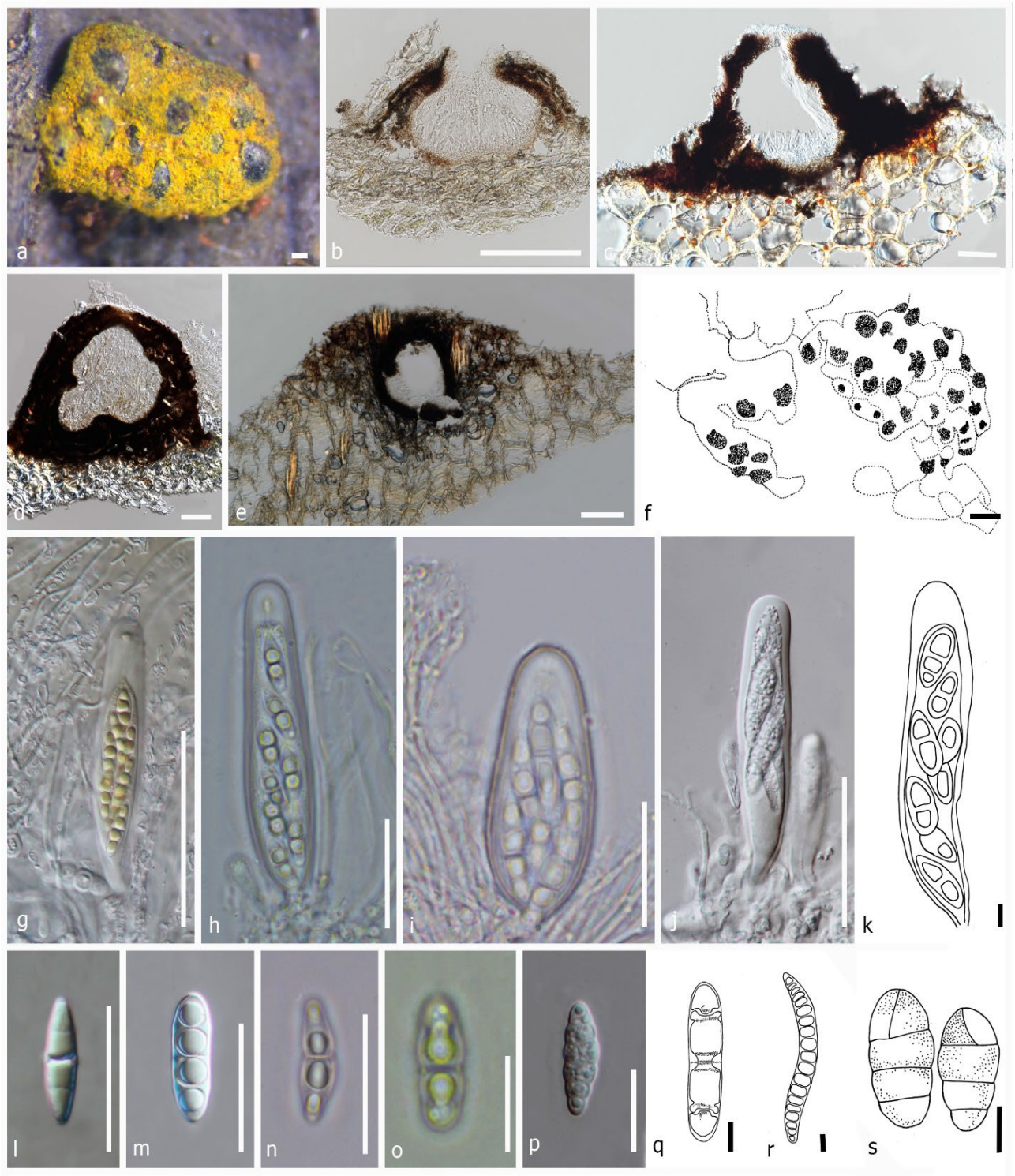


Figure 93 – Vertical section through ascomata, asci, paraphyses and ascospores of *Trypetheliales*. a–f Vertical section through ascomata (a *Astrothelium* sp., b *Alloarthopyrenia italica*, c *Trypetheilaceae* sp., d *Pseudopyrenula endoxanthoides*, e *Bogoriella pandanicola*, f *Polycoccum trypethelioides*). g–k Asci and Paraphyses (g *Pseudopyrenula endoxanthoides*, h *Arthopyrenia callunae*, i *A. viridescens*, j *Bogoriella pandanicola*, k *Polycoccum pulvinatum*). i–s Ascospores (l, m *Pseudopyrenula endoxanthoides*, n *A. viridescens*, o *Arthopyrenia callunae*, p *Bogoriella pandanicola*, q *Aptrootia terricola*, r *Polymeridium pleurothecium*, s *Bogoriella decipiens*) (drawn from Nelsen et al. 2014b, Ertz et al. 2015, Aptroot & Lücking 2016, Zhang et al. 2017c). Scale bars: a, b = 100 µm, c, g, j = 50 µm, d, h, j, l–n, p = 20 µm, e = 200 µm, f, k = 5 µm, r, s = 10 µm.

These taxa are mostly found in tropical lowland to lower montane regions, including rainforests, dry forests, and savannas (Hongsanan et al. 2020a). In some species such as *Marcelaria purpurina*, the copious red pigment of the ascomata has been historically utilized as a dye by Amazonian indigenous tribes (Sambo 1940, Daly & Millozza 2007) and as a treatment for headaches by the Bolivian Chácobo people. As the second-largest lichenized family, *Trypetheliaceae* members play a significant role in lichen communities, particularly in wet and dry tropical forests and savanna ecosystems (Komposch & Hafellner 2000, 2003, Rivas Plata et al. 2008, Aptroot 2013, Menezes et al. 2018).

Chemical diversity

Trypetheliaceae produces polyketide-derived aromatic compounds synthesized through an acetyl-polymalonyl pathway (Elix & Stocker-Wörgötter 2008). These compounds, including xanthones, anthraquinones, and perylenequinones, often contribute to the colorful appearance of their ascomata or thalli (Stensiö & Wachtmeister 1969, Culberson & Culberson, 1970, Mathey & Hoder 1978, Harris 1984, Mathey et al. 1987, 1994, Aptroot 1991b, Mathey & Lukins 2001, Manojlovic et al. 2010).

Secondary metabolites have been used for taxonomic characterization, and Aptroot et al. (2013a) considered the presence or absence of metabolites sufficient for species segregation. However, the utility of the secondary metabolite lichexanthone for species identification in *Trypetheliaceae* has been questioned, as its presence can vary (Harris 1991, 1995, 1998). Sometimes, lichexanthone is produced on the thallus surface, while yellow to orange or red anthraquinones and perylenequinones are often found in the medulla of the thalline layer covering the perithecia or superficially on various parts of the thallus (Hongsanan et al. 2020a). Further molecular studies are required to ascertain the reliability of using these metabolites for species delimitation in *Trypetheliaceae*.

Other relevant data and future recommendations

Arthopyreniaceae is a heterogenous group that was introduced to accommodate lichenized and non-lichenized fungi (Watson 1929). *Arthopyrenia salicis* and an unidentified *Arthopyrenia* species are placed in *Pleosporales* based on molecular data. *Arthopyrenia salicis* formed a close clade to bambusicolous genera *Roussoella* and *Roussoellopsi*s but the former differs in having periphysoids produced in a gelatinized matrix while the latter have paraphysoids and oblong to fusiform, hyaline spores lacking striations (Hino & Katumoto 1965, Hyde 1997, Tanaka et al. 2009, Schoch et al. 2009a, Nelsen et al. 2011a, b). Mapook et al. (2020a) introduced a novel genus, *Setoarthopyrenia*, to accommodate *Setoarthopyrenia chromolaenae*, which clustered with *Arthopyrenia* sp. (UTHSC: DI16-362) in *Pleosporales*, showing high similarity in BLAST research results. However, due to the lack of available data for *Arthopyrenia* sp. (UTHSC: DI16-362), the authors did not provide a morphological comparison between these two species. *Arthopyrenia* was found to be polyphyletic in phylogenetic analyses by Thiyagaraja et al. (2021a). Many *Arthopyrenia* species have also been transferred to *Naetrocymbe* (Harris 1995), but this genus lacks molecular data. Therefore, detailed morpho-molecular investigations are needed to resolve their taxonomic placement. Genera such as *Polypyrenula*, *Novomicrothelia* and *Pseudobogoriella* are facultatively associated with algae, while *Alloarthopyrenia*, *Julella*, and *Arthopyrenia sensu stricto* are recorded as non-lichenized saprobic fungi on bark (Hyde et al. 2013, Aptroot & Lücking 2016, Hongsanan et al. 2020b). However, the nutritional mode of species that are loosely associated with or without algae is largely unknown.

Tubeufiales **Boonmee & K.D. Hyde, Fungal Diversity 68(1): 245 (2014)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

The order *Tubeufiales* (*Pleosporomycetidae*, *Dothideomycetes*) was established by Boonmee et al. (2014) with *Tubeufiaceae* as the type family based on morphology and phylogenetic analysis of combined LSU, SSU and TEF1-α sequence data. Currently, *Tubeufiales* accommodates *Bezerromycetaceae*, *Tubeufiaceae*, and *Wiesneriomycetaceae*, based on DNA molecular data (Wijayawardene et al. 2022a, Hyde et al. 2024b). Among these, *Tubeufiaceae* is the largest family within the order *Tubeufiales* (Wijayawardene et al. 2022a). It was introduced by Barr (1979a) based on the generic type *Tubeufia* and included five genera i.e. *Letendraeopsis*, *Melioliphila*, *Podonectria*, *Rebentischia*, and *Thaxteriella*. There are 53 accepted genera in the family *Tubeufiaceae*, including *Acanthohelicospora*, *Acanthophiobolus*, *Acanthostigma*, *Acanthostigmina*, *Acanthotubeufia*, *Acrogenihelicosporium*, *Aquaphila*, *Berkleasmium*, *Bifrontia*, *Boerlagiomyces*, *Camporesiomyces*, *Chaetosphaerulina*, *Chlamydotubeufia*, *Dematiohelicoma*, *Dematiohelicomyces*, *Dematiohelicosporum*, *Dematiotubeufia*, *Dictyospora*, *Discotubeufia*, *Excipulariopsis*, *Helicangiospora*, *Helicoarctatus*, *Helicodochium*, *Helicohyalinum*, *Helicoma*, *Helicomyces*, *Helicosporium*, *Helicotruncatum*, *Helicotubeufia*, *Hyalohelicoon*, *Hyalohelicotubeufia*, *Hyalohelisphora*, *Kamalomyces*, *Kevinhydea*, *Lichenotubeufia*, *Manoharachariella*, *Muripulchra*, *Neoacanthostigma*, *Neochlamydotubeufia*, *Neohelicoma*, *Neohelicomyces*, *Neohelicosporium*, *Neomanoharachariella*, *Neotubeufia*, *Paraheliconyces*, *Pleurohelicosporium*, *Pseudohelicoon*, *Pseudohelicosporium*, *Pseudotubeufia*, *Tamhinispora*, *Thaxteriella*, *Tubeufia*, and *Zaanenomyces*. Among them, there are 31 genera, namely *Acanthohelicospora*, *Acanthostigmina*, *Acrogenihelicosporium*, *Berkleasmium*, *Camporesiomyces*, *Chlamydotubeufia*, *Dematiohelicoma*, *Dematiohelicomyces*, *Dematiohelicosporum*, *Helicangiospora*, *Helicoarctatus*, *Helicodochium*, *Helicohyalinum*, *Helicoma*, *Helicomyces*, *Helicosporium*, *Helicotruncatum*, *Helicotubeufia*, *Hyalohelicoon*, *Hyalohelisphora*, *Hyalohelicotubeufia*, *Neoacanthostigma*, *Neohelicomyces*, *Neohelicosporium*, *Paraheliconyces*, *Pleurohelicosporium*, *Pseudohelicoon*, *Pseudohelicosporium*, *Pseudotubeufia*, *Thaxteriella*, *Thaxteriellopsis*, and *Tubeufia*. with coiled conidia, and eight genera, *viz*. *Acanthophiobolus*, *Bifrontia*, *Boerlagiomyces*, *Chaetosphaerulina*, *Lichenotubeufia*, *Hyalohelicoon*, *Hyalohelicotubeufia*, and *Thaxteriella*, only have morphological data available, and their systematic evolutionary relationships have not been confirmed by molecular data (Lu et al. 2018b, Jayasiri et al. 2019, Liu et al. 2019b, Lu & Kang 2020, Kuo & Goh 2021, Xu et al. 2021, Li et al. 2022b, Wijayawardene et al. 2022a, Ma et al. 2023b, 2024). *Tubeufiaceae* species are mostly saprobic on terrestrial woody substrates and some are from freshwater habitats (Lu et al. 2018b, Lu & Kang 2020, Li et al. 2022b, Ma et al. 2023b). The sexual morphs of *Tubeufiaceae* are characterized by superficial ascomata, a pseudoparaphysate hamathecium, bitunicate asci, and many septate, hyaline to pale brown cylindrical ascospores (Boonmee et al. 2014, Lu et al. 2018b). The asexual morphs of *Tubeufiaceae* are hyphomycetous, mostly helicosporous, some are chlamydosporous and phragmosporous (Zhao et al. 2007, Boonmee et al. 2014, Lu et al. 2018b). The other two families, *Bezerromycetaceae* includes *Bezerromyces*, *Honghemyces*, and *Neorhamphoria* and *Wiesneriomycetaceae* includes *Parawiesneriomyces*, *Phalangispora*, *Pseudogliophragma*, *Setosynnema*, *Speiropsis*, and *Wiesneriomyces* (Wijayawardene et al. 2022a, Yang et al. 2023a).

History

The order *Tubeufiales* was introduced by Boonmee et al. (2014) based on the type family, *Tubeufiaceae*. Subsequently, Suetrong et al. (2014) introduced a second family *Wiesneriomycetaceae* to *Tubeufiales* based on morphology and molecular data. Bezerra et al. (2017a) excluded *Wiesneriomycetaceae* from *Tubeufiales*. Instead, they introduced two orders within *Dothideomycetes*, *viz*. *Bezerromycetales* and *Wiesneriomycetales*, based on phylogenetic analysis of combined ITS, LSU, and SSU sequence data. Liu et al. (2017b) studied the divergence time of the three orders, *Bezerromycetales*, *Tubeufiales* and *Wiesneriomycetales*, which are 14 (stem ages 147), 189 (stem age 268 MYA), and 40 MYA (stem ages 186 MYA), respectively. Therefore, they excluded *Bezerromycetales* and *Wiesneriomycetales*, and transferred *Bezerromycetaceae* and *Wiesneriomycetaceae* as families of *Tubeufiales* (*Dothideomycetes*) based on divergence times (Liu

et al. 2017b). Additionally, the genus *Xiliomyces* within *Bezerromycetaceae* was introduced with only one species, *X. brasiliensis* by Bezerra et al. (2017a). However, Crous et al. (2021b) identified *Xiliomyces brasiliensis* as *Bezerromyces pseudobrasiliensis* within *Bezerromycetaceae* based on DNA sequence data and morphological characteristics (Crous et al. 2021b). The latest studies excluded the genera *Artocarpomyces* and *Podonectria*, and added the genus *Excipulariopsis* within *Tubeufiaceae* (Xu et al. 2021, Wijayawardene et al. 2022a, Yang et al. 2023a). Currently, there are 62 genera in *Tubeufiales* (Lu et al. 2018b, Kuo & Goh 2021, Xu et al. 2021, Li et al. 2022b, Wijayawardene et al. 2022a, Ma et al. 2023b, 2024, Yang et al. 2023a).

General description

Tubeufiales species exhibit both sexual and asexual morphs (Suetrong et al. 2014, Bezerra et al. 2017a, Lu et al. 2018b). The sexual morph of *Tubeufiales* typically features ellipsoid, filiform, fusiform ascospores (Suetrong et al. 2014, Bezerra et al. 2017a, Lu et al. 2018b). The asexual morph of *Tubeufiales* can have various types of conidia, including chlamydosporous, dictyosporous, helicosporous, phragmosporous, and scolecosporous (Suetrong et al. 2014, Bezerra et al. 2017a, Lu et al. 2018b, Ma et al. 2024). *Tubeufiaceae* is known to encompass both sexual and asexual morphs (Lu et al. 2018b), whereas *Bezerromycetaceae* and *Wiesneriomycetaceae* have been reported to exhibit only their sexual and asexual morphs.

Sexual morph: *Ascomata* superficial, oval and bright, *Hamathecium* pseudoparaphysate, *Asci* bitunicate, *Ascospores* septate, hyaline to pale brown, cylindrical to long subfusiform, obovoid or ellipsoidal, fusiform to filiform (Boonmee et al. 2014, Bezerra et al. 2017a, Lu et al. 2018b); Asexual morph: *Conidia* hyphomycetes, mostly helicoid, some have cylindrical, ellipsoidal or ovoid, globose to subglobose, filiform, fusiform (adapted from Zhao et al. 2007, Crous et al. 2016b, Lu et al. 2018b, Kuo & Goh 2021, Wanasinghe et al. 2023, Yang et al. 2023a, Ma et al. 2024) (Figs. 94, 95, 96, 97, 98, 99). For a more complete description of the other five genera, see Ma et al. (2024), which are listed as *Acrohelicosporium*, *Hyalohelicoon*, *Hyalohelisphora*, *Hyalotubeufia*, and *Pseudohelicospo -rium*.

Families included in *Tubeufiales*

Bezerromycetaceae J.D.P. Bezerra, C.M. Souza-Motta & Crous
Tubeufiaceae M.E. Barr
Wiesneriomycetaceae Suetrong, Rungjind. Somrith. & E.B.G. Jones

Evolution

The classification of fungi at higher taxonomic levels has been subjective (Liu et al. 2016b). With the development of molecular methods and the availability of fossil calibration data, it has become possible to use divergence time as a standardized criterion for classification at higher taxonomic levels (Liu et al. 2016b, 2017b, Hongsanan et al. 2020b). Liu et al. (2017b) studied the divergence time of the largest class, *Dothideomycetes*. They found that divergence times (crown age) for most orders were between 100 and 220 MYA, while divergence times for most families were between 20 and 100 MYA. However, the two orders, *Bezerromycetales* and *Wiesneriomycetales*, were 14 (stem ages 147) and 40 MYA (stem ages 186 MYA), respectively (Liu et al. 2017b). Therefore, Liu et al. (2017b) identified *Bezerromycetaceae* and *Wiesneriomycetaceae* as families of *Tubeufiales* (*Dothideomycetes*) based on divergence times.

Justification of order and problems

Currently, about 286 helicosporous species are distributed across 31 genera of *Tubeufiales* (Linder 1929, Zhao et al. 2007, Boonmee et al. 2011, 2014, Lu et al. 2017a, b, c, 2018a, b, Luo et al. 2017, Liu et al. 2019b, Li et al. 2022b, Wijayawardene et al. 2022a, Ma et al. 2023b, 2023c, Xiao et al. 2023a, Yang et al. 2023b, Ma et al. 2024, Peng et al. 2025). Among them, the genus *Xenosporium* was introduced by Penzig & Saccardo (1902) with *X. mirabile* as type species. Before 2007, a total of 18 species of *Xenosporium* had been discovered. None of the authors were successful in obtaining molecular data (Zhao et al. 2006, 2007).

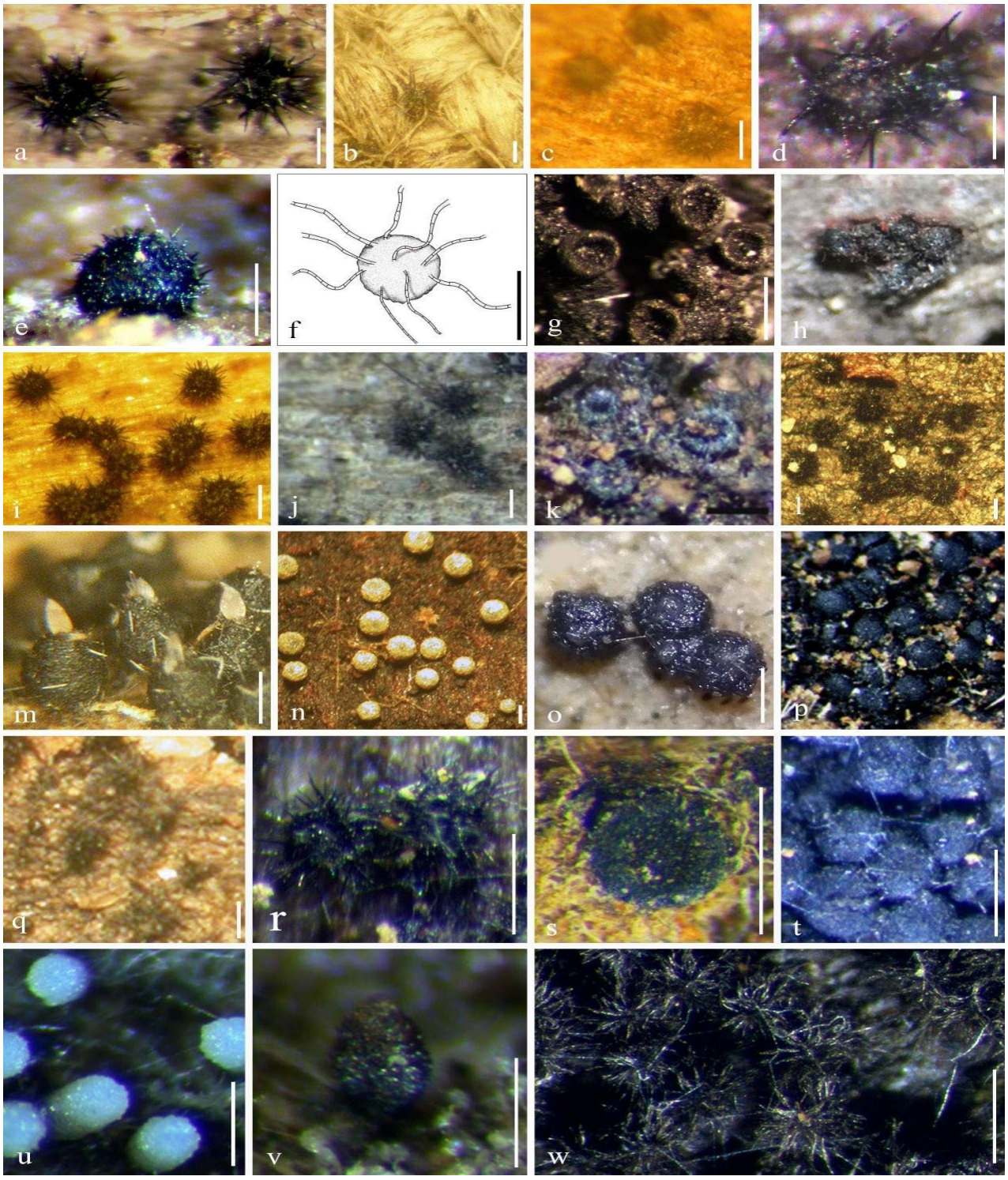


Figure 94 – Colonies morphology of the sexual *Tubeufiales.* a *Acanthohelicospora pinicola*. b *Acanthophiobolus helminthosporus*. c *Acanthostigma chiangmaiense*. d *Acanthostigmina minuta*. e *Berkleasmium fusiforme*. f *Bezerromyces brasiliensis*. g *Bifrontia compactior*. h *Camporesiomyces mali*. i *Chlamydotubeufia huaikangplaensis*. j *Dictyospora thailandica*. k *Discotubeufia browneae*. l *Helicangiospora lignicola*. m *Dematiotubeufia chiangraiensis*. n *Neohelicoma fagacearum*. o *Helicotubeufia guangxiensis*. p *Kamalomyces thailandicus*. q *Neoacanthostigma fusiforme*. r *Neochlamydotubeufia fusiformis*. s *Neorhamphoria garethjonesii*. t *Neotubeufia krabiensis*. u *Tubeufia filiformis*. v *T. filiformis*. w *T. latispora*. (Photos were adapted from Boonmee et al. 2011, 2014, 2016, Brahmanage et al. 2017, Chaiwan et al. 2017, Lu et al. 2017b, 2018b, Liu et al. 2018b, Jayasiri et al. 2019, Phookamsak et al. 2019, Hyde et al. 2020b, redrawn from Bezerra et al. 2017a).

Scale bars: s, t, w = 500 µm, f = 250 µm, d, e, g, j, o, r, u, v = 200 µm, a, b, i, l–n, q = 100 µm, c = 50 µm.



Figure 95 – Ascomata morphology of *Tubeufiales.* a *Acanthohelicospora pinicola*. b *Acanthophiobolus helminthosporus*. c *Acanthostigma chiangmaiense*. d *Acanthotubeufia filiformis*. e *Acanthostigmina minuta*. f *Berkleasmium fusiforme*. g *Bifrontia compactior*. h *Camporesiomyces* mali. i *Chlamydotubeufia huaikangplaensis*. j *Dictyospora thailandica*. k *Discotubeufia browneae*. l *Helicangiospora lignicola*. m *Dematiotubeufia chiangraiensis*. n *Neohelicoma fagacearum*. o *Helicotubeufia guangxiensis*. p *Honghemyces pterolobii*. q *Kamalomyces thailandicus*. r *Lichenotubeufia cryptica*. s *Neoacanthostigma fusiforme*. t *Neochlamydotubeufia fusiformis*. u *Neorhamphoria garethjonesii*. v *Neotubeufia krabiensis*. w *Tubeufia filiformis*. x *T. latispora*. (Photos were obtained from Boonmee et al. 2011, 2014, 2016, Brahmanage et al. 2017, Chaiwan et

al. 2017, Lu et al. 2017b, 2018b, Liu et al. 2018b, Jayasiri et al. 2019, Phookamsak et al. 2019, Hyde et al. 2020b, redrawn from Promputtha 2010, Flakus et al. 2019, Wanasinghe et al. 2022). Scale bars: e, u, w = 200 µm, h = 150 µm, a, b, f, i, j, l–q, s, v, x, = 100 µm, c, d, g, t = 50 µm, k = 30 µm, r = 25 µm.

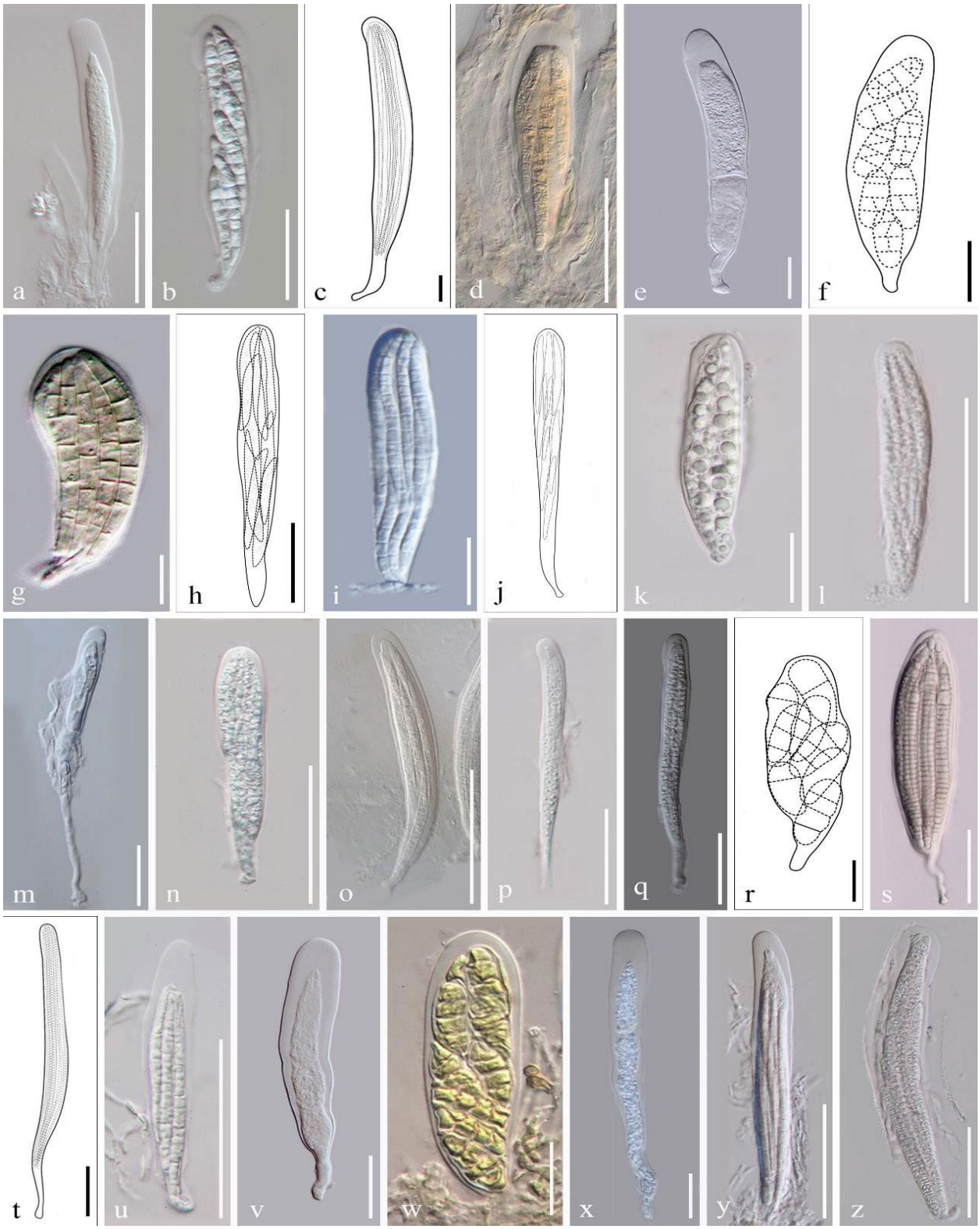


Figure 96 – Asci morphology of *Tubeufiales.* a *Acanthohelicospora pinicola*. b *Acanthostigma chiangmaiense*. c *Acanthotubeufia filiformis*. d *Acanthostigmina minuta*. e *Berkleasmium fusiforme*. f *Bezerromyces brasiliensis*. g *Bifrontia compactior*. h *Boerlagiomyces velutinus*. i *Camporesiomyces mali*. j *Chaetosphaerulina yasudae*. k *Chlamydotubeufia huaikangplaensis*. l *Dictyospora*

thailandica. m *Discotubeufia browneae*. n *Helicangiospora lignicola*. o *Dematiotubeufia chiangraiensis*. p *Neohelicoma fagacearum*. q *Helicotubeufia guangxiensis*. r *Honghemyces pterolobii*. s *Kamalomyces thailandicus*. t *Lichenotubeufia cryptica*. u *Neoacanthostigma fusiforme*. v *Neochlamydotubeufia fusiformis*. w *Neorhamphoria garethjonesii*. x *Neotubeufia krabiensis*. y *Tubeufia filiformis*. z *T. latispora* (Photos were adapted from Hino 1938, Boonmee et al. 2011, 2014, 2016, Brahmanage et al. 2017, Chaiwan et al. 2017, Lu et al. 2017b, 2018b, Liu et al. 2018b, Jayasiri et al. 2019, Phookamsak et al. 2019, Hyde et al. 2020b. redrawn from Promputtha & Miller 2010, Bezerra et al. 2017a, Flakus et al. 2019). Scale bars: l, o = 100 μm; a, d, n, s, y, z = 50 μm, b, f = 30 μm, t = 25 μm, e, i, k, m, p, q, u–x = 20 μm, c, g, r = 10 μm.

Thus, *Xenosporium* is classified as *Tubeufiaceae* in the Index Fungorum database but lacks sufficient morphological and phylogenetic support (Lu & Kang 2020). Kuo & Goh (2021) introduced two new species and one new record of *Xenosporium*, confirming its phylogenetic placement within the *Tubeufiales*. Ma et al. (2023c) introduced a new species, *Tubeufia muriformis*, and found that it is morphological similarity to *Xenosporium* rather than *Tubeufia*. Additionally, Kuo & Goh (2021) conducted a phylogenetic analysis and revealed that species of *Xenosporium* and *Tubeufia* cluster with strong support. Therefore, based on morphological comparison and DNA sequence data, Ma et al. (2024) classified *Xenosporium* species within *Tubeufia*.

Significance

Ecological and economic roles

Most species of *Tubeufiales* have a worldwide distribution and are common saprobes on decaying wood (Boonmee et al. 2011, 2014, Lu et al. 2018b, Lu & Kang 2020). They are mostly discovered in aquatic and terrestrial habitats and are widely distributed in tropical to subtropical regions (Zhao et al. 2007, Boonmee et al. 2011, 2014, Lu et al. 2018b, Lu & Kang 2020). Some literature report *Tubeufiales* species as plant endophytes (Flewelling et al. 2013, Bezerra et al. 2017a, Sati & Pathak 2017). They can be saprobic, endophytic, and play important roles in ecological cycling, medicine, and environmental protection (Lu et al. 2018b, Lu & Kang 2020).

Chemical diversity

Tubeufiales taxa, especially the helicosporous members, have the potential to produce a number of bioactive compounds. For example, species from genera such as *Helicoma*, *Helicosporium*, *Neohelicomyces*, and *Tubeufia* can produce secondary metabolites with novel structures and significant biological activity. These metabolites are especially notable for their antitumor and antimicrobial activity (Itazaki et al. 1990, Nakai et al. 1991, Hu et al. 2006, Lee et al. 2013, Zeng et al. 2022c, Qian et al. 2023).

Other relevant data and future recommendations

Tubeufiales species, especially the helicosporous members, are reported to have high diversity worldwide, yet their morphology is very similar (Linder 1929, Goos 1986, Zhao et al. 2007, Boonmee et al. 2011, 2014, Lu et al. 2018b, Ma et al. 2023c). Since they have highly similar morphological characteristics, it was difficult to identify helicosporous hyphomycete taxa based solely on morphological comparisons (Linder 1929, Pirozynski 1972, Goos 1985, 1986, 1989, Zhao et al. 2007, Lu et al. 2018b, Hsieh et al. 2021, Lu et al. 2022, Tian et al. 2022). Therefore, they require multigene phylogenetic analyses to correctly identify taxa. Consequently, collecting additional fresh specimens or obtaining valid specimens on loan is necessary to resolve the issue of uniform classification for these genera or species.

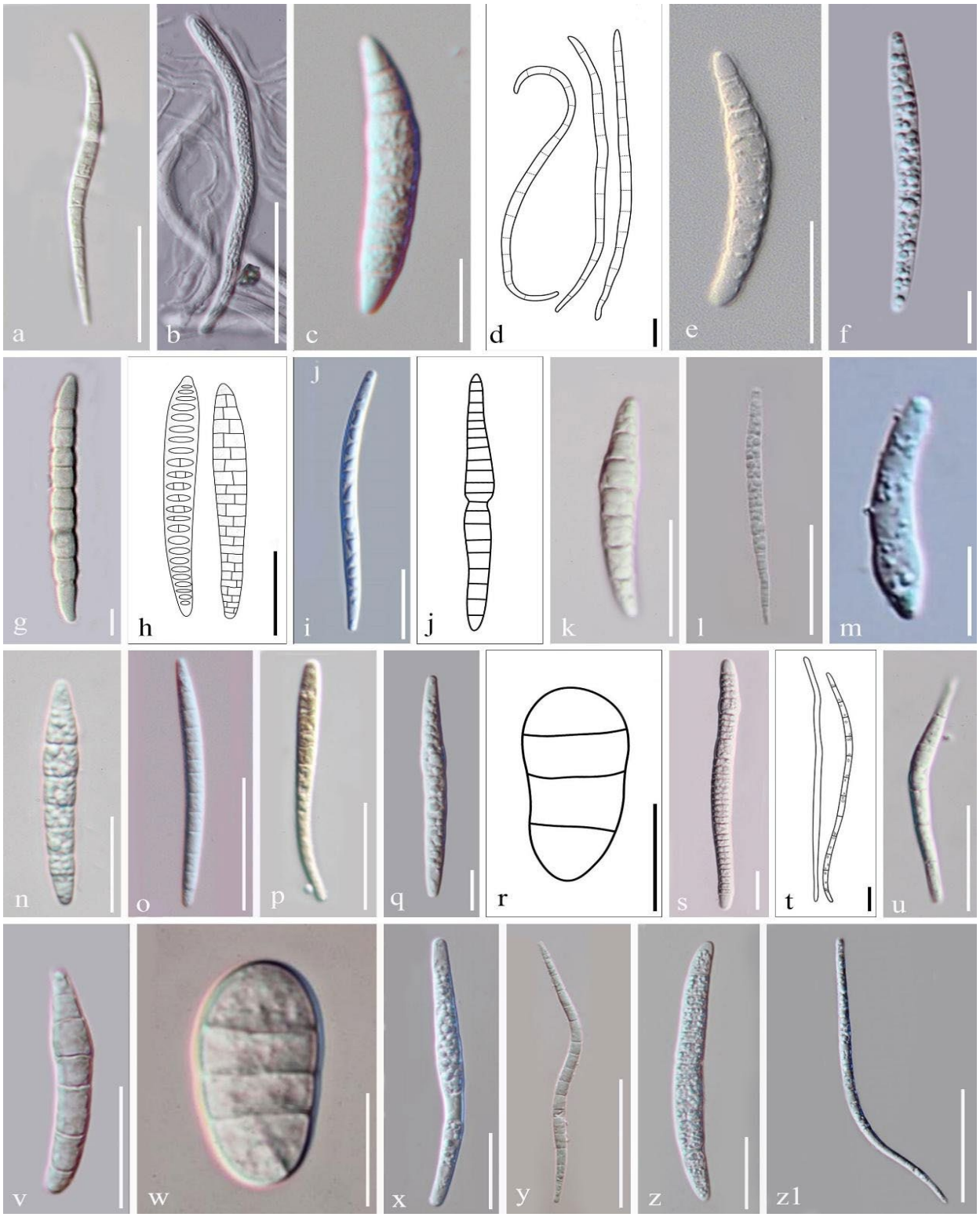


Figure 97 – Ascospores morphology of *Tubeufiales.* a *Acanthohelicospora pinicola*. b *Acanthophiobolus helminthosporus*. c *Acanthostigma chiangmaiense*. d *Acanthotubeufia filiformis*. e *Acanthostigmina minuta*. f *Berkleasmium fusiforme*. g *Bifrontia compactior*. h *Boerlagiomyces velutinus*. i *Camporesiomyces mali*. j *Chaetosphaerulina yasudae*. k *Chlamydotubeufia huaikangplaensis*. l *Dictyospora thailandica*. m *Discotubeufia browneae*. n *Helicangiospora lignicola*. o *Dematiotubeufia chiangraiensis*. p *Neohelicoma fagacearum*. q *Helicotubeufia guangxiensis*. r *Honghemyces pterolobii*. s *Kamalomyces thailandicus*. t *Lichenotubeufia cryptica*. u *Neoacanthostigma fusiforme*. v *Neochlamydotubeufia fusiformis*. w *Neorhamphoria garethjonesii*. x *Neotubeufia krabiensis*. y *Tubeufia filiformis*. z *T. latispora*. z1 *Tubeufia tectonae* (Photos were

adapted from Boonmee et al. 2011, 2014, 2016, Brahmanage et al. 2017, Chaiwan et al. 2017, Lu et al. 2017b, 2018b, Liu et al. 2018b, Jayasiri et al. 2019, Phookamsak et al. 2019, Hyde et al. 2020b. redrawn from Promputtha & Miller 2010, Flakus et al. 2019). Scale bars: b = 100 µm, h 90–120×12–14 µm, e, l, o, z1 = 50 µm, a, i, k, n, s, u, v, x. z = 20 µm, c, d, f, m, p–r, t, w = 10 µm, g = 5 µm.

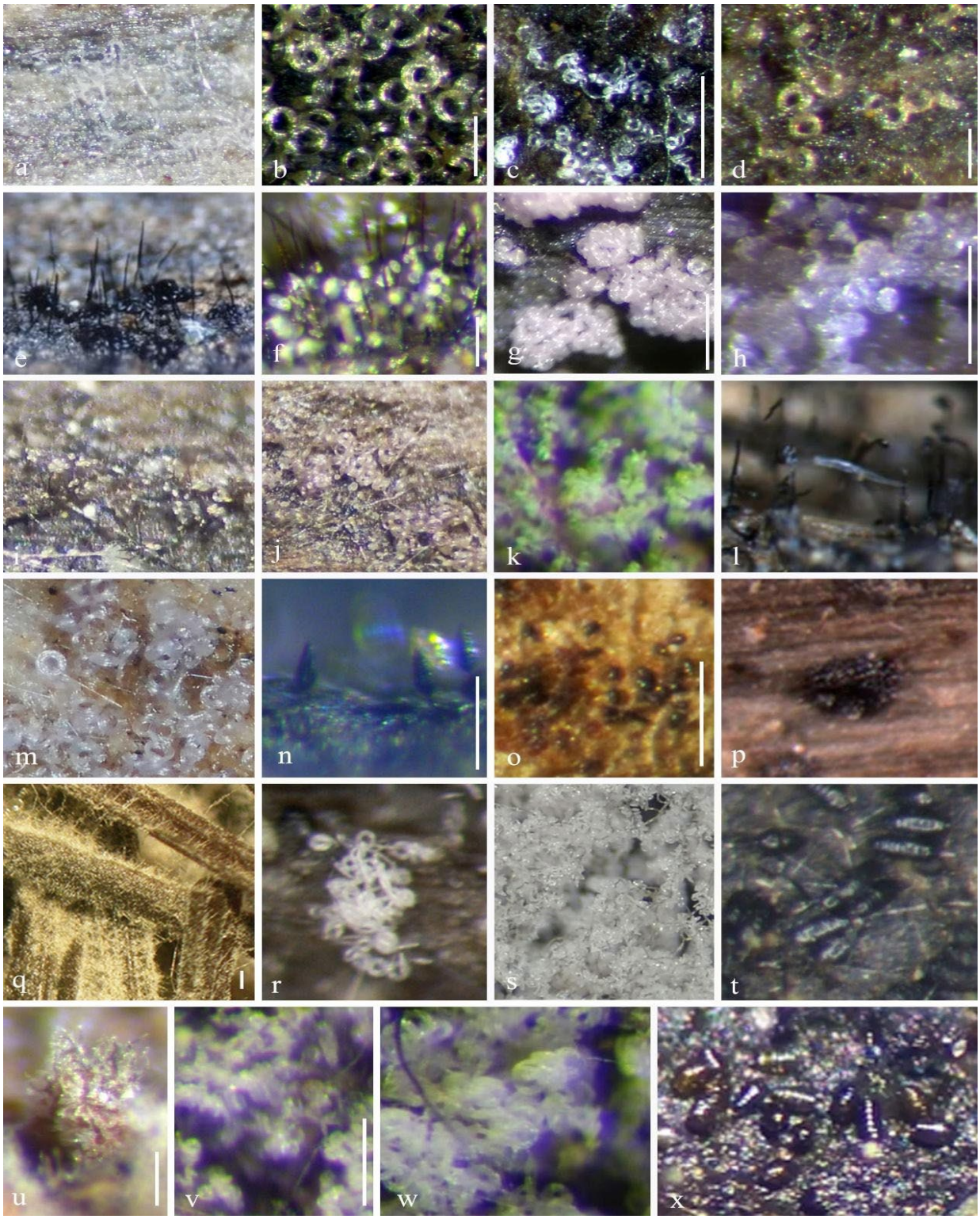


Figure 98 – Colonies morphology of the asexual *Tubeufiales.* a *Aquaphila albicans*. b *Berkleasmium longisporum*. c *Dematiohelicomyces helicosporous*. d *Dematiohelicosporum guttulatum*. e *Excipulariopsis narsapurensis*. f *Helicoarctatus aquaticus*. g *Helicoarctatus aquaticus*. h *Helicohyalinum infundibulum*. i *Helicoma guttulatum*. j *Helicoma longisporum*. k *Helicosporium multidentatum*. l *Helicotruncatum* palmigenum. m *Helicotubeufia guangxiensis*. n *Kevinhydea*

brevistipitata. o *Manoharachariella tectonae*. p *Muripulchra aquatic*. q *Neoacanthostigma fusiforme*. r *Neohelicomyces aquaticus*. s *Neohelicosporium parvisporum*. t *Neomanoharachariella aquatic*. u *Pleurohelicosporium parvisporum*. v *Pseudohelicomyces aquaticus*. w *Pseudotubeufia hyalospora*. x *Pseudohelicoon subglobosum*. (Photos were adapted from Doilom et al. 2017, Luo et al. 2017; Liu et al. 2018b, Lu et al. 2018a, 2018b, 2022, Liu et al. 2019b, Li et al. 2022b, Tian et al. 2022, Ma et al. 2023b, Xiao et al. 2023a, Yang et al. 2023b). Scale bars: c = 500 µm, b, h, o = 200 µm, d, f, g, n, u, v = 100 µm, q = 10 µm.



Figure 99 – Conidia morphology of *Tubeufiales.* a *Acanthohelicospora pinicola*. b *Aquaphila albicans*. c *Berkleasmium longisporum*. d *Dematiohelicoma pulchrum*. e *Dematiohelicomyces helicosporous*. f *Dematiohelicosporum guttulatum*. g *Excipulariopsis narsapurensis*. h *Helicangiospora lignicola*. i *Helicoarctatus aquaticus*. j *Helicodochium aquaticum*. k *Helicohyalinum infundibulum*. l *Helicoma guttulatum*. m *Helicoma longisporum*. n *Helicomyces colligatus*. o *Helicosporium multidentatum*. p *Helicotruncatum palmigenum*. q *Helicotubeufia guangxiensis*. r *Kevinhydea brevistipitata*. s *Manoharachariella tectonae*. t *Muripulchra aquatic*. u *Neoacanthostigma fusiforme*. v *Neohelicomyces aquaticus*. w *Neohelicosporium parvisporum*. x *Neomanoharachariella aquatic*. y *Parawiesneriomyces syzygii*. z *Phalangispora constricta*. z1 *Pleurohelicosporium parvisporum*. z2 *Setosynnema yunnanense*. z3 *Speiropsis simplex*. z4 *Wiesneriomyces* sp. z5 *Pseudogliophragma indicum*. z6 *Zaanenomyces quadripartis*. z7 *Tamhinispora indica*. z8 *Thaxteriella roraimensis*. z9 *Thaxteriellopsis lignicola*. z10 *Pseudohelicomyces aquaticus*. z11 *Pseudotubeufia hyalospora*. z12 *Xenosporium* sp. z13 *Pseudohelicoon* sp. (Photos were obtained from Boonmee et al. 2014, Doilom et al. 2017, Luo et al. 2017, Liu et al. 2018b, Lu et al. 2018a, 2018b, 2022, Liu et al. 2019b; Li et al. 2022b; Tian et al. 2022, Ma et al. 2023b, Xiao et al. 2023a, Yang et al. 2023b, redrawn from Matsushima 1971, Samuels & Muller 1978, Nawawi & Webster 1982, Subramanian & Sekar 1982, Zhao et al. 2007, Rajeshkumar & Sharma 2013, Mel'nik et al. 2014, Crous et al. 2016b, 2021b). Scale bars: c = 100 μm, e, f, q = 50 μm, t = 40 μm, g, v = 30 μm, b, p, z = 30 μm, i–k, m, n, z7, z12, z13 = 20 μm, x = 15 μm, a, d, l, o, r, s, u, w, y, z1–z3, z5, z6, z10, z11 = 10 μm, h = 5 μm.

Valsariales **Jaklitsch, K.D. Hyde & Voglmayr, Fungal Diversity 73: 167 (2015)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

The order *Valsariales* was introduced by Jaklitsch et al. (2015), and contains a single family *Valsariaceae*. *Valsariaceae* is typified by *Valsaria insitiva* and includes three genera, *viz*. *Bambusaria*, *Myrmaecium* and *Valsaria*. *Valsariaceae* is characterized by multi-perithecioid, ostiolate ascomata immersed in eu- or pseudostromata, bitunicate, cylindrical asci, without obvious fissitunicate dehiscence, and dark brown, bicellular ascospores, budding in artificial culture. Asexual morphs of *Valsariaceae* were reported as hyphomycetes, coelomycetes, or budding yeast-like conidia, or produce arthrospores (Jaklitsch et al. 2015, Pem et al. 2019a). Members of *Valsariaceae* are widely distributed, from Europe to the topics, and occur on decayed wood, bark or culms of tree-like grasses (bamboo) (Jaklitsch et al. 2015). Most species of *Valsariaceae* are reported from continent of Europe, however only *Bambusaria* was collected from a tropical region (India and Thailand).

History

Valsaria was introduced by Cesati & De Notaris (1863) with *V. insitiva* as the type species. The placement of *Valsaria* was initially controversial, as most researchers considered it as having unitunicate asci (Barr 1978, 1990b, Glawe 1985, Huhndorf 1992). Later Ju et al. (1966) identified that *Valsaria* should have bitunicate asci, even though, the fissitunicate feature was not noticeable, they placed *Valsaria* in *Dothideomycetes*. Jaklitsch et al. (2015) introduced a new family *Valsariaceae* and new order *Valsariales* to accommodate valsaria-like taxa, based on morphological and phylogenetic studies, and accepted three genera (*Bambusaria*, *Myrmaecium* and *Valsaria*) in *Valsariaceae*.

General description

The typical characters of sexual morph of valsaria-like taxa are that multi-perithecioid ascomata are gregariously immersed in eu- or pseudostromata, and produce bitunicate asci without obvious

fissitunicate dehiscence, and bicellular ascospore with ornamentations (Jaklitsch et al. 2015). *Valsaria* usually forms pseudostromata, which are immersed or erumpent from bark to superficial on wood and contains 4–12 ascomata. The surface of stromata is usually irregularly tubercular. The ectostroma of *Valsaria* are black, and frequently form substellate-stellate structures around the ostiolar openings (Jaklitsch et al. 2015, Pem et al. 2019a). *Valsaria* taxa produce brown to dark brown ascospores with finely tuberculate, dotted, or reticulate surface ornamentation. *Myrmaecium* forms eu- or pseudostromatic, immersed, erumpent to superficial stromata on bark, or rarely decorticated wood. *Myrmaecium* taxa usually produce stromata with a variety of color (orange, yellow to brownish-yellow, grey to tan, or hyaline to reddish-brown), when stromata are obvious, and eustromatic. *Myrmaecium* species produce dark brown ascospores with reticulate or labyrinthine surface ornamentation. *Bambusaria* is characterized by immersed, erumpent to superficial, globose to irregular, black eustromatic fruiting bodies with ostiolar necks, bitunicate asci with an ocular chamber, and ellipsoid to broadly fusiform or biconic, brown ascospores with labyrinthine to coarsely reticulate ornamentation (Jaklitsch et al. 2015). Ju et al. (1966) mentioned that *Valsaria* form four types of asexual morphs.

Sexual morph: *Ascomata* perithecioid, clustered or immersed in eu- or pseudostromata. *Ostiole* periphysate, generally with a neck. *Hamathecium* of true, apically free paraphyses. *Asci* bitunicate, cylindrical, usually without obvious fissitunicate dehiscence. *Ascospores* brown to dark brown, bicellular, budding in artificial culture. Asexual morph: Coelomycetous in nature substrate, and hyphomycetous and/or coelomycetous in culture. On natural substrates: when present, multiloculate conidiomata resembling stromata, immersed to erumpent, globose to irregular, dark. *Locules* with a dark brown, pseudoparenchymatous wall, internally lined by dense palisades of lageniform phialides. *Phialides* densely packed, lageniform to cylindrical. *Conidia* oblong, allantoid, ellipsoid or bullet-shaped, 1-celled, hyaline, smooth (Figs. 100, 101).

Families included in *Valsariales*

Valsariaceae Jaklitsch, K.D. Hyde & Voglmayr

Justification of order and problems

Valsaria have more than 140 records in Index Fungorum (2023), while only seven species (*V. insitiva*, *V. lopadostomoides*, *V. neotropica*, *V. ostryae*, *V. robiniae*, *V. rudis*, *V. spartii*) are reported with sequences (Jaklitsch et al. 2015, Pem et al. 2019a, Li et al. 2023b). Twenty-five epithets of *Myrmaecium* are listed in Index Fungorum, however only three species *viz*. *M. fulvopruinatum*, *M. rubricosum*, *M. rubrum* have molecular data in GenBank. *Bambusaria* is monotypic, with *B. bambusae* as the type species. A new collection from Thailand was designated as the reference specimens with ITS-LSU, RPB2 and TEF1-α genes.

As lacking enough sequence data, the classification of *Myrmaecium* and *Valsaria* species remain problematic. Ju et al. (1966) moved 19 *Valsaria* species to *Myrmaecium* based on morphological characteristics. Jaklitsch et al. (2015) mentioned that 182 names of the above genera can be found in Index Fungorum (2025). Most existing species of *Myrmaecium* were described with hyaline ascospores. They are probably synonyms (Jaklitsch et al. 2015). Fresh collections of *Myrmaecium* and *Valsaria* are needed to obtaining molecular data for determining the species placement.

Significance

Ecological and economic roles

Members of *Valsariaceae* have widely geographical distribution, with the reports most from Europe and America, and particularly from Southeast Asia (Schweinitz 1822, Ellis & Everhart 1892, Eriksson 2014, Ju et al. 1966, Jaklitsch et al. 2015). Most *Valsaria* taxa occur in arm climate areas in Europe. Li et al. (2023c) re-described a new record of *V. insitiva* from Sichuan, China, which is in a subtropical climate. Only *Bambusaria bambusae* was reported from tropic regions (India, and Thailand). *Myrmaecium* has a worldwide distribution and usually found on sun-exposed, corticated logs and branches of conifers and broad-leaved trees (Jaklitsch et al. 2015).

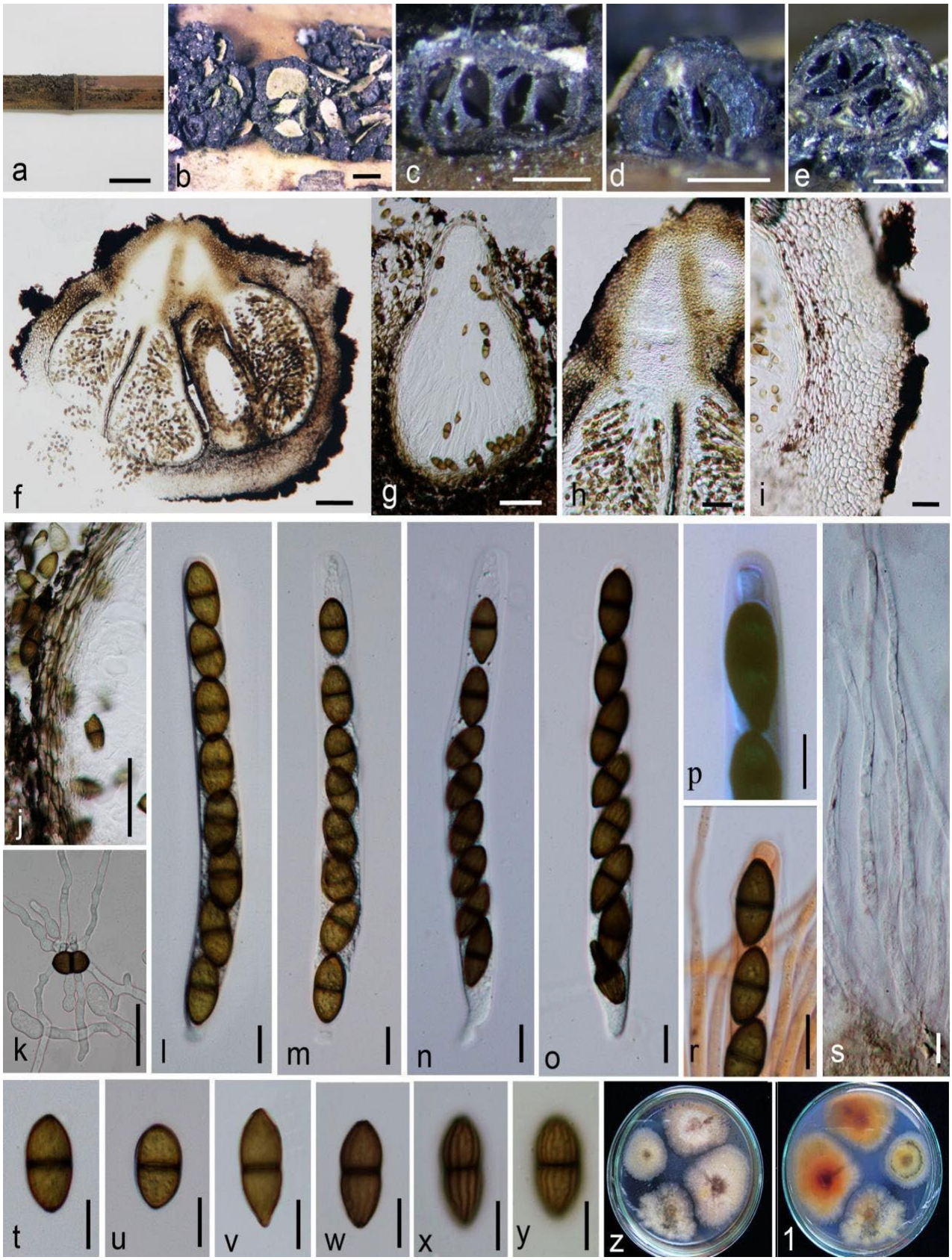


Figure 100 – *Bambusaria bambusae*. a Bamboo specimen. b–e Black stromata on host surface. f Section of stroma. g Section of ascoma. i, j Peridium. k Germinating ascospore. l–o Asci. p, r Asci apices. r Paraphyses. t–y Dark brown ascospores. z, 1 Culture on PDA. Scale bars: b–e = 1 mm, f, g = 500 µm, h = 100 µm. i, j = 50 µm. k–y = 10 µm.

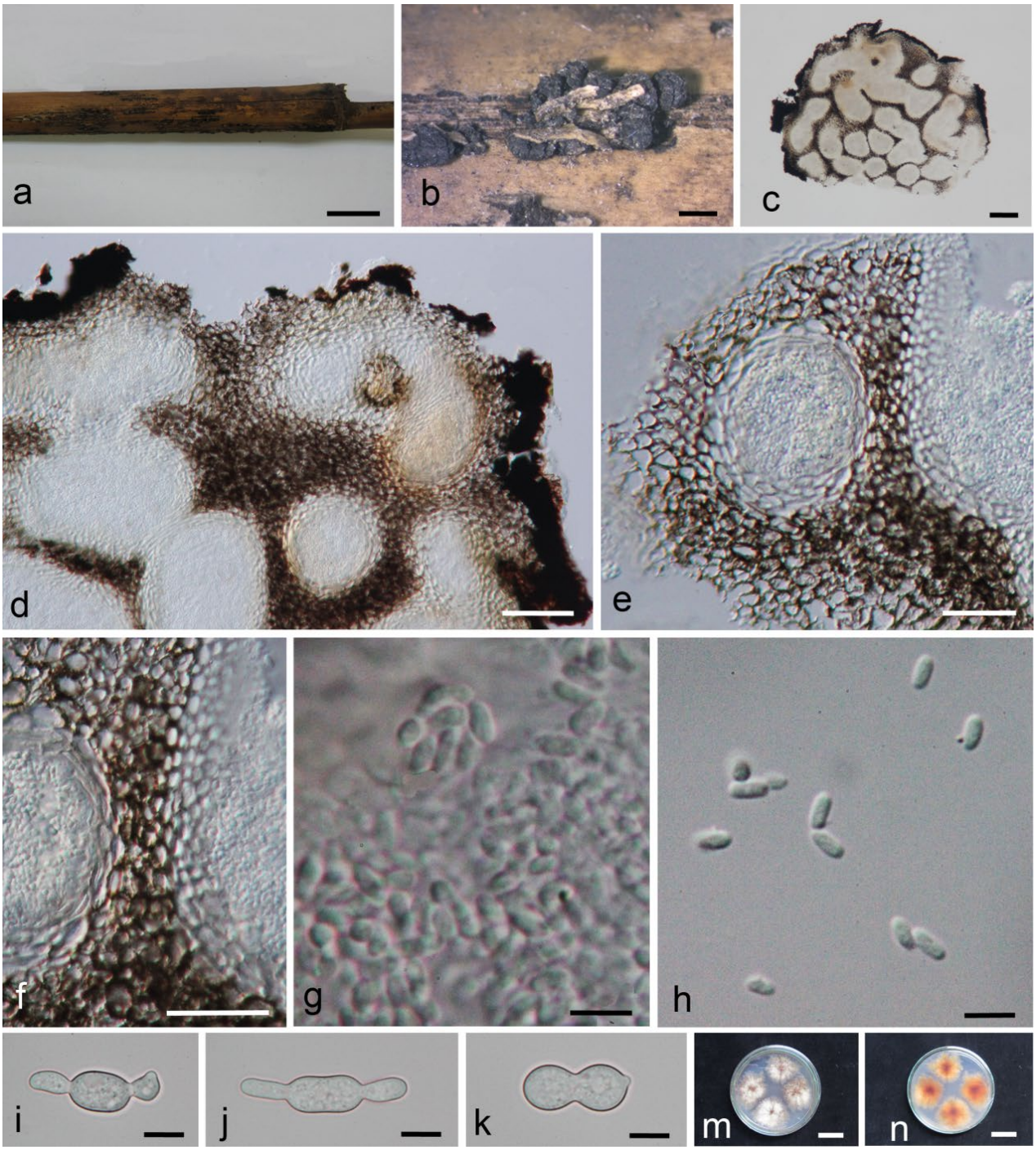


Figure 101 – Asexual morph of *Bambusaria bambusae* on natural host. a–k Asexual morph on natural host. a bamboo specimen. b Black conidiomata on host. c–e Sections of conidiomata with locules. g, h Hyaline conidia. i–k Geminating conidia from PDA. Scale bars: a = 3 mm, b = 500 µm, c = 100 µm, d, e = 50 µm, g, h = 5 µm, i–k = 10 µm.

Chemical diversity

Stromata of *Myrmaecium* generally have chemical reactions, and change to purple or pink in KOH reagent, and yellow to greenish in lactic acid (Jaklitsch et al. 2015). However, ionomidotic reaction is not reported from *Bambusaria* and *Valsaria*. Briggs et al. (1965) isolated a new pigment, produced from *Valsaria rubricosa* (current name: *Myrmaecium rubricosum*), and named the new compound as *Valsarin*. Later more chemical compounds were extracted from *Myrmaecium* by researchers (Bohman 1969, Briggs et al. 1972, Lam et al. 1972).

Other relevant data and future recommendations

Interestingly, ascospores of *Valsaria* and especially *Myrmaecium* remain viable for long periods of time. Ju et al. (1966) and Jaklitsch et al. (2015) obtained a culture of *Myrmaecium fulvopruinatum* from a 12-year-old specimen and a culture of *M. rubricosum* from a nearly 11-year-old specimen respectively. Stromata of *Myrmaecium* species contain compound *Valsarin*, which cause ionomidotic reaction, and present variety pigments. This can be important identifying characters for determining *Myrmaecium* taxa.

***Venturiales* Y. Zhang ter, C.L. Schoch & K.D. Hyde, Fungal Diversity 51(1): 251 (2011)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Pleosporomycetidae*

Introduction

Venturiales was introduced for two families, *viz*. *Sympoventuriaceae* (*Sympoventuria* and allied genera) and *Venturiaceae* (*Venturia* and related genera). Subsequently, *Cylindrosympodiaceae* was added by Shen et al. (2020a) to include *Cylindrosympodium* as the type genus. Thus, currently, three families are accepted in *Venturiales*. The members of this order are distributed in the temperate and tropical areas of the world, with diverse lifestyles. For instance, some species of the *Venturiales* are known to cause leaf spots, necroses, scab diseases, leaf, and fruit deformations on plants and some are opportunistic neurotropic pathogens of aquatic animals or humans. There are many records of *Venturiales* as saprobes in the soil or plant debris, with some thermophilic species living in hot springs (Schoch et al. 2009b, Zhang et al. 2011b, Hyde et al. 2013, Giraldo et al. 2014b, Samerpitak et al. 2014, Tennakoon et al. 2021). The species are characterized by ascomata, with or without setae, mostly with an evanescent hamathecium, 8-spored, broadly or usually obclavate asci usually lacking a pedicel, hyaline, light greenish-olivaceous to brown, 1-septate, symmetrical, asymmetrical or apiosporous ascospores and hyphomycetous asexual states (Zhang et al. 2011b, Hyde et al. 2013). Based on phylogeny, this order is closely related to *Microthyriales*, *Natipusillales* and *Asterinales* (Hyde et al. 2013, Shen et al. 2020a), and the divergence time is estimated as 184 MYA (Hongsanan et al. 2020a).

History

Venturiales was introduced by Zhang et al. (2011b) to accommodate *Venturiaceae* as the type family. *Venturiaceae* genera were initially accommodated in various families, such as *Coleroa* in *Trichosphaeriaceae*, *Gibbera* in *Cucurbitariaceae*, *Stigmatea* in *Stigmateaceae* and *Venturia* in *Pleosporaceae* (Winter 1887). Petrak (1924, 1927, 1947) investigated the morphological similarities between some genera (*Antennularia*, *Coleroa*, *Eriosphaeria*, *Gibbera*, *Trichosphaeria* and *Venturia*) and used this evidence to demonstrate a potential taxonomic link between those taxa. Thus, Müller & von Arx (1950) introduced *Venturiaceae* in *Pseudosphaeriales* to accommodate morphologically similar genera such as *Antennularia*, *Coleroa*, *Endostigme*, *Gibbera*, *Spilosticta*, *Stigmatea* and *Venturia*. von Arx (1952) carried out an in-depth assessment of the *Venturiaceae* species on the basis of morphological characteristics (immersed, semi-immersed or superficial ascomata with or without setae, filiform pseudoparaphyses, clavate, obclavate, bitunicate, 8-spored (sometimes 4-spored) asci, hyaline, pale-olivaceous to brown, and 1-septate, often asymmetrical ascospores), and eventually accepted 12 genera in the family. This number later increased to 25 (Müller & von Arx 1962) and to 30 (von Arx 1952), respectively.

Valid morphological descriptions and illustrations for *Venturiaceae* were provided by Barr (1979a), who illustrated them as setose ascomata and hyaline, olive to greenish-brown, obovate to oblong, generally 1-septate ascospores as main morphological characteristics. Subsequently, Barr (1968, 1979a) assigned this family in *Pleosporales* based on its "Pleospora-type of centrum and bitunicate asci". However, subsequent molecular analyses did not support this placement (Kodsueb et al. 2006, Kruys et al. 2006, Winton et al. 2007). Based on data on morphology, phylogeny, and

ecology, Zhang et al. (2011b) redefined *Venturiaceae* in *Venturiales* and accepted two families (*Sympoventuriaceae* and *Venturiaceae*). Recently, *Cylindrosympodiaceae* was added to *Venturiales* by Shen et al. (2020a), and, thus, three families are currently accepted.

General description

Sexual morph: *Ascomata* immersed, erumpent to superficial, scattered or gregarious, or as locules in a stroma or below a blackened clypeus, globose, subglobose, or dome-shaped or flat-conical, with or without seta around papilla or covering whole ascomata, ostiolate. *Hamathecium* composed of narrowly cellular, mostly evanescent, and rarely persistent pseudoparaphyses. *Asci* 8-spored, bitunicate, fissitunicate, broadly or usually obclavate, usually lacking a pedicel. *Ascospores* hyaline, light greenish-olivaceous to brown, 1-septate, symmetrical, asymmetrical or apiosporous. Asexual morph: *Conidiophores* solitary or loosely to densely fasciculate, arising from supra-epidermal hyphae, arising from small to moderately large stromata, or formed in sporodochia; conidiophores often reduced to conidiogenous cells or composed of several vertical cells, erect, cylindrical, pyriform, subclavate, narrowly obclavate, slightly to distinctly geniculate-sinuous, unbranched or occasionally branched, pale olivaceous to dark brown, sometimes paler at tips, smooth to somewhat verruculose. *Conidiogenous* cells integrated, mono- to polyblastic, percurrently proliferating or sympodial, with terminal or lateral conidiogenous loci, sometimes denticle-like, truncate at apex to slightly convex, thin-walled. *Conidia* solitary or mostly catenate, in simple or branched chains, subcylindrical, ampulliform to fusoid-ellipsoid, acicular, straight, slightly curved or coiled, truncate at base, septate or aseptate, subhyaline, pale to dark brown, mostly olivaceous, rarely constricted at septa, smooth to verruculose, pointed or rounded to truncate at ends, thin-walled (adapted from Shen et al. 2020a) (Fig. 102).

There are two main phases in the disease life cycle of members of *Venturiales*, *viz*. sexual or primary phase and asexual or secondary phase (Bowen et al. 2011). In the primary phase, the sexual morph of the fungus overwinters in infected leaves or on the ground with fruiting bodies (pseudothecia). During suitable climatic conditions (in spring), the ascospores become mature and are released from the pseudothecia to the air (Belete & Boyraz 2017, Chatzidimopoulos et al. 2020). The released ascospores are carried by the wind to newly emerging leaves and fruits of healthy trees. When conditions are favorable, ascospores initiate their germination process, germ tubes penetrate the cuticle through appressoria and differentiate into multi-layered, pseudoparenchymatous structures called stromata. The stromata and the conidia that they produce cause the characteristic leaf and fruit lesions in the trees (Bowen et al. 2011). The conidia are dispersed by wind and rain-splash from the lesions, germinate on wet surfaces, infect the tissue, and again produce lesions in leaves and fruits (Shafi et al. 2019). In this way, multiple secondary infection cycles take place over a growth season (Belete & Boyraz 2017, Chatzidimopoulos et al. 2020).

Families included in *Venturiales*

Cylindrosympodiaceae Crous, M. Shen & Y. Zhang ter
Sympoventuriaceae Y. Zhang ter, C.L. Schoch & K.D. Hyde
Venturiaceae E. Müll. & Arx ex M.E. Barr

Venturiales genera *incertae sedis*
Cylindrosympodioides Crous & M.J. Wingf.
Lasiobotrys Kunze

Evolution

The divergence time for *Venturiales* has been estimated as 184 MYA (stem age, Hongsanan et al. 2020a). As has been reported for *Capnodiales*, the ancestral form of the *Venturiales* is likely to have a saprobic lifestyle and their pathogenic role appears to be a novel evolutionary state (Abdollahzadeh et al. 2020, Shen et al. 2020a). Recent studies also indicate that the *Venturiales* is terminally clustered in phylogeny trees as some other orders, such as *Pleosporales* and *Capnodiales* (Crous et al. 2009c, Zhang et al. 2009c, Shen et al. 2020a). However, in order to adapt to a lifestyle

associated with plants and fungi, ancestors of the saprobic lifestyle usually lost the enzymes that break down plant cell walls and develop effector-like secreted proteins (as in ectomycorrhizas, ECM) (Kohler et al. 2015, Martin et al. 2016). Therefore, the ancestral state appears to have a saprobic life mode at the ordinal level and class level (*Dothideomycetes*) (Haridas et al. 2020).

Justification of order and problems

Traditionally, morphology-based identification was the main means for identifying *Venturiales* and taxa have been established using brief descriptions along with line drawings (Petrak 1924, Von Arx 1952, Barr 1979a). However, it is difficult to identify the *Venturiales* species solely based on morphology due to the phenotypic plasticity, which generally result in erroneous interpretations. Thus, recent studies used a combination of molecular and morphological approaches for species delimitation and identification, taxonomic classification, and phylogenetic inference in the *Venturiales* (Kodsueb et al. 2006, Kruys et al. 2006, Winton et al. 2007, Zhang et al. 2011b, Hyde et al. 2013, Shen et al. 2020a).

The sexual morphs of *Venturiales* species have overlapping morphological characteristics (small to medium-sized ascomata, with or without setae, broadly or usually obclavate asci, hyaline, light greenish-olivaceous to brown, 1-septate, symmetrical, asymmetrical, or apiosporous ascospores), and thus the asexual morph proved to be more reliable for species identification (Schubert et al. 2003). Mostly, conidial apparatus including conidiophores, conidiogenous cells, and conidia, have been widely used for species delimitation in taxonomic studies (Hyde et al. 2013, Shen et al. 2020a). However, morphology data combined with phylogeny is the best approach for *Venturiales* species delimitation.

Significance

Ecological and economic roles

Species in *Venturiales* have a wide range of life modes. Most species cause fungal diseases, such as apple scab (*Venturia inaequalis*), poplar shoot blight (*V. populina*), pear scab (*V. pyrina*), soybean black leaf blight (*Arkoola nigra*) and black knot disease of cherry (*Dibotryonmorbosum*) (Walker & Stovold 1986, Newcombe 2003, Bowen et al. 2011). Some species are opportunistic neurotropic pathogens of aquatic animals or humans (e.g., *Ochroconis globalis* infecting Atlantic salmon, lung infection by *Ochroconis* spp. *Verruconis gallopava* for zoonoses in broiler house chickens and trumpeters) (Samerpitak et al. 2014, 2019). The species inhabit soil, dung and dead leaves, stalks, or twigs of various higher plants and act as saprobes (Tennakoon et al. 2021). They can be found in living leaves, twigs as endophytes as well (Shen et al. 2020a, Tazik et al. 2020). Some *Venturiales* members have been recorded as thermophilic, living in hot springs (Schoch et al. 2009b, Machouart et al. 2014, Giraldo et al. 2014b).

The host-specificity of *Venturiales* species has yet to be studied, despite having been collected from various plant families (e.g., *Arecaceae*, *Asparagaceae*, *Dicksoniaceae*, *Fabaceae*, *Lauraceae*, *Moraceae*, *Myrtaceae*, *Pandanaceae*) (Tibpromma et al. 2018, Shen et al. 2020a, Tazik et al. 2020, Tennakoon et al. 2021). They have cosmopolitan distribution, as they have been recorded from both temperate and tropical countries (e.g., Australia, Canada, China, Cuba, Greece, France, India, Italy, Malaysia, Netherlands, New Zealand, South Africa, Switzerland, Thailand, the United Kingdom) (Seifert et al. 2011, Shen et al. 2020a, Tazik et al. 2020, Tennakoon et al. 2021).

Chemical diversity

There are currently no records pertaining to chemical compound analyses of *Venturiales* species.

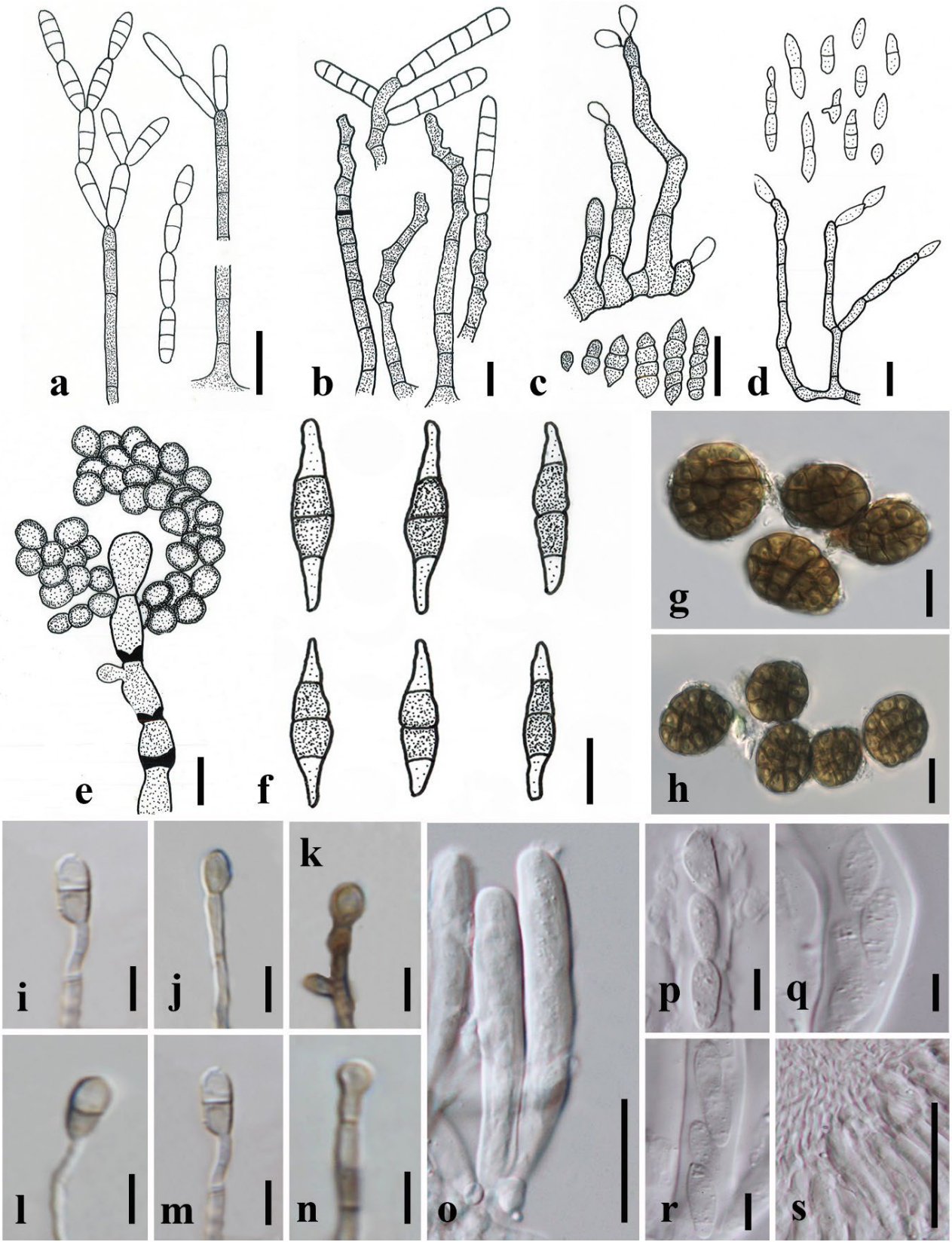


Figure 102 – Sexual and asexual morphologies of *Venturiales* species. a *Septonema fasciculare* (Delgado et al. 2019). b *Cylindrosympodium sosae* (Castañeda-Ruiz et al. 2012). c *Acroconidiella indica* (Prasher & Verma 2015). d *Fusicladium aromaticum* (Schubert & Braun 2005). e *Echinocatena arthrinioides* (Campbell & Sutton 1977). f *Verruconis hainanensis* (Qiao et al. 2019). g, h *Yunnanomyces pandanicola* (Tennakoon et al. 2021). i–n *Verruconis soli* (Yasanthika et al. 2023). o–s *Apiosporina collinsii*. Scale bars: a, c = 20 µm, b, d, e–h = 10 µm, i–n, p–r = 6 µm, o, s = 30 µm.

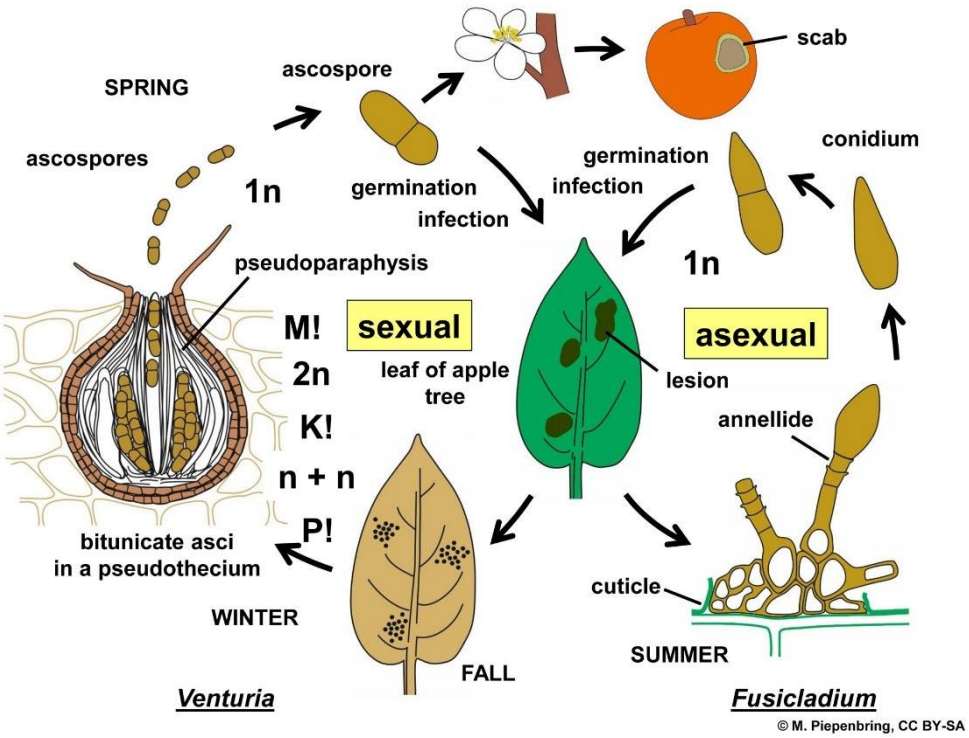


Figure 103 – Sexual and asexual life cycles of *Venturiales* (From Mycological teaching diagrams by Meike Piepenbring (2023)). Abbreviations: **1n** = haploid, **2n** = diploid, **P!** = plasmogamy, **K!** = karyogamy, **M!** = meiosis. Black and white circles represent haploid nuclei of different mating types, circles of both colors represent diploid nuclei.

Other relevant data and future recommendations

Despite having a cosmopolitan distribution, most members of the *Venturiales* lack molecular data. For example, only 31 species of *Fusicladium* have molecular data out of the 81 species, and 58 *Venturia* species out of the 123 species (Hongsanan et al. 2020a). Some genera are highly diverse (e.g., *Fusicladium*), while some have fewer species (e.g., *Apiosporina*: 3 species, *Atopospora*: 4 species, *Dimerosporiopsis*: 2 species, *Magnohelicospora*: 2 species, *Matsushimaea*: 4 species, *Scolecobasidiella*: 2 species, *Sympoventuria*: 3 species), or monotypic genera (e.g., *Clavatispora*, *Echinocatena*, *Metacoleroa*, *Mycosisymbrium*, *Pseudoparodiella*, *Veronaeopsis*) (Hongsanan et al. 2020a). To define the phylogenetic position of some genera in *Venturiales*, there is a lack molecular data (e.g., *Atopospora*, *Dimeriella*, *Pseudoparodiella*). Thus, additional collections are needed to clarify the phylogenetic placement of those genera.

Zeloasperisporiales **Hongsanan & K.D. Hyde, Cryptogamie, Mycologie 36(3): 306 (2015)**

Subphylum : *Pezizomycotina*
Class : *Dothideomycetes*
Subclass : *Incertae sedis*

Introduction

Zeloasperisporiales was introduced by Hongsanan et al. (2015a) to accommodate *Zeloasperisporiaceae* based on phylogenetic analysis using LSU and SSU sequence data. This order represents a distinct lineage within *Dothideomycetes*, separate from *Microthyriales*, and is sister to the clade of the freshwater order *Natipusillales*. *Zeloasperisporiales* is identified as a distinct order due to its unique morphological characteristics. The estimated divergence time for *Zeloasperisporiales* is 180 MYA according to Hongsanan et al. (2020a). Over the years, additional species have been added to this genus, and some have been linked to sexual morphs, further expanding our understanding of this fungal group.

History

The order *Zeloasperisporiales* was formally established by Hongsanan et al. (2015a). Prior to this, *Zeloasperisporium* was initially introduced as *incertae sedis* genus in *Dothideomycetes* to accommodate *Z. hyphopodioides*, a species that was isolated from the air in Cuba (Castañeda et al. 1996, Wijayawardene et al. 2014a). At that time, the taxonomic placement of *Zeloasperisporium* was not well-defined. Based on its phylogenetic placement at the base of the *Venturiaceae* clade, *Zeloasperisporium* was classified within the family *Venturiaceae* by Crous et al. (2007d). Further taxonomic revisions occurred as additional species were discovered. Two species found on leaves of *Eucalyptus* and *Clivia* collected in Australia and South Africa respectively, were introduced based on asexual morphological characteristics and molecular data by Cheewangkoon et al. (2009) and Crous et al. (2015d). While Crous et al. (2015d) introduced *Zeloasperisporiaceae* to accommodate the sexual genus *Neomicrothyrium* and the asexual genus *Zeloasperisporium*. Hongsanan et al. (2015a) linked morphs by adding more species and subsequently synonymized *Neomicrothyrium* under *Zeloasperisporium*. Hongsanan et al. (2015a) also introduced two new species of *Zeloasperisporium* that were found on leaves of *Ficus benjamina* and *Wrightia religiosa* collected in Thailand. Phylogenetic analyses provided strong support for the recognition of *Zeloasperisporium* species as a distinct family and order within the *Dothideomycetes* (Hongsanan et al. 2015a, 2020a). Jayasiri et al. (2018b) introduced *Z. pterocarpi*, a species found on carpel of fallen pod of *Pterocarpus* collected in Thailand, while Hyde et al. (2023) recently established *Z. spartii* from decaying stems of *Spartium junceum* collected in Yunnan, China.

General description

Morphological characteristics of *Zeloasperisporium* include both sexual and asexual morphs. The appearance of its sexual morph and coelomycete state on host surface show microthyrium-like, with flattened thyriothecia, a lack of obvious ostioles, an upper peridial wall comprising cells radiating from the center, and a poorly-developed base. The asexual morph can be found in both nature and on artificial media, with hyphomycetes characters (Figs. 104, 105). However, coelomycetes structures of *Zeloasperisporium* was recently found by Hyde et al. (2023).

Sexual morph: Appearing as small black dots, or in air. *Superficial hyphae* present or absent. *Thyriothecia* superficial, solitary, circular, flattened, brown to dark brown, easy removed, base poorly developed, ostiole absent. *Upper wall* composed of ellipsoid angular cells, radiating from the center to the outer rim. *Pseudoparaphyses* not observed. *Asci* 8-spored, bitunicate, fissitunicate, globose to ovoid or clavate, broadly obpyriform, apedicellate, with an apical ocular chamber. *Ascospores* 2–3-seriate or irregularly arranged, obovoid to clavate, 1-septate, slightly constricted at the septum, widest in upper cell, hyaline, smooth-walled or verrucose, surrounded by a thin mucilaginous sheath, or without mucilaginous sheath in some species (Wu et al. 2011, Crous et al. 2015d, Jayasiri et al. 2018b). Asexual morph: *Hyphomycetous*, *hyphae* branched, septate, constricted at the septa, hyaline or pale brown to brown, smooth-walled, micronematous conidiogenous present or absent. *Conidiophores* reduced to conidiogenous cells, *Conidiogenous cells* arising as lateral hyphal branches, cylindrical to subcylindrical, straight or slightly curved, unbranched, slightly tapering towards the apex, brown, slightly thick-walled. *Conidial proliferation* sympodial, with one to several conidiogenous loci, mostly crowded at the apex, protuberant of conidial scars thickened-refractive. *Conidia* fusiform to obclavate or cylindrical, straight to curved, 1–3-septate, distinctly or slightly constricted at the septum, tapered towards the apex, toward a protruding scar, somewhat thickened and darkened refractive, hyaline to pale brown to brown, smooth-walled or verrucose (Adapted from Hongsanan et al. 2015a and Jayasiri et al. 2018b); *Coelomycetous*, *Conidiomata* on surface of host have the same appearance as in the sexual morph, upper wall composed of ellipsoid angular cells, arranged in parallel radiating lines from the center to the outer rim covering the host, with a poorly developed basal layer and an irregular margin, outer cell layers darker than central cell layers, ostioles lacking. *Pycnidial wall*, thin-walled, pale brown, large cells of *textura angularis*. *Conidiogenous cells* globose to subglobose, simple, hyaline or light yellow, smooth-walled. *Conidia* lunate to fusiform,

straight or curved, wide in the middle, tapering on both sides, 2 transverse septa, hyaline, thin- and smooth-walled (adapted from Hyde et al. 2023).

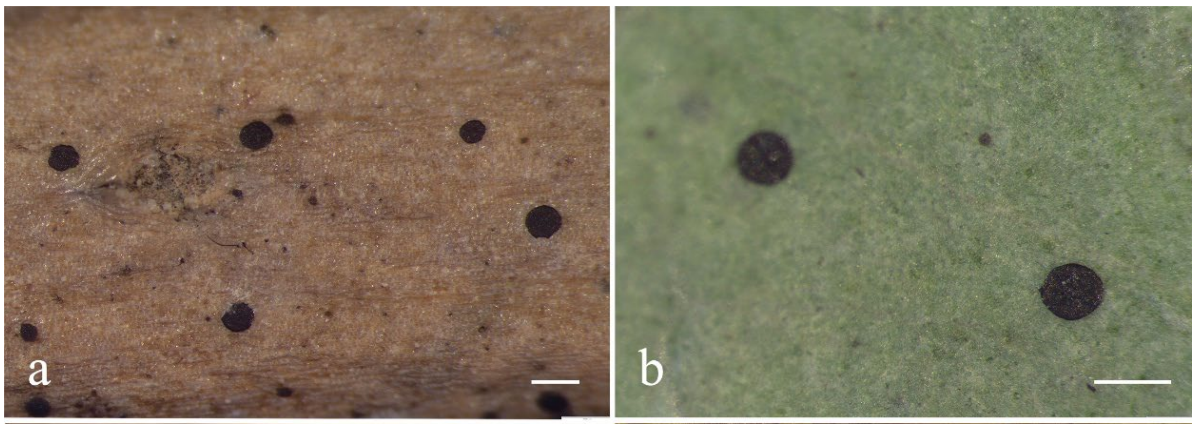


Figure 104 – Thyriothecial morphology of *Zeloasperisporiales*. a *Zeloasperisporium* spp. on stem. b *Zeloasperisporium* spp. on leaves. Scale bars: a, b = 300 μm.

Families included in *Zeloasperisporiales*

Zeloasperisporiaceae Crous

Evolution

The evolutionary of the *Zeloasperisporiales* is estimated to date back approximately 180 MYA, as determined by Hongsanan et al. (2020a). This order is placed as a distinct lineage within the *Dothideomycetes*. Notably, it shows a sister relationship to *Natipusillales*, a family of freshwater fungi characterized by a markedly different morphology (Hongsanan et al. 2015a, 2020a, Hyde et al. 2023). Currently, the relationship between these two orders remains undefined. However, further exploration involving the discovery of additional species within both orders and their related clades promises to shed light on their taxonomic placement and contribute to a deeper understanding of the evolutionary history of both orders. Within the *Zeloasperisporiales* itself, synanamorphs, are found in different host conditions, such as those isolated from the air, plant stems and leaves. Further investigation into the evolutionary relationships among species within this order is needed.

Justification of order and problems

The establishment of the *Zeloasperisporiales* is well-supported by both phylogenetic analysis and morphology. Its distinctiveness from related orders within the *Dothideomycetes*, as well as its phylogenetic placement, justifies its classification as a separate order. However, the order has unique features and challenges in understanding relationship with the freshwater order *Natipusillales*.

Significance

Ecological and economic roles

Most of the species within the *Zeloasperisporiales* are associated with plant surfaces, including leaves and stems. They are found on both living and dead plant material. Their sexual morph occurrence is often observed during the cold season (December to February) in Thailand (Hongsanan et al. 2015a, Jayasiri et al. 2018b). While the exact ecological roles of these fungi remain to be explored, their presence on plant surfaces suggests potential interactions with host plants. Understanding these interactions may have implications for plant health and ecosystem dynamics. Regarding economic roles, there is limited information available about the economic significance of *Zeloasperisporium* species. Further research is needed to explore any potential impacts on agriculture, forestry, or other industries.

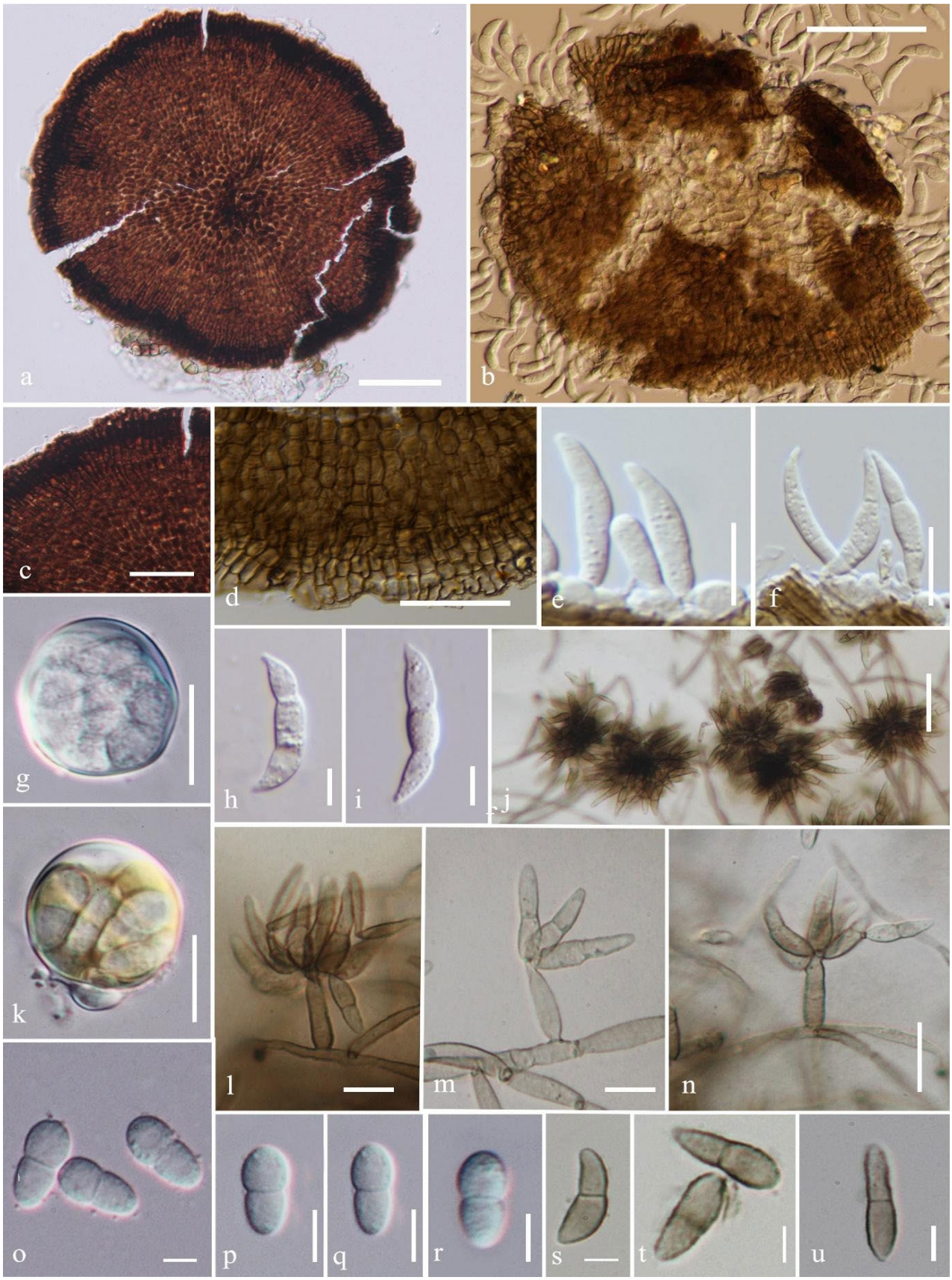


Figure 105 – Sexual morph and Asexual morph of *Zeloasperisporiales.* (a, c, g, j–l, n, o, t = *Zeloasperisporium wrightiae*; b, d–f, h, i = *Z. spartii*; m, p–s, u = *Z. ficusicola*). a Thyriothecium. b Pycnothyrium. c Upper wall of thyriothecium. d Upper wall of pycnothyrium. e, f Conidiogenous cells and growing conidia. h, i Conidia. j, l–n Conidia on conidiogenous cells with sympodial

proliferation. g, k Asci. o–r Ascospores. s–u Conidia. (adapted from Hongsanan et al. 2015a, Hyde et al. (2023). Scale bars: a, b = 50 μm, c, d = 20 μm, e, f, i–k, g, j–n = 10 μm, h, i, o–v = 5 μm.

Chemical diversity

There is no report about chemical diversity for the species in *Zeloasperisporiales*.

Other relevant data and future recommendations

In addition to the taxonomic and ecological aspects, future research on *Zeloasperisporiales* should focus on revealing the nutritional modes of sexual and asexual morphs and their interactions with host plants. Investigating the roles of appressorium-like organs at the margin of thyriothecium in nutrient acquisition would be a valuable area of study. Furthermore, continued exploration and taxonomic revisions may lead to the recognition of additional species and further insights into their evolutionary history.

***Eurotiomycetes* O.E. Erikss. & Winka, Myconet 1(1): 6 (1997)**
***Arachnomycetales* Gibas, Sigler & Currah, Studies in Mycology 47: 134 (2002)**

Subphylum : *Pezizomycotina*
Class : *Eurotiomycetes*
Subclass : *Eurotiomycetidae*

Introduction

Arachnomycetales comprises two genera *viz*. *Arachnomyces* and *Onychocola*. *Onychocola* was considered as the anamorph of *Arachnomyces*. Following the single name nomenclature, *Arachnomyces* was proposed as a valid name according to its priority (Sun et al. 2019). The generic type *Arachnomyces* comprised 15 valid species (Species Fungorum 2025) with *A*. *nitidus* as the type. The genus is characterized by appendaged cleistothecial ascomycetes producing smooth, oblate, reddish-brown ascospores (Gibas et al. 2002a). *Onychocola* was described to accommodate *O*. *canadensis* which caused onychomycosis. *Onychocola* shows a similar formation of hyaline arthroconidia and isolation from the human nail with other non-dermatophyte fungi such as *Natlrassia* and *Scytalidium*. However, *Onychocola canadensis* has not been observed to invade tissues. Its pathogenic status in human disease and its occurrence in the environment need further study (Sigler & Congly 1990). Susceptibility tests *in vitro* showed that the fungus was resistant to cycloheximide, but sensitive to benomyl and common antifungal drugs (Sigler & Congly 1990). The genus presently accommodates four species (Species Fungorum 2025) that are reported solely based on their asexual morph.

History

Arachnomycetales was established to accommodate a single family *Arachnomycetaceae* (Gibas et al. 2002a) and two genera, *Arachnomyces* and *Onychocola*. *Arachnomyces* was initially placed in *Perisporiaceae*. Later it was considered as a member of *Onygenaceae sensu lato* (Malloch & Cain 1970a) which was originally established for the stipitate cleistothecial ascomycetes (Malloch & Cain 1970a). Abbott et al. (1996) considered the genus to be placed within *Gymnoascaceae* (*Onygenales*) based on having smooth oblate ascospores and an inability to degrade keratin. However, the genus differs from *Onygenales* in the membranous cleistothecia and *Onychocola* arthroconidial anamorph. Currah (1985) did not accept this placement. Gibas et al. (2002a) transferred this genus to a newly established family *Arachnomycetaceae* and the order *Arachnomycetales* based on SSU phylogenetic analysis. The genus formed a sister clade to *Eurotiales*. *Arachnomyces* was introduced to accommodate *A*. *nitidus* and *A*. *sulphureus* without designating the type species (Massee & Salmon 1902). These two taxa formed cleistothecial ascomycetes with long dark peridial appendages and ascospores clustered in globose asci. Later, *A*. *flavidulus* was described (Saccardo, P.A. Sylloge Fungorum XXIV) to the genus. Malloch & Cain (1970a) introduced the fourth species *A*. *minimus* and listed *A*. *nitidus* as lectotype. This was accepted by Abbott et al. (1996) who followed this designation when they amended the genus. Malloch & Cain (1970a) further synonymized *Anixiopsis*

peruviana under *Arachnomyces peruvianus* and listed *A. flavidulus* as a doubtful species because of the distinct ascospores morphology. *Arachnomyces* was assumed to have a close association to *Aphanoascus* and was later synonymized as *Anixiopsis* (Apinis 1968) based on examination of the type material which showed similar peridium in the surface appearance and color with similar shape and color of ascospores.

Later it was confirmed that *Arachnomyces* could be distinguished from *Aphanoascus* based on sexual morphology and pure culture. Subsequently, *Anixiopsis peruviana* was synonymized under *Arachnomyces* based on pure culture. However, *Anixiopsis peruviana* was further transferred to *Xanthothecium peruvianum* based on having glabrous ascomata and by echinulate ascospores (Von Arx & Samson 1973). Gibas et al. (2002b) established the second heterothallic *Arachnomyces* species, *A. kanei* which also formed superficial white onychomycosis. *Arachnomyces peruvianus* has been reported to cause cutaneous infection (Brasch et al. 2017). Rodríguez-Andrade et al. (2021) recently reported two new *Arachnomyces* species, *viz*. *A. bostrychodes* and *A. graciliformis* from clinical specimens in the USA. *Onychocola* was introduced by Sigler & Congly (1990) for a species reported from nails of three native-born Canadian females which caused great toenail infection. The fungus was identified as *Onychocola canadensis* and was characterized by forming hyaline, round to barrel-shaped arthroconidia, hyaline hyphae of varying width, and broad thick-walled brownish hyphae under direct microscopic examination (Sigler & Congly 1990).

General description

The sexual morph of *Arachnomyces* is characterized by brightly colored cleistothecial ascomata bearing setae, and by its production of an onychocola-like (Sigler et al. 1994) or a malbranchea-like (Udagawa & Uchiyama 1999) asexual morph which has lytic dehiscence and sometimes with schizolytic dehiscence. The sexual morph of *A. nodosetosus* was linked to the asexual morph of *Onychocola canadensis* on the basis of producing nodose, circinate to loosely coiled setae (Sigler et al. 1994).

Sexual morph: *Ascomata* cleistothecia, non-ostiolate. *Setae* coiled or circinate, straight and tapered, slightly nodose. *Peridium* membranous of textura angularis. *Asci* evanescent, eight spored. *Ascospores* oblate, lightly pigmented, lacking germ pores. Asexual morph: *Arthroconidia* or *Aleurioconidia*. *Arthroconidia* alternate, cylindrical to irregularly swollen, regularly swollen in persistent chain, sclerotia present or absent. *Colonies* greyish-brown, white to pale brown, smooth to finely asperulate, coarsely verrucose, setae strongly nodose, tip circinate or loosely coiled (Figs. 106, 107).

Families included in *Arachnomycetales*

Arachnomycetaceae Gibas, Sigler & Currah

Justification of order and problems

Onychocola canadensis is mainly identified based on growth parameters, the presence of elliptic arthroconidia in chains, together with rough vegetative hyphae, and brown hyphae with dark superficial deformities, which can be found in 4–6-week-old cultures. However, the characteristics of the cultures that are older than 4 weeks or before the third week can lead to misidentification. For example, *Trichophyton rubrum* shows a similar morphological appearance to *Onychocola canadensis* in 3-week-old culture. Stuchlík et al. (2011) reported two different appearances of onychomycosis caused by *Onychocola canadensis*. One with distal and lateral onycholysis with conspicuous black pigmentation, while another case was reported with distal and lateral subungual onychomycosis with yellow discoloration. Thus, morphological characters are important for the identification of *Onychocola canadensis* from other medically important fungi. However, *Onychocola* spp. are mostly overlooked due to their slow growth (Stuchlík et al. 2011).

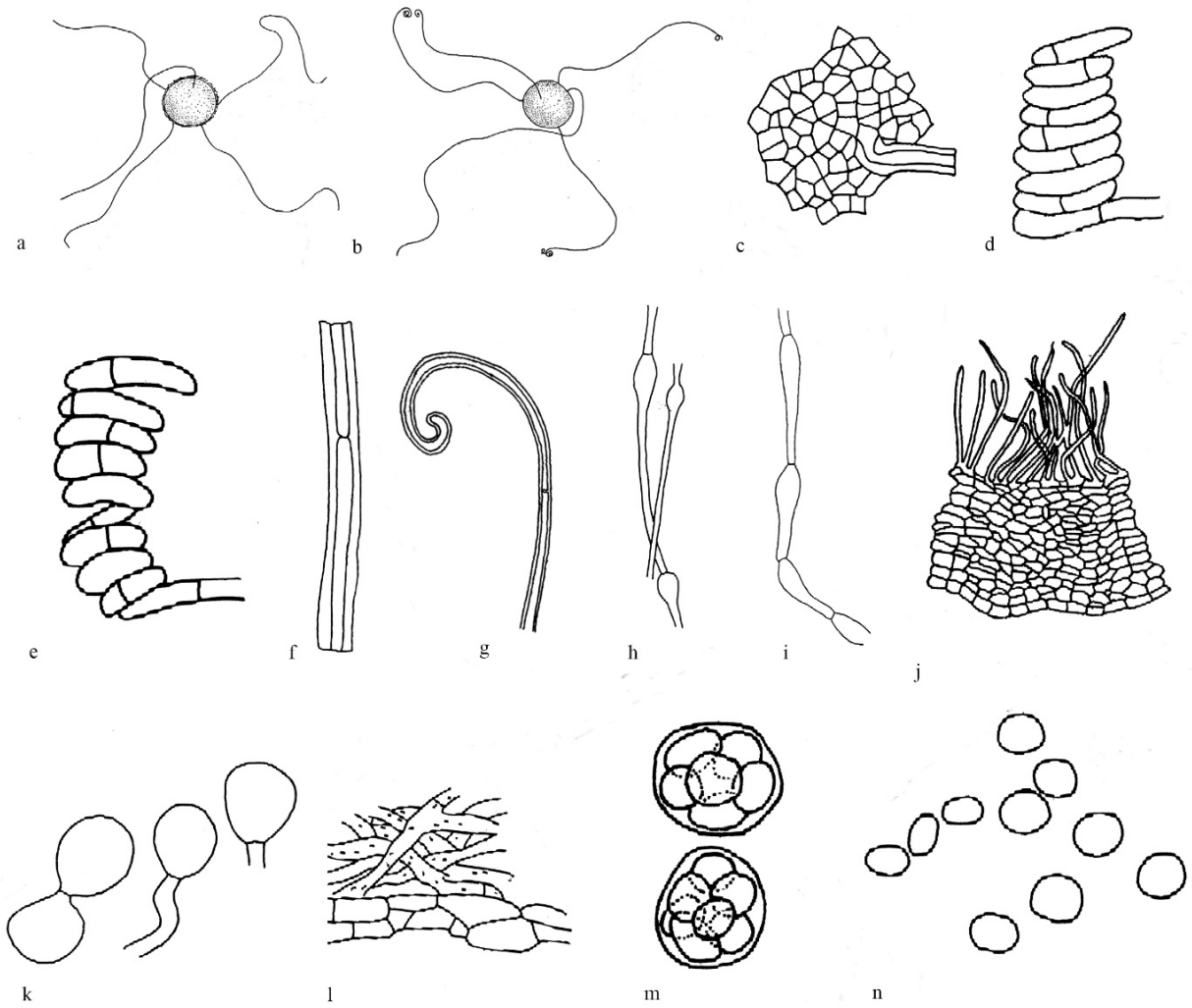


Figure 106 – Sexual morph of *Arachnomycetales*. a, b Ascocarp (a *Arachnomyces sulphureus* X 650, b. *A. nitidus* (X 1500)). c Surface view of peridium (*A. nitidus* X 650). d, e Ascocarp initial (d (*A. minimus* X 1500, e *A. peruvianus* X 1500). f, g Detail of ascomata appendage (f *A. nitidus* X 1500, g *A. minimus* X 1500). h, i Ampulliform swellings (h *A. minimus* X 1500, i *A. peruvianus* X 1500). j Cross-section of peridium showing paraphyses-like tissue (*A. minimus* X 650). k Swollen cells from vicinity of ascocarp initial (*A. minimus* X 1500). l Peridium cross section showing nature of the tomentose layer (*A. sulphureus* X 1500). m Asci (*A. minimus* X 1500). n Ascospores (*A. sulphureus* X 1500) (redrawn from Malloch & Cain 1970a).

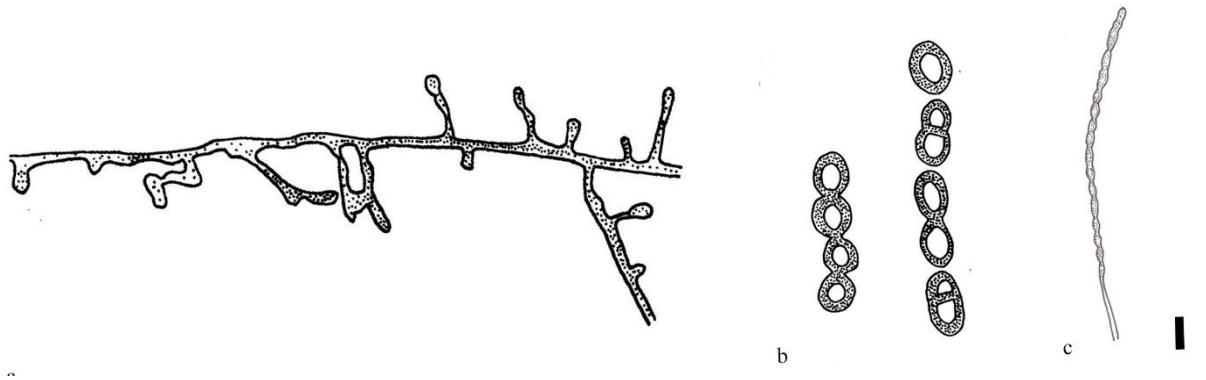


Figure 107 – Asexual morph of *Arachnomycetales* (*Onychocola canadensis*). a Arthroconidia in persistent chains, showing irregular swelling, 6043 × 395. b Mature conidia seceding by schizolysis.

c Swollen arthroconidia in persistent chains (redrawn from Sigler & Congly 1990, Gibas et al. 2002a, b). Scale bars: c = 10 µm.

Significance

Ecological and economic roles

Arachnomyces species are reported from decomposing grasses and human nails but, their distribution and habitat are poorly understood. *Arachnomyces nitidus* has been reported from grass stems and rat dung in the UK, hay dung compost and dead grass in Canada and ox dung in India. *Arachnomyces sulphureus* was also observed on rotten straw from an old bee's nest in the UK (Massee & Salmon 1902). *Arachnomyces nodosetosus* causes nail and skin infections (Sigler & Congly 1990). *Arachnomyces kanei* causes non-dermatophytic onychomycosis (Sigler et al. 1994, Gibas et al. 2002b). The role of *Arachnomyces glareosus* in nail infections is uncertain, but several isolates of this species were obtained from nail or skin scrapings taken from patients for diagnostic purposes (Gibas et al. 2002a). *Onychocola canadensis* has been frequently reported in elderly females who often worked as gardeners or farmers. This suggests that the probable source of the infection was from soil (Gupta et al. 1997). *Onychomycosis* can be caused by dermatophytes, non-dermatophytic moulds and yeasts and causes an important disease in developed countries that affects toe or finger nails. Dermatophytes are responsible for most infections. Following the initial report of *Onychocola canadensis* from Canada, several new cases were reported in New Zealand, France, and the UK (Sigler et al. 1994, Campbell et al. 1997, Contet-Audonneau et al. 1997, Koenig et al. 1997,). The prevalence of onychomycosis has been estimated at 2.6% in Spain (Sais et al. 1995), 2.7% in the UK (Roberts 1992), 6.8% in Canada (Gupta et al. 2001) and 8.4% in Finland (Heikkila & Stubb 1995).

Chemical diversity

Onychocola sclerotica is a rare keratinophilc fungus that produces compounds such as three cyclotetrapeptides with an 'aa' sequence of L-N-methyl-phenylalanine, L-valine or Lisoleucine, L-N-methyl-phenylalanine, and L-valine or Lisoleucine (Pérez-Victoria et al. 2012).

Chaetothyriales M.E. Barr, Mycotaxon 29: 502 (1987)

Subphylum : *Pezizomycotina*
Class : *Eurotiomycetes*
Subclass : *Chaetothyriomycetidae*

Introduction

The order *Chaetothyriales* is classified within the *Eurotiomycetes* of the subphylum *Pezizomycotina* (Gueidan et al. 2014a, Wijayawardene et al. 2020, Hyde et al. 2024b). Members of this order are cultured since only a few decades and consequently, the classification status of this order is constantly updated with the description of new species and genera. The order was proposed by Barr (1976) based on specimens that were collected with visible sexual fruitbodies. Subsequently, eight families were recognized: *Chaetothyriaceae*, *Coccodiniaceae*, *Herpotrichiellaceae*, *Metacapnodiaceae*, *Microtheliopsidaceae*, *Pyrenotrichaceae*, *Strigulaceae*, and *Trichopeltidaceae* (Barr 1987a, b). Phylogenetic data proved that most of these did not belong to this order. For example, the *Coccodiniaceae* include four genera with a few epilithic and epiphytic species that have varied morphology and are challenging to cultivate and sequence. Most researchers hypothesize an affinity to *Capnodiales* in *Dothideomycetes* (Winka et al. 1998b, Hyde et al. 2013, Réblová et al. 2013), or have remained *incertae sedis*. The family *Pyrenotrichaceae* (de los Angeles Herrera-Campos et al. 2005) has been suggested to belong to *Chaetothyriales* (Wijayawardene et al. 2020), but no sequence data are available to support this. Out of the original eight families, only two are recognized: *Chaetothyriacea*e and *Herpotrichiellaceae*. Recent reviews now acknowledge five described families: *Chaetothyriaceae*, *Cyphellophoraceae*, *Epibryaceae*, *Herpotrichiellaceae*, and *Trichomeriaceae* (Barr 1976, 1987b, Réblová et al. 2013, Gueidan et al. 2014a). Beside this, Quan

et al. (2020, 2023) identified four clades that may represent the level of families but need more taxon sampling for statistical support. These four clades are *Domatiaceae*, *Muellerella* (Muggia et al. 2021b), *Paracladophialophoraceae* (Crous et al. 2018a) and *Phaeosaccardinula* (Kirk et al. 2008b).

History

Chaetothyriaceae had provisionally been introduced by Hansford (1946) with *Chaetothyrium*, based on *C. guaraniticum* as the type species. Many members of this family have been documented since the 19th century, categorized by their ascomata found on natural substrates. However, culture and sequence data exist for only a small portion of these species. As a result, a comprehensive description of the family *Chaetothyriaceae* is forthcoming. The family *Herpotrichiellaceae* was introduced by Munk (1953) with *Herpotrichiella* (Petrak 1914) as the type genus. *Cyphellophoraceae* was described by Réblová et al. (2013) for a group previously known as the 'europaea-clade' within *Herpotrichiellaceae* (de Hoog et al. 2011b) and raised to family level by Réblová et al. (2013) with *Cyphellophora* (de Vries 1962) as the type genus and *C. laciniata* as the type species. *Epibryaceae* was introduced by Gueidan et al. (2014b) with *Epibryon* (Döbbeler 1978) as the type genus which has *E. plagiochilae* as the type species. This species was described with molecular data (Stenroos et al. 2010) in a detailed overview of the genus, and is accepted as a reference for this group of phylogenetically consistent moss endophytes. *Trichomeriaceae* was introduced by Chomnunti et al. (2012) with *Trichomerium* as type genus. Members of this family are 'sooty mold's colonizing inert substrates such as leathery plants (Chomnunti et al. 2014). The family also comprises *Knufia* and relatives containing rock-colonizing species (Isola et al. 2016), as well as some ant-associated fungi (Vasse et al. 2017, Quan et al. 2021).

The scientific history of the order *Chaetothyriales* can be divided into two periods: the phenotypic era, which focused on the sexual states of the genera *Capronia* and *Trichomerium* in their natural environments, and the predominantly molecular phase, which primarily used asexual states in culture and recognized numerous genera. However, traditional morphological classification systems do not align well with recent phylogenetic data. Classical studies relied on fruitbodies found on lichenized rock or decorticated wood, with dried voucher specimens preserved in herbaria (Barr 1976). During the second half of the 20th century, a separate line of research developed, focusing almost entirely on living cultures (Beatrice Schol-Schwarz 1968, de Hoog et al. 2003). Since that time, species descriptions were mainly according to their molecular data. Conflicts between old and new methods has resulted in duplication of description for some species for sexual versus asexual states, such as *Capronia semiimmersa* and *Phialophora americana*. Some morphologically and phylogenetically defined genera in *Herpotrichiellaceae* are randomly mixed. Therefore, the nomenclature of *Chaetothyriales* needs revision. New and unexpected habitats continuously reveal a vast array of novel species. These include fungi associated with ants, inhabitants of rocks, waterborne opportunists affecting fish and crabs, plant endophytes, toxin-associated species, and rare pathogens causing severe infections in humans.

General description

Sexual morph: *Ascomata* superficial, immersed to erumpent through cracking or splitting of the host tissue, solitary to gregarious, with periphysate ostioles, with or without papilla. *Peridium* composed of several layers, outer layers of dark brown cells, inner layers of hyaline to light brown flattened cells. *Hamathecium* lacking or comprising filiform, hyaline, septate paraphyses. *Asci* 4–8-spored, bitunicate, fissitunicate, oblong, clavate to nearly cylindrical, oval, sessile or short pedicellate, with or without an ocular chamber, forming in a basal layer, often interspersed with and covered by cellular remnants of interthecial tissues. *Ascospores* overlapping 1-multi-seriate, irregularly arranged, ellipsoid to broadly obovoid, fusiform to cylindrical, hyaline or lightly pigmented, yellowish to brownish, aseptate or 1–2- trans-septate, or muriform, thin-walled, with or without a gelatinous sheath or appendages, guttulate or eguttulate. Asexual morph: cultures slow growing, greyish to olivaceous black; hyphae consistently melanized. *Conidial* production highly polymorphic: (1, 2) phialidic or annellidic with small, intercalary or discrete phialides or annellides,

producing mucous clumps of ellipsoidal to falcate, one-celled or septate conidia; 3) sympodial from differentiated, erect stalks producing one- or two-celled, non-catenate conidia, 4) catenate in short or long acropetal chains, from non- or slightly differentiated conidiophores; 5) multiseptate conidia with different arms being produced from undifferentiated hyphae (Fig. 108).

Families included in *Chaetothyriales*

Chaetothyriaceae Hansf. ex M.E. Barr
Coccodiniaceae Höhn. ex O.E. Erikss.
Cyphellophoraceae Réblová & Unter.
Epibryaceae S. Stenroos & Gueidan
Herpotrichiellaceae Munk
Lyrommataceae Lücking
Microtheliopsidaceae O.E. Erikss.
Paracladophialophoraceae Crous
Pyrenotrichaceae Zahlbr
Trichomeriaceae Chomnunti & K.D. Hyde (= *Strelitzianaceae* Crous & M.J. Wingf.)

Chaetothyriales family *incertae sedis*
Metacapnodiaceae S. Hughes & Corlett

Chaetothyriales genera *incertae sedis*
Bacillicladium Hubka, Réblová & Thureborn
Bahusutrabeeja Subram. & Bhat
Euceramia Bat. & Cif.
Hyaloscolecostroma Bat. & J. Oliveira
Lichenodiplis Dyko & D. Hawksw. (= *Laeviomyces* D. Hawksw.)
Lichenodiplisiella S.Y. Kondr. & Kudratov
Melanina Grube, Muggia & de Hoog
Minutoexcipula V. Atienza & D. Hawksw.
Muellerella Hepp ex Müll. Arg.
Sarcinomyces Lindner
Staninwardia B. Sutton
Uncispora R.C. Sinclair & Morgan-Jones

Evolution

The earliest lineages of *Chaetothyriales* are represented by black fungi that engage in various forms of symbiosis with lichens, such as endolichenic fungi (Arnold et al. 2009) and lichen-associated fungi (Muggia & Grube 2018). Sun-exposed rock surfaces, which are the preferred habitat of lichens, are characterized by extreme fluctuations in temperature and humidity. These harsh conditions foster the development of species-rich communities of chaetothyrialean fungi. Chaetothyrialean lichen-associated fungi have been known for 30 years (Petrini et al. 1990), but their taxonomic diversity and phylogenetic position have been clarified only during the past decade (Hofstetter et al. 2007, Arnold et al. 2009, Quan et al. 2020). Since the pioneering molecular studies of lichenized and non-lichenized rock-inhabiting fungi in *Chaetothyriomycetes* by Ruibal et al. (2008) and the investigation of their evolutionary origins by Gueidan et al. (2011), these fungi have been repeatedly reclassified due to the increasing volume of sequence data. The ancestral *Chaetothyriales* found in lichen-associated fungi and rock-inhabiting fungi are of significant interest due to their role in the evolution of various lifestyles and habitats. *Pleostigmataceae* and their ancestral relatives serve as a cradle of diversification, possessing nascent traits that have further developed in more derived families. The thallus of all chaetothyrialean members is uniformly melanized. Melanin is a crucial compound with various functions that enhance survival in extreme conditions (Moreno et al. 2017). Teixeira et al. (2017) showed specific gene family expansions in 23 genomes of members of *Herpotrichiellaceae*: alcohol (ADH) and aldehyde dehydrogenases

(ALDHS), membrane transport proteins, and a diverse ensemble of cytochrome P450 family members (CYPs), which all are considered as essential for survival under extreme conditions. A wide array of mechanisms related to nutrient acquisition was also observed, aligning with oligotrophy consistent with the ancestral lifestyle on bare, sun-exposed rock (Quan et al. 2020). Derived groups of rock-colonizing species are found in the genus *Knufia* and relatives in the family *Trichomeriaceae* (Isola et al. 2016). All of these fungi exhibit extreme tolerance, thriving in environments with high or low temperatures, limited nutrients, desiccation, and solar irradiation.

Justification of order and problems

The family *Herpotrichiellaceae* was initially introduced by Munk (1953), with the genus *Herpotrichiella* as the type genus. However, it was later discovered that the type species of this genus is actually a homotypic synonym of *Capronia pilosella*. Currently, this family is one of the largest within the order *Chaetothyriales*, comprising 18 genera (Hyde et al. 2024b). In recent years, extensive investigations of various novel and unexpected habitats have led to the discovery of numerous new species. A comparison with the past reveals that in the last two years alone, 6 new genera and 37 new species have been added. Traditionally, descriptions of new species relied mainly on their morphological characteristics. However, over the past two decades, with the widespread application of molecular biology techniques, the approach to describing new species has shifted towards a systematic methodology based on gene sequences. These differing classification standards have resulted in an arbitrary mixing of genera and species in terms of morphology and phylogeny. Currently, *Exophiala* comprises 75 known species, with new species being continuously described, leading species with polyphyletic clustering. Another significant genus, *Cladophialophora*, also faces taxonomic challenges as its strains have primarily been described based on morphological features but have been found dispersed among four different families/groups. Additionally, the classical genus *Phialophora* encounters similar issues, with 22 species described to date, but the taxonomic status of many species remains unclear. It is evident that relying solely on morphological characteristics to describe new species is insufficient to address classification issues, necessitating additional methods to complement them. *Herpotrichiellaceae* species are commonly found in human-dominated environments, with new species continually being discovered. A comprehensive systematic analysis of this family can help clarify existing taxonomic confusion, resolve issues of duplication and wrong identification, and establish reliable standards for the introduction of new genera and species.

Significance

Ecological and economic roles

Species of the family *Herpotrichiellaceae* are typically isolated from toxic sources, such as sites contaminated with hydrocarbons (Prenafeta-Boldú et al. 2001), fuel tanks, pumps of gasoline, diesel vehicles (Isola et al. 2021), and railroad ties (Döğen et al. 2013). These habitats are considered unfavorable for colonization by most fungi, but do not hinder the growth of some black yeasts, allowing for selective isolation of such fungi (Quan et al. 2019) utilizing toxic aromatic hydrocarbon compounds. Some black yeasts also exhibit significant capability to tolerate high concentrations of heavy metals in solution, which are toxic to most other organisms. For instance, species of the genus *Exophiala*, particularly *Exophiala sideris*, have been repeatedly isolated from environments contaminated with arsenic, with an observed half-maximal inhibitory concentration (IC50) for As(V) (Seyedmousavi et al. 2011). *Exophiala mesophila* is also capable of growth at an IC50 for Cr(VI) significantly higher than reported for other microorganisms (Chen & Hao 1998). The fish pathogen *Exophiala pisciphila* has also been isolated multiple times from the roots of plants growing in soil contaminated with heavy metals, and *in vitro* analysis has shown that this fungus exhibits IC50 values for Pb(II), Cd(II), and Zn(II) of 0.8, 0.3, and 1.5 g/L, respectively (Zhang et al. 2008). Similarly, *Exophiala salmonis* has been isolated as an endophyte from the roots of the herbaceous plant *Astragalus adsurgens* (Chu et al. 2019).

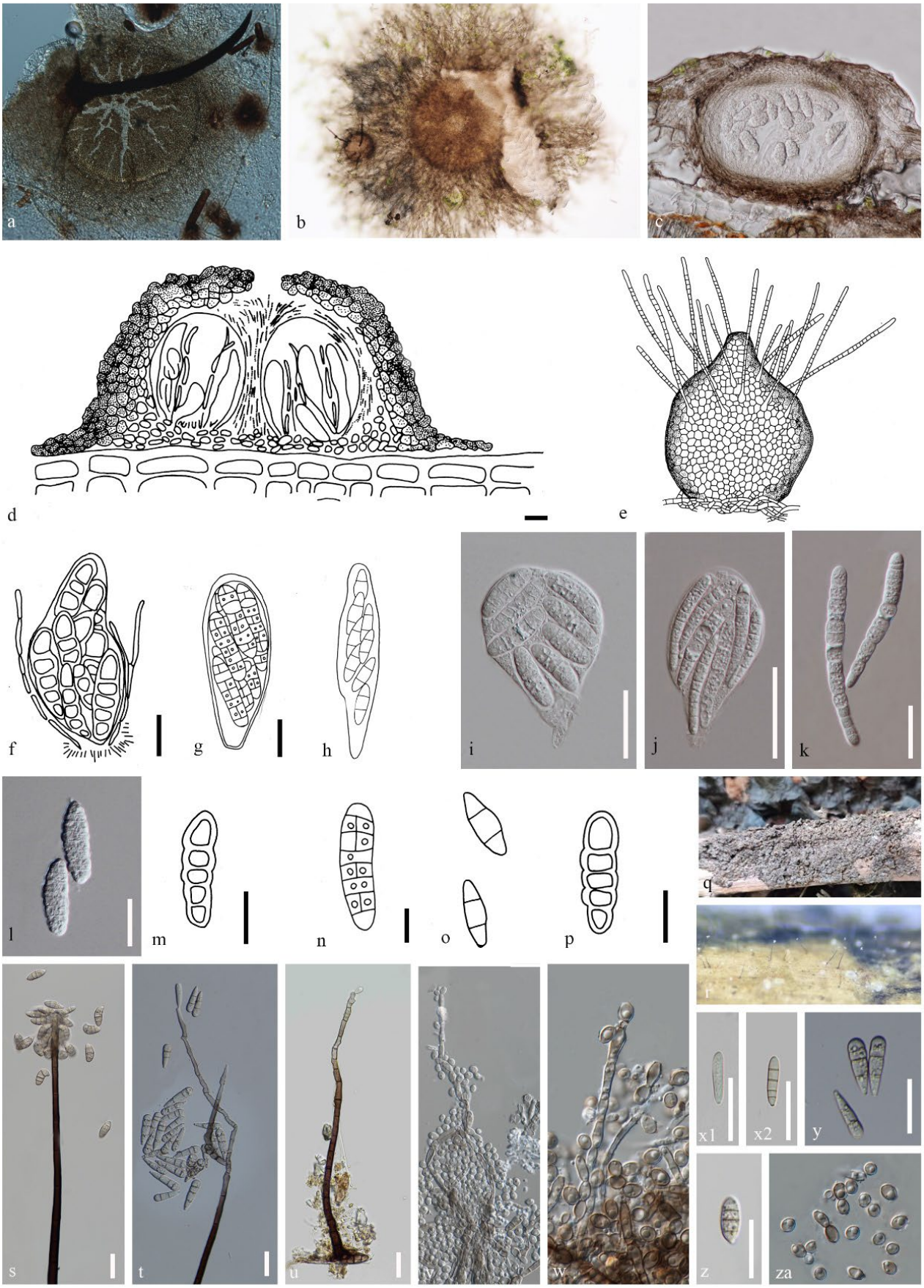


Figure 108 – Sexual and asexual morph of *Chaetothyriales.* a, b, Ascomata on substrate (a *Longihyalospora ampeli,* b *Ceramothyrium longivolcaniforme*). c–e Sections of ascoma (*M. aquaticum*), (c *Ceramothyrium longivolcaniforme*, d *Euceramia palmicola*, e *Trichomerium*

coffeicola). f–h (f *Euceramia palmicola*, g *Treubiomyces pulcherrimus*, h *Treubiomyces pulcherrimus*), i *Ceramothyrium longivolcaniforme*, j *Longihyalospora ampeli*), k *Longihyalospora ampeli*, l *Ceramothyrium longivolcaniforme*, m, p *Euceramia palmicola*, n *Treubiomyces pulcherrimus*, o *Treubiomyces pulcherrimus*). q, r Colonies on substrate (q *Rhinocladiella* sp. r *Thysanorea curvata*). s–w Conidiophores & Conidiogenous cells (s *Thysanorea curvata*, t *Thysanorea* sp., u *Thysanorea amniculi*, v, w *Rhinocladiella* sp.). x1–za Conidia (x1, x2 *Thysanorea amniculi*, y *Thysanorea* sp., z *Thysanorea curvata*, za *Rhinocladiella* sp.). (redrawn from Chomnunti et al. 2012, Tian et al. 2021). Scale bars: d, f, m, n, p = 10 µm, g, s, u, z = 20 µm, i, l, t, y = 30 µm, j = 50 µm, k = 20 µm, x1, x2 = 25 µm.

These characteristics can be engineered for the development of new biodegradation or bioremediation techniques, aiding in the breakdown of toxic substances in polluted environments or preventing the bioaccumulation of heavy metals in edible plant products.

Special ecology

In recent years, a large number of chaetothyrialean strains have been isolated from unique environments such as rock surfaces and ant nests. This not only enriches the fungal resources of this order but also helps us understand their evolutionary trajectories and deepen our understanding of the special relationships between these black yeasts and their environments. Chaetothyrialean taxa are found on exposed structures like ant nests or nest walls, where they must adapt to high temperatures, dryness, extreme solar radiation, and possible nutrient deficiencies. These fungi are exposed to a variety of compounds produced by ants within their nests. Mayer et al. (2021) analyzed the volatile organic compounds (VOCs) present in ant nests in tropical rainforests and hypothesized that *Chaetothyriales* associated with ants may play a crucial role in removing harmful volatiles that could affect vulnerable larvae lacking external skeletal protection. Given the biodiversity, wide distribution, and diverse nesting activities of ant species, as well as their specific functions in ant-plant associations, a rich diversity of fungi associated with these arthropods has been discovered (Quan et al. 2021, Voglmayr & Jaklitsch 2011), with more discoveries expected in further research.

Clinical presentation and pathogenicity

Chaetothyriales includes numerous pathogens causing human infections, ranging from severe to nearly asymptomatic. Species are distributed among 11 genera in three derived families: *Herpotrichiellaceae* (*Cladophialophora*, *Exophiala*, *Fonsecaea*, *Phialophora*, *Rhinocladiella*, *Veronaea*), *Trichomeriaceae* (*Arthrocladium*, *Knufa Bradymyces*) and *Cyphellophoraceae* (*Anthopsis*, *Cyphellophora*). In addition to infecting humans, infections in cold-blooded aquatic animals such as fish, frogs, toads, and crabs are also common (Boeger et al. 2005). Janse et al. (2024) noted that infections in fish are limited to bony fish, whereas cartilaginous fish and marine turtles are mainly affected by *Fusarium* species. Infections caused by black yeasts and their close relatives are notorious for their potential to cause severe disfigurement and death. The neurotropic species *Cladophialophora bantiana* is ranked among the top ten most feared fungi (Hyde et al. 2018a). Recently discovered rare genetic immunodeficiencies in humans, particularly mutations in the caspase recruitment domain-containing protein 9 (CARD9), have provided new insights into these clinical syndromes (Glocker et al. 2009). Fungi associated with CARD9 deficiency reported to date include members of *E. dermatitidis*, *E. spinifera*, *Veronaea botryosa*, and the *Phialophora verrucosa* complex. Particularly *Phialophora* responds to the human CARD9 inherited immune disorder (Song et al. 2021); the disease is otherwise mainly found with dermatophytes and with *Candida albicans*. The clinical features of CARD9-related infection are similar to chromoblastomycosis, a skin disorder caused by members of *Fonsecaea* and *Cladophialophora*, and an immunogenic relation has been hypothesized (Sobianski Herman et al. 2024). Possibly all severe, chronic, highly disfiguring, and often fatal infections caused by classical chaetothyrialean fungi are attributed to such or related genetic immunodeficiencies.

Exophiala, *Cladophialophora* and *Phialophora* are the most important genera within the family *Herpotrichiellaceae*, with many species causing severe infections belonging to these genera. The

most common disease caused by members of *Chaetothyriales* is chromoblastomycosis (CBM). This is a (subcutaneous) infection, where the pathogen transforms into "muriform cells" of equal diameter within tissues. The disease has been recognized by the World Health Organization (Hay et al. 2019) as a "neglected tropical disease (NTDs)".

A recent meta-analysis of extensive data collected from the "Atlas of Clinical Fungi" indicates that *Chaetothyriales* exhibit low resistance to antifungal drugs within the fungal kingdom, with significant variation within the order (Niu et al. 2024). MIC90 and GM data demonstrate significant sensitivity of *Chaetothyriales* to azole drugs, with only a few strains showing deviation. Resistance percentages are usually below 10%, whereas black melanized opportunistic pathogens in *Capnodiales*, *Dothideales*, *Pleosporales*, *Sordariales* and *Venturiales* show resistance ranges exceeding 50% for ITZ, PCZ, and VCZ (Niu et al. 2024), but are much less frequently observed in clinical settings. Infections *in vivo* are often recalcitrant despite the low MIC values of commonly used drugs, and therefore infections caused by members of *Chaetothyriales* remain a significant therapeutic challenge. The exact mechanisms of drug action in relation to host immunity will continue to be an important research question to better understand why diseases recur and develop resistance during treatment.

Coryneliales **Seaver & Chardón, Sci. Surv. Porto Rico & Virgin Islands 8 (1): 40 (1926)**

Subphylum : *Pezizomycotina*
Class : *Eurotiomycetes*
Subclass : *Coryneliomycetidae*

Introduction

Coryneliales is a small order in *Eurotiomycetes*, *Ascomycota* which comprises 58 species assigned to eight genera and one family. Its members are mainly plant pathogens with immersed in host tissue mycelium and erumpent coriaceous to carbonaceous stromata. Most representatives of the *Coryneliales* are biotrophic on the leaves of *Podocarpaceae* and are distributed mainly in the Southern Hemisphere. Most species are known in sexual state only (Geiser et al. 2006, Crous et al. 2019a).

History

Corynelia was published by Fries (1823) to describe *Corynelia uberata*, a species parasitizing *Afrocarpus falcatus* (syn. *Podocarpus falcatus*). Saccardo (1886, 1891) introduced a new family, *Coryneliaceae*, within *Sphaeriales*. At the same time, Cooke (1892) placed *Corynelia* in *Perisporiaceae*. Fitzpatrick (1920) doubted that the placement of *Corynelia* in both *Sphaeriales* and *Perisporiales* was correct, due to the lack of typical *Sphaeriales* ostiolum. To solve the problem, Seaver & Chardón (1926) established a new order *Coryneliales* in which to place *Corynelia*. Thereafter, authors included *Coryneliaceae* in *Erysiphales* (Clements & Shear 1931), *Sphaeriales* (Hansford 1946, Müller & von Arx 1973) or considered *Coryneliales* as an order of uncertain position (Funk 1963, Eriksson 1982). Based on the phylogenetic analysis of the SSU gene region, Winka (2000) placed *Coryneales* in its current class, *Eurotiomycetes*. Wood et al. (2016) introduced a new sub-class, *Coryneliomycetidae* based on multi-locus phylogenetic analysis. This work made it finally possible to state the place of *Coryneliales*. Wood et al. (2016) also provided updated descriptions, selected types and epitypes of different taxa, and published a detailed historical summary of *Coryneliales*.

General description

The characteristic features of *Coryneliales* are pseudothecial mazaedial ascomata with initially double-walled asci with the outer layer deliquescing, without an apical release mechanism resulting in passive ascospore release and producing spermogonia (Johnston & Minter 1989, Geiser et al. 2006, Wood et al. 2016). The same characters are specific to *Coryneliomycetidae* and differentiate this subclass from *Eurotiomycetidae* (cleistothecia/gymnothecia with prototunicate asci) and

Chaetothyriomycetidae (perithecia with bitunicate/fissitunicate asci) within *Eurotiomycetes* (Geiser et al. 2006, Hibbett et al. 2007, Wood et al. 2016). According to Assefa et al. (2014), the anamorph of some *Corynelia* species previously described as pycnidia or spermagonia (Fitzpatrick 1920, 1942, Benny et al. 1985) needs re-evaluation and confirmation by molecular methods.

Sexual morph: *Stromata* reduced or cushion-like, developing to variously-shaped loculate fertile extensions that form ascomata or spermogonia. *Spermogonia* sessile, with minute ostiole, spermatia unicellular, elongate, hyaline. *Ascomata* clustered or individual, pseudothecial, with a mazaedial chamber above the ascus-bearing base, black, thick- and smooth or rough-walled, opening by an ostiole or dehiscence grooves. *Interascal tissue* absent. *Asci* clavate, spathulate to capitate, mostly 8-spored or 2–3-spored, initially thick double-walled, the outer layer breaking and sloughing away with elongation, becoming long-stalked, and thin-walled, without apical release mechanism, evanescent. *Ascospores* aseptate, dark, variable, smooth-walled to prominently ornamented, aggregating in a mass above the ascus layer. Sexual propagules do not germinate in culture (adapted from Wood et al. 2016). Asexual morph: *Conidiomata* pycnidial, globose, ostiolate, brown to black, separate or aggregated in a brown stroma. *Conidiophores* arising from inner cells of the pycnidial wall, hyaline, smooth, simple, ampulliform or more frequently elongate, subcylindrical, branched, septate. *Conidiogenous cells* subcylindrical to doliiform, hyaline, smooth, terminal and intercalary, phialidic. *Conidia* hyaline, aseptate, ellipsoid to solitary, mostly somewhat curved, smooth, granular, apex obtuse, tapered towards base, truncate, sometimes with 1–2 guttules (Figs. 109, 110).

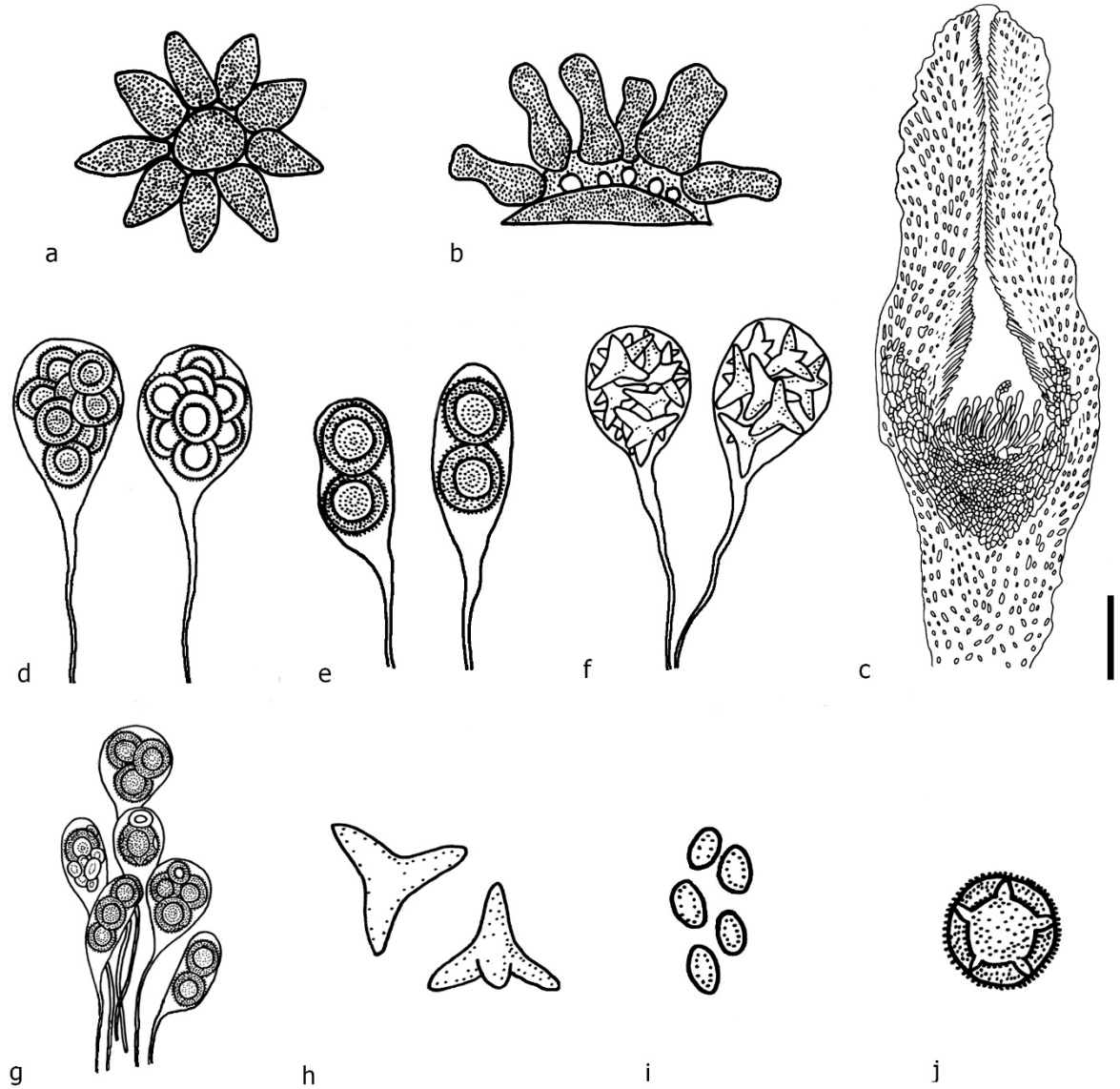


Figure 109 – Sexual morph of *Coryneliales*. a, b Perithecia (a *Corynelia brasiliensis*, b *C. nipponensis*). c Young ascoma from host tissue showing textura porrecta tissue type (c *Caliciopsis pleomorpha*). d–f Asci (d *Corynelia oreophila*, e *Corynelia bispora*, f *Tripospora tripos*, g *Corynelia portoricensis*). h–j Ascospores (h *Tripospora tripos*, i *Caliciopsis calicioides*, j *Corynelia oreophila*) (redrawn from Fitzpatrick 1920, Pascoe et al. 2018). Scale bars: a, b × 11, d–i × 700, j × 1000, c = 40 µm.

Families included in *Coryneliales*

Coryneliaceae Sacc. ex Berl. & Voglino

Evolution

According to Wood et al. (2016), *Coryneliales* can serve as an ideal subject for studies of the evolution of the *Ascomycota*. They proposed *Coryneliomycetidae* as a transition stage between the prototunicate *Eurotiomycetidae* and the bitunicate *Chaetothyriomycetidae*.

Justification of order and problems

Since its establishment by Seaver & Chardón (1926), the taxonomic placement of *Coryneliales* remained unclear due to the combination of the unitunicate asci and ascolocular development. To solve this problem, Tim (1971) proposed the new corynelioid type of centrum. Johnston & Minter (1989) showed that the asci of the *Coryneliales* are bitunicate with the outer layer deliquescing. The taxonomic position of *Coryneliales* within *Eurotiomycetes* was phylogenetically stated by Winka (2000), and later confirmed by Geiser et al. (2006) and Wood et al. (2016).

Significance

Ecological and economic roles

The economic significance of members of *Coryneliales* is not well-understood and underestimated (Assefa et al. 2014). Most representatives of *Corynelia* are obligate parasites on plants of the genera *Afrocarpus* and *Podocarpus*. They cause disease on the leaves, cones and young stems, but also destroy seed embryos and can kill seedling trees (Fitzpatrick 1920, 1942, Benny et al. 1985, Minter 2006, Assefa et al. 2014). This may cause both economic and ecological effects because the host trees are widely used as a source of timber, edible oil, and medicinal products, and are well-known commercially as podo or East African Yellow-Wood. Its fruit also serves as a food source for birds, bats and other animals (Breitenbach 1963, Geldenhuys 1993, Negash 1995, Assefa et al. 2014).

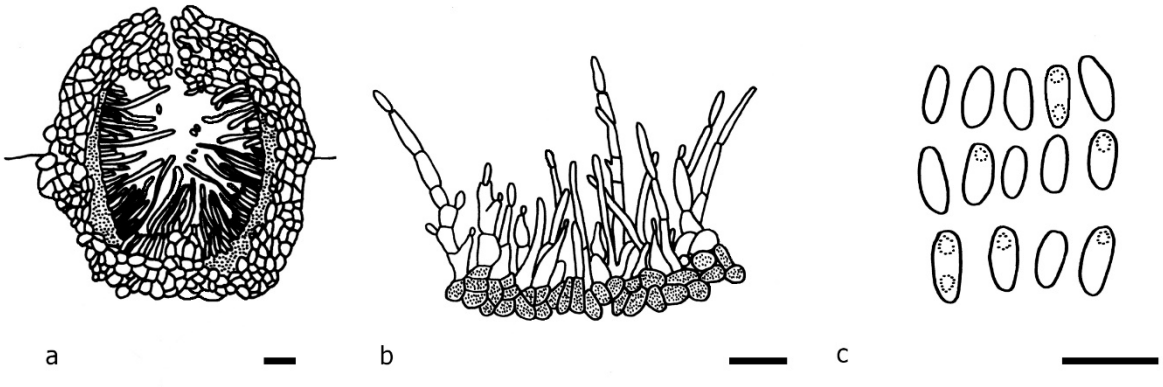


Figure 110 – Asexual morph of *Coryneliales*. a Pycnidium. b Conidiophores and conidiogenesis. c Conidia (a–c *Caliciopsis pleomorpha*) (redrawn from Pascoe et al. 2018). Scale bars: a–c = 10 µm

Chemical diversity

No chemical substances were reported in *Coryneliales*.

Other relevant data and future recommendations

Further detailed investigation of *Coryneliales* particularly using molecular analyses, is required, and further species diversity within the order is expected. There are some concerns about the continued existence of these obligate pathogens (e.g., Wood et al. 2016) because the host trees *Podocarpaceae* are under threat from over exploitation. There is also little known about their co-evolution.

Cryptocaliciales **M. Prieto, Etayo & Olariaga, Mycological Progress 20(7): 894 (2021)**

Subphylum : *Pezizomycotina*
Class : *Eurotiomycetes*
Subclass : *Cryptocaliciomycetidae*

Introduction and History

Cryptocaliciales was recently established to accommodate a single family (*Cryptocaliciaceae*), a genus (*Cryptocalicium*) and a species (*C. blascoi*) that was reported on the inner side of loose bark strips of *Juniperus oxycedrus* from Spain (Prieto et al. 2021). The order was placed in the newly established subclass *Cryptocaliciomycetidae* which formed a distinct lineage and was sister to *Eurotiomycetidae* in the multigene phylogenetic analysis based on LSU, SSU, ITS, mtSSU, RPB1, RPB2 and MCM7 sequence data. The presence of clavate, bitunicate and evanescent and pedicellate asci supported the placement of the order between *Eurotiomycetidae* and the *Coryneliomycetidae*. However, *Cryptocaliciales* differs to the latter subclasses in the formation of tiny fruiting structures (which are difficult to observe using 10–20 × magnification) among calicioid fungi with hemi amyloid reaction of asci, the presence of hamathecial filaments and the dark violet pigment granules that turn blue-green in KOH. The order further differs from the subclass *Mycocaliciomycetidae* with mazaediate stipitate ascomatal opening by clavate asci, whereas the latter has cylindrical asci without iodine reactions (Tibell & Wedin 2000).

General description

The sexual morph of *Cryptocaliciales* is characterized by tiny fruiting structures, hemi amyloid reaction of asci, the presence of hamathecial filaments and the dark violet pigment granules that turn blue-green in KOH while the asexual morph is observed in the axenic culture in Hyphomycete-like morph.

Sexual morph: *Ascomata* apothecioid, 0.15–0.36 mm high (mazaedium excluded), stalked, mazaediate. *Stalk* cylindrical, sometimes broader at the base, straight, seldom bent, smooth, black and shiny. *Capitulum* urniform to hemispherical, dark violaceous brown when wet, black, and shiny when dehydrated, monocephalic, with an ochre disc. *Hamathecium* composed of regularly scattered sterile elements, protruding over mature asci. *Subhymenium* poorly differentiated from the medullary excipulum, composed of a *textura angularis-globulosa* with more or less isodiametrical hyphae, pale brown in water, and green in IKI and amyloid in KOH+IKI. *Ectal excipulum* poorly differentiated from the medullary excipulum, composed of periclinal-arranged hyphae, of *textura prismatica* in surface view, with cells progressively shorter towards the margin of the capitulum, and pale brown, thick-walled with pigment granules. *Medullary excipulum* 15–20 µm thick, composed of a *textura angularis-globulosa* cells with more or less isodiametrical hyphae, and hyaline to very pale brown, thin-walled, 2–4 µm broad, and non-gelatinized. *Asci* clavate, bitunicate with a pedicel, initially thick-walled (wall 1 µm) and becoming thin-walled, evanescent and 8-spored. *Ascospores* disperse passively and are globose to subglobose, rarely ellipsoid, hyaline inside the asci, pale brown when mature, with a homogeneous content, with two-minute refractive bodies in Congo Red, smooth when viewed in a light microscope, (3)3.3– 4(4.7) × 2.8– 3.5 (4) µm, and slightly thick-walled (0.2–0.4 µm). Asexual morph: Hyphomycete-like, observed only in culture on MEA, superficial, effuse, convex to obtusely conical, initially even, later wrinkled-cerebriform, cauliflower- like, cream white, tomentose and pale brownish ochre in reverse. *Conidiophores* 30–48 µm long, basally branched, formed by 2–6(8) catenulate segments. *Segments* irregular in shape, usually cylindrical to

subglobose, often triangular or angled, constricted at septa and connected to each other by 1–3, thin, 1 µm broad appendices, easily disarticulating in microscopic preparations, 5–9 × 3–6.5 µm. *Conidiogenous* cells cylindrical to ovoid, 5–12 × 1.5–4 µm, bearing one simple apical conidiogenous locus, 1 µm broad, to which immature conidia are attached. *Conidia* single, first pyriform then subglobose, slightly truncate at the basal end, thin-walled, smooth, hyaline, with small oily droplets, 2.3–3 µm (adapted from Prieto et al. 2021) (Fig. 111).

Families included in *Cryptocaliciales*

Cryptocaliciaceae Etayo, Olariaga & M. Prieto

Evolution

Cryptocaliciales shows open ascomata (apothecioid). The study conducted on the evolution of ascomata showed that closed ascomata (both perithecioid and cleistothecioid) forms have derived from apothecioid ancestors in the *Eurotiomycetes* (Prieto et al. 2021).

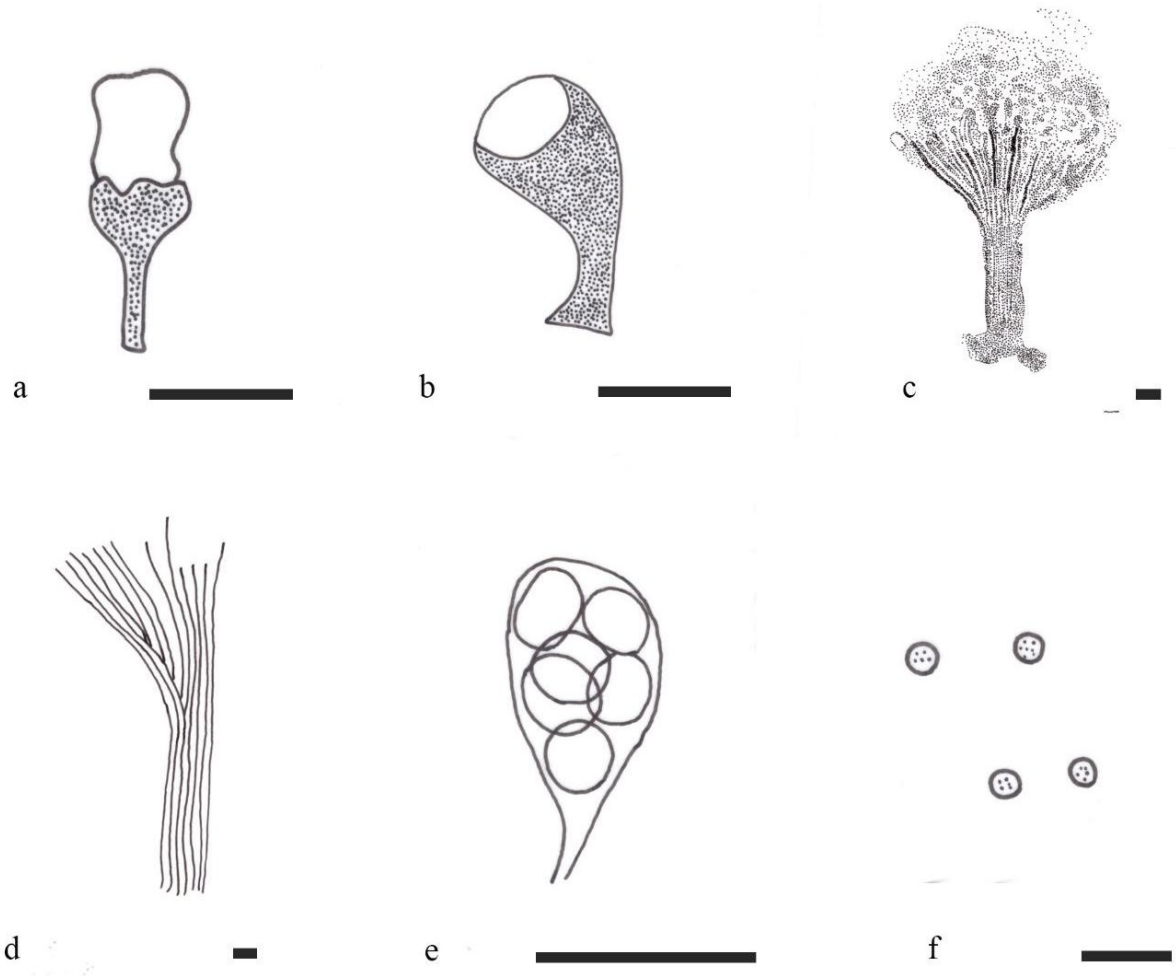


Figure 111 – Morphology of *Cryptocaliciales* (*Cryptocalicium blascoi*). a, b, c. Ascomata. d Stalk surface in water. e Ascus. f Ascospores (drawn from Prieto et al. 2021). Scale bars: a–c = 100 µm, d–f = 10 µm.

Justification of order and problems

The phylogenetic placement of *Cryptocaliciales* between *Eurotiomycetidae* and *Coryneliomycetidae* supports either the inclusion of both *Coryneliomycetidae* and *Cryptocaliciomycetidae* within the *Eurotiomycetidae* or the description of a new subclass (*Cryptocaliciomycetidae*).

Significance

Ecological and economic roles

The saprotrophic inoperculate ascomycetes species *Cryptocalicium blascoi* grows on the inner part of bark strips of *Juniperus oxycedrus* and *J. thurifera* trees. Few ascomata occur on solid resin drops in continental Mediterranean areas in Spain. They are restricted to well-preserved stands of ancient *Juniperus* and *Cupressus*. However, these taxa might have a wider distribution, because they could have easily been overlooked due to their small ascomata (Prieto et al. 2021).

Chemical diversity

Data is lacking regarding chemical diversity within this order.

Eurotiales G.W. Martin ex Benny & Kimbr. Mycotaxon 12 (1): 23 (1980)

= *Aspergillales* C.E. Bessey, University of Nebraska Studies 7: 304 (1907)
Subphylum : *Pezizomycotina*
Class : *Eurotiomycetes*
Subclass : *Eurotiomycetidae*

Introduction

Eurotiales is one of the major orders of *Ascomycota* which consists of many important fungal genera. It contains over 1200 species assigned to 28 genera and five families (Houbraken et al. 2020, Wijayawardene et al. 2022a, Hyde et al. 2024b). *Eurotiales* is characterized by cleistothecial ascomata with bright walls, thin-walled, evanescent, clavate or saccate asci, sometimes forming chains with variable ascospores which are usually small, aseptate, often ornamented, and with equatorial crests or furrows. This order is often named *Aspergillales* rather than *Eurotiales*. This order is vast and widespread that one of its members *Penicillium chrysogenum* was once declared to be among the most common eukaryotic life forms on Earth (Malloch 2022). Concerning the occurrence of anamorphic and teleomorphic stages, it is notable that most *Eurotiales* taxa were reported to reproduce asexually. However, the sexual mode of reproduction is a focus of research because there are different views about the existence of their teleomorphs. The *Aspergillaceae*, one of the largest families, consists of about 14 genera and 978 species (Wijayawardene et al. 2020, 2022a). The species that produce asci inside cleistothecia, stromata, or are surrounded by hülle cells and mainly have oblate to ellipsoidal ascospores with a furrow or slit are generally included in this family. The family contains some of the important fungal genera, such as *Aspergillus* and *Penicillium*. The species of this family are cosmopolitan in distribution and are highly adaptable to extreme environmental conditions. *Trichocomaceae* is another family of this order with about 180 species belonging to nine genera (Wijayawardene et al. 2022a).

The members of this family are generally saprobic with aggressive colonization strategies. *Talaromyces* is reported to be an important genus found useful in both industry and medicine. Another family *Elaphomycetaceae* consists of two genera namely *Elaphomyces* and *Pseudotulostoma*. *Elaphomyces* is one of the most important ectomycorrhizal fungal genera in temperate and subarctic forest ecosystems and contains more than 100 species. In contrast, *Pseudotulostoma* contains only two species, one reported from Guyana and Japan (Index Fungorum 2025, MycoBank 2025). The remaining two families are also taxonomically important as they have unique and distinctive characteristics. *Thermoascaceae* was proposed by Apinis (1967), containing only two genera *Paecilomyces* and *Thermoascus*. *Paecilomyces* consists of both plant pathogenic and entomopathogenic fungal species whereas, *Thermoascus* accommodates soil inhabiting taxa that are characterized by the production of heat-resistant ascospores.

Penicillaginaceae, the last family of this order was proposed by Houbraken et al. (2020) during a re-evaluation of the relationships between families and genera of the *Eurotiales* using a nine-gene sequence dataset. Recently, Hyde et al. (2024b) also outlined all fungi and fungus-like taxa and confirmed the inclusion of five families under the order *Eurotiales.*

History

Eurotiales was proposed by Martin (1941) and later validated by Benny & Kimbrough (1980). The species in this order are widespread, abundant, diverse, and widely distributed; therefore, these taxa were classified and placed in different orders by several researchers. They were placed under *Aspergillales* by Luttrell (1951a). Separately, these species were classified as *Eurotiales* (Martin 1941, Ainsworth 1961, 1971, Alexopoulos 1962, Fennell 1973, Muller & Loeffler 1976, Alexopoulos & Mims 1979), *Gymnascales* (Clements & Shear 1931), *Hypocreales* (Cain 1956b, Malloch 1979), *Perisporales* (Clements & Shear 1931) and *Plectascales* (Gaumann 1928, Nannfeldt 1932, Langeron & Vanbreuseghem 1965, Dennis 1968, 1978, Wehmeyer 1975). Fennell (1973) included nine families in her treatment of *Eurotiales*. However, Benny & Kimbrough (1980) placed only two families, *Cephalothecaceae* and *Trichocomaceae,* in this order. Benny & Kimbrough (1980) validated both *Eurotiales*, and also three more orders *Ascosphaeriales*, *Microascales* and *Onygenales*. They proposed the characteristics of this order as: coiled ascogonia; ascospores lacking or present as hyaline or variously colored, lacking ostioles, stromatic or astromatic, consisting of hyphae or pseudoparenchyma; asci one-celled, globose, evanescent, irregularly disposed, consisting of eight spored ascospores, hyaline or variously colored, smooth, and ornamented; anamorph usually consisted of phialoconidia.

General description

Eurotiales sometimes referred to as an order of "sac fungi", contain taxa known as green and blue molds. The members of this order are generally characterized based on common characteristics that include: bright-walled cleistothecial ascomata, thin-walled, evanescent, clavate or saccate asci, sometimes forming chains, and ascospores which are variable but usually small, aseptate, often ornamented, and with equatorial crests or furrows. However, each family and genus possess distinct anamorphic and telomorphic characteristics that define their taxonomic placement. The genera of *Aspergillaceae* produce asci inside cleistothecia, and stromata, or are surrounded by Hülle cells. They mainly have oblate to ellipsoidal ascospores with a furrow or slit. The general characters of the monotypic family *Penicillaginaceae* include the production of ampulliform to acerose phialides that have relatively fine, long, narrowed necks, and conidia with conspicuous disjunctors. However, they also share some common characteristics with other *Penicillium* species: production of penicillium-like conidiophores, green shades conidia, inability to grow on Czapek's agar (CYA) medium at 37 °C and moderate growth on CREA without acid production (Guevara-Suarez et al. 2020, Houbraken et al. 2020). Members of the *Thermoascaceae* family are characterized by the production of firm, somewhat sclerotioid, pseudoparenchymatous cleistothecia and the formation of ascospores lacking a furrow or slit. These are thermotolerant or thermophilic in nature (Houbraken & Samson 2011, Houbraken et al. 2020). *Trichocomaceae* is characterized by formation of lanceolate phialides, asci borne within a tuft or layer of loose hyphae and ascospores lacking a slit or furrows (Houbraken & Samson 2011).

The members of *Eurotiales* reproduce both asexually and sexually, but many predominantly reproduce asexually only. The anamorphs of *Eurotiales* generally form chains of conidia that emerge from awl-shaped phialides or flask-shaped conidiogenous cells (Houbraken & Samson 2011, Rossman et al. 2016, Wijayawardene et al. 2017b, Houbraken et al. 2020). The number of sexual morphs observed per genera are: *Ascospirella* (1), *Dendrosphaera* (1), *Dichlaena* (2), *Evansstolkia* (1), *Hamigera* (8), *Leiothecium* (2), *Monascus* (2), *Paecilomyces* (5), *Penicilliopsis* (3), *Penicillium* (64), *Pseudohamigera* (1), *Pseudopenicillium* (3), *Rasamsonia* (4), *Sagenomella* (1), *Sclerocleista* (2), *Talaromyces* (40), *Thermoascus* (7), *Thermomyces* (1), *Trichocoma* (1), *Warcupiella* (1), *Xeromyces* (1). In total, 295 species of *Eurotiales* have been reported to produce sexual morphs. The highest numbers of sexual morphs were reported from the genera *Penicillium* and *Talaromyces*. *Aspergillus* contains sexual morphs with different structures, including eurotium-type, neosartorya-type, emericella-type, petromyces-type, chaetosartorya-type, fennellia-type and neopetromyces-type (Houbraken & Samson 2017, Houbraken et al. 2020). *Talaromyces* sexual morph have been observed in *Biverticillium*, *Penicillium* and *Rasamsonia* (Benjamin 1955, Houbraken et al. 2012b). Other types

of sexual morphs observed in *Eurotiales* are emericella-type (Section *Nidulantes* series *Aurantiobrunnei*), fennellia-type (Section *Usti* series *Monodiorum*), eupenicillium-type (Series *Thiersiorum*) neosarotya-type (Section *Fumigati*, Series *Fennelliarum*) (Samson et al. 2007, 2011, Hubka et al. 2017), and chaetosartorya-type (*Aspergillus*) (Houbraken & Samson 2017).

Sexual morph: *Ascomata* cleistothecial**,** bright-walled. *Asci* thin-walled, evanescent, clavate or saccate asci sometimes forming chains. *Ascospores* very variable but usually small, aseptate, often ornamented, and with equatorial crests or furrows. Asexual morph: *Conidia* mostly chains, emerge from awl-shaped phialides or flask-shaped conidiogenous cells (Houbraken & Samson 2011, Rossman et al. 2016, Wijayawardene et al. 2017b, Houbraken et al. 2020) (Fig. 112).

Families included in *Eurotiales*

Aspergillaceae Link (= *Monascaceae* J. Schröt.)
Elaphomycetaceae Tul. ex Paol.
Penicillaginaceae Houbraken, Frisvad & Samson
Thermoascaceae Apinis
Trichocomaceae E. Fisch.

Evolution

Fungal evolutionary studies remain a crucial task for biologists and mycologists because of the lack of fossil evidence and obscure morphology (Sugiyama 1998, Berbee & Taylor 2001). Houbraken et al. (2020) provided a detailed account of evidence regarding the evolution of taxa included in *Eurotiales,* emphasizing the ectomycorrhizal association. Mead et al. (2021) studied the diverse evolutionary analysis of the genomes of 18 *Aspergillus* strains representing 13 species. They found dozens of gene families that were present only in a given pathogen, as well as dozens of genes whose evolutionary rates differed between a given pathogen and the rest of the taxa (Mead et al. 2021). The relationship of *Penicillium* to other genera of *Trichocomaceae* was investigated by phylogenetic analysis based on partial RPB1, RPB2 (RNA polymerase II genes), Tsr1 (putative ribosome biogenesis protein) and Cct8 (putative chaperonin complex component TCP-1) gene sequences, which reflected the polyphyletic nature of *Penicillium*. Houbraken & Samson (2011) revealed that 15 lateral gene transfer events were from bacteria that occurred during the evolution of *Penicillium* (Petersen et al. 2023).

Justification of order and problems

The species of *Eurotiales* share common characteristics which justify their taxonomic placement in this order. The members of *Trichocomaceae* are known for their production of organic acids and diverse enzymes (that degrade a wide variety of complex biomolecules), secondary metabolites and mycotoxins (Geiser et al. 2006, Pitt & Hocking 2009, Samson et al. 2010). After the introduction of the family *Trichocomaceae* (Fischer 1897), its classification was studied extensively, but based only on the phenotypic characters of teleomorphs, not any anamorphs (Malloch & Cain 1972, Subramanian 1972, Malloch 1985, 1986, von Arx 1986). The formation of lanceolate phialides, asci within a tuft or layer of loose hyphae and ascospores without slit differentiated them from other families and justified their placement in this order (Houbraken & Samson 2011). *Penicillaginaceae* is named after the sole genus in this family, *Penicillago*.

The presence of penicillium-like conidiophores with long, narrow neck phialides justified the placement of *Penicillago* in *Eurotiales*. This genus was originally named *Penicillago* because of its close phylogenetic relationship with *Penicillium* (Guevara-Suarez et al. 2020), but it was found to be distantly related to *Penicillium* in the *Aspergillaceae* and formed a unique lineage in *Eurotiales* (Houbraken et al. 2020). The production of cleistothecia is a uniting character of *Elaphomycetaceae,* which placed them in *Eurotiales*. The members of *Elaphomycetaceae* represent one of the few independent lineages of mycorrhizal symbiosis (Tedersoo et al. 2010, Houbraken et al. 2020). The genera *Thermoascus* and *Paecilomyces* in *Thermoascaceae* are thermotolerant or thermophilic in nature and form ascospores lacking a furrow or slit, however, they are differentiated from *Trichocomaceae* by the production of asci from croziers (Houbraken & Samson 2011).

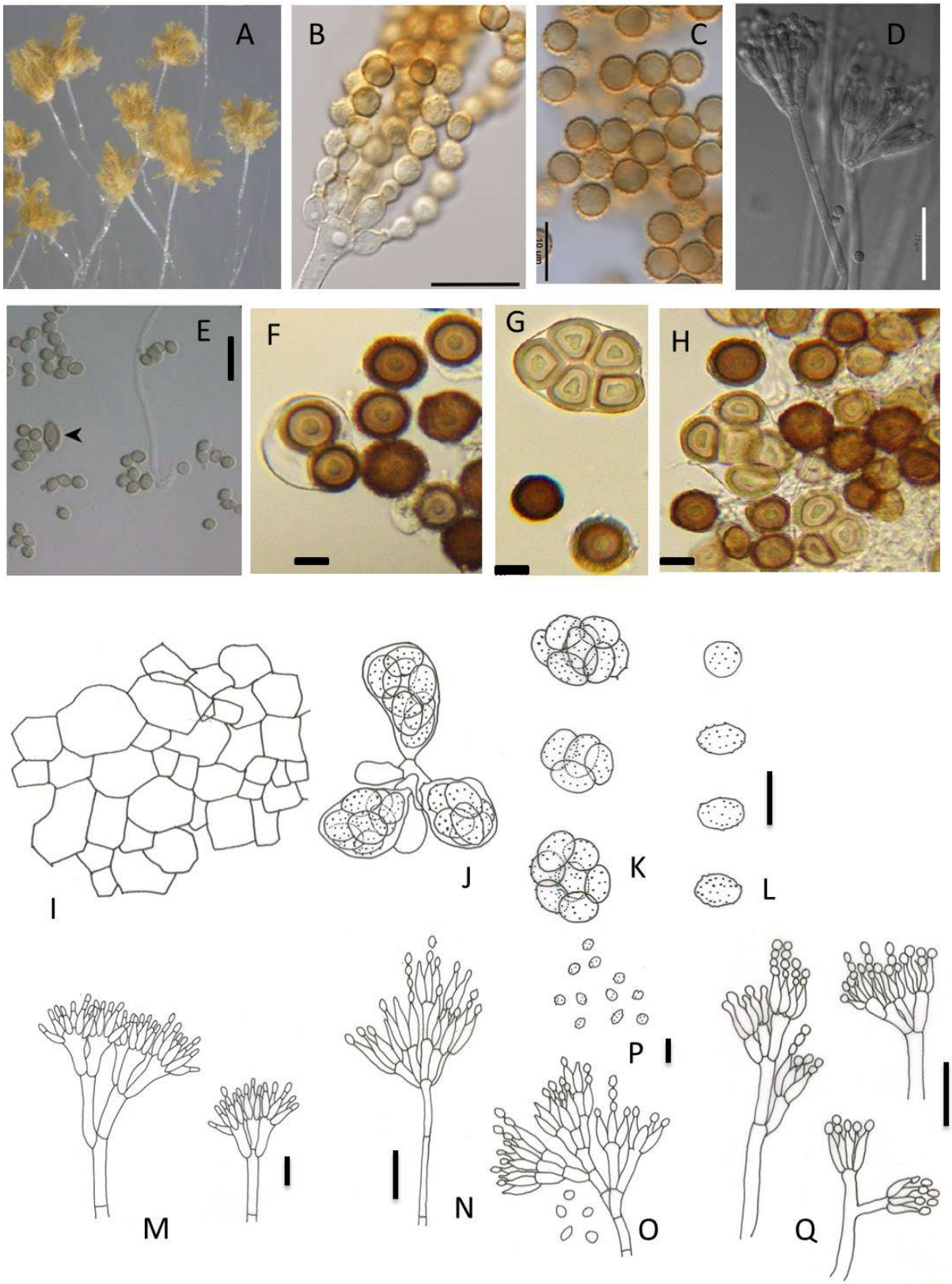


Figure 112 – *Aspergillus tamarii* A, B Conidiophore with attached conidia. C Conidia (*Talaromyces quii*). D Typical biverticillate symmetric conidiophores. E Normal and large-sized conidia (Photo credit to Dr. KC Rajeshkumar of NFCCI Pune India). *Elaphomyces muricatus.* F–H Asci and ascospores (from Roman 2013) (*Thermoascus taitungiacus*). I Portion of ascomal peridium. J Asci. K Ascospores in evanescent asci L. Ascospores (Redrawn from Chen & Chen 1996) (*Penicillium persicinum*). M Conidiophores and conidia (Redrawn from Wang et al. 2004a) (*Acidotalaromyces lingorum*). N, O Conidiophores with attached conidia. P Conidia (Redrawn from Stolk 1969*).*

(*Penicillago kabunica*). Q Conidiophores and conidia (Redrawn from Baghdadi 1968). Scale bars: B, D = 20 µm C, E–P = 10µm, Q = 15µm.

Significance

Ecological and economic roles

The taxa of *Eurotiales* are mainly saprotrophic in nature and are found in a wide range of habitats, including soil, wood, dung, and animal debris (such as hair, horn, and feathers). Some members cause spoilage of certain foods (Frisvad et al. 2019); others are used in many industrial operations and preparations, or cause diseases in animals (Seyedmousavi et al. 2015, Nguyen et al. 2023). Two genera, *Aspergillus* and *Penicillium*, are found on all types of substrates. They grow as saprobes on a variety of substrates such as soil, plant and animal debris, and other dead organic matter. They may also appear as phytopathogens on different plant hosts (Zakaria 2024). Species are found in variable environments all over the world, though they have been observed most frequently during autumn and winter in the Northern Hemisphere (Low et al. 2005, Crous et al. 2020c). *Aspergillus proliferans*, *A. parasiticus*, *A. nomius*, and *A. lentulus* are important aflatoxin producers.

Mycotoxins such as ochratoxin A and patulin can occur in foods and feeds contaminated by *Penicillium* species, e.g., *Penicillium citrinum* (Perrone & Susca 2017). *Paecilomyces variotii* can also cause food spoilage. Many of these taxa are important human pathogens and indoor contaminants which cause a variety of disorders of the respiratory tract, lungs and many carcinogenic effects (Sklenář et al. 2020, Nguyen et al. 2023). *Aspergillus fumigatus* is also an extremely dangerous pathogen, causing aspergillosis. Over 60 *Aspergillus* species are reported as medically relevant pathogens. For humans, these include a range of diseases such as infection to the external ear, skin lesions, and ulcers (Frisvad et al. 2019, van den Brule et al. 2019). *Aspergillus carbonarius* and *Aspergillus ochraceus* produce ochratoxin A (OTA), which contaminates grapes and coffee (Bayman et al. 2002). *Acidotalaromyces* can cause wood rot in Europe. It grows on acid agar media (pH 3.5) and potentially produces biotechnologically interesting enzymes (Houbraken et al. 2020).

Many members of *Eurotiales* have properties useful to industrial applications and products (Hyde et al. 2019). *Aspergillus oryzae* is used in the food industry for fermentation. Soy sauce (*A. oryzae*), blue-veined cheese (Roquefort) (*P. roqueforti*) and camembert cheese (*P. camemberti*) are produced with the help of taxa of *Eurotiales*. Many useful organic acids and enzymes of industrial importance and many pharmaceutically important compounds are produced by members of *Eurotiales*. The production of citric acid (by *Aspergillus niger*), enzymes (by *Rasamsonia emersonii* and *Thermomyces lanuginosus*) and pharmaceuticals, including lovastatin (*Aspergillus terreus*), mycophenolic acid (*Penicillium brevicompactum*) and the antibiotic, penicillin (*P. rubens*) are some important examples of beneficial aspects of these taxa (Houbraken et al. 2012a, 2014, Nielsen et al. 2017, Frisvad et al. 2019, Hyde et al. 2019). Many species of this order are used in the fermentation of foods and beverages, such as soy sauce, chocolate, soft drinks, vitamins, black tea, and fruit juices (Houbraken et al. 2020). *Aspergillus flavus* AF36, a non-carcinogenic, aflatoxin-free strain can be applied to soil as a component of pesticides. It germinates and out-competes aflatoxin-producing strains of *A. flavus* (Urquhart et al. 2018). Overall, *Eurotiales* are known as prolific producers of a wide range of chemical compounds that may be either beneficial or harmful to humans and the environment.

Eurotiales contains some taxa having both saprobic and parasitic life cycles (e.g., *Coccidioides immitis* and *C. posadasii*) (Fisher et al. 2002). The members of this order can have either positive or negative impacts on human activities. *Aspergillus*, *Paecilomyces*, *Penicillium*, *Rasamsonia* and *Talaromyces* are well-known as causes of food spoilage, mycotoxin production, environmental contaminants and even animal and plant pathogens. *Aspergillus* commonly occurs in the environment. If inhaled for an extended time, this can cause Aspergillosis in humans (Hocking 2006, Feofilovaa et al. 2009, Houbraken et al. 2020). In addition, mycotoxins (aflatoxins) are produced by *A. flavus*. Human pathogens and indoor contaminants are produced by *A. fumigatus*, *A. flavus* and *A. versicolor* (Ismaiel & Papenbrock 2015, van den Brule et al. 2019). However, its industrial uses encompass production of acids and enzymes such as cellulases, pectinase, amylases

and other enzymes that degrade complex polysaccharides (Mojsov 2016). Other uses of *Aspergillus* include: *A. niger* in the production of citric acid, *A. oryzae* in soy sauce, and *A. terreus* in the production of pharmaceuticals.

Penicillium, another genus of this order, has many useful industrial applications, including the production of blue-veined cheese by *P. roqueforti*, and camembert cheese by *P. camemberti*. The most well-known product of many species of *Penicillium* is penicillin. This was the world's first antibiotic, which was discovered by Alexander Fleming during World War II. However, *Penicillium* can also have some harmful impacts on animals and plants. Citrinin, patulin, penicillic acid, ochratoxin A and citreoviridin, are some important mycotoxins produced by different species of *Penicillium* that negatively affect liver or kidney functions (Ismaiel & Papenbrock 2015, Frisvad et al. 2019). Other species of *Penicillium* have a range of differing beneficial and harmful impacts on animals, plants, and the environment.

Chemical diversity

Taxa of *Eurotiales* produce a broad range of chemicals that are used in different industrial processes. *Aspergillus ochraceus* produces diverse structural products, including polyketides, nonribosomal peptides, diketopiperazine alkaloids, benzodiazepine alkaloids, pyrazines, bis-indolyl benzenoids, nitrobenzoyl sesquiterpenoids, steroids and useful industrial enzymes (Chen et al. 2016a, 2022a). The endophytic taxa of this order (*Penicillium cinnamopurpureum*, *P. olsonii*, *Talaromyces T. verruculosum*, *T. atroroseus* and *T. minioluteus*) produce phenolic compounds: hydroxybenzoic acids, flavanols and hydroxycinnamic acids (Rocha et al. 2020). Secondary metabolites (chrysophanol, 7,7'-biphyscion, secalonic acid D, mannitol, and trehalose) were isolated from extracts of *Phialomyces macrosporus* (da Silva Brandão et al. 2019). Sixty-two secondary metabolites, representing a variety of structural classes, including polyketides, terpenoids, peptides, and those of mixed biosynthetic origins, were isolated and characterized from extracts of solid-phase cultures of the endophytic taxon *Silybum marianum* (Raja et al. 2015b). Two secondary metabolites (kongiilines A and B), two asperphenamate derivatives (asperphenamates B and C) and 16 other known compounds were isolated from *Penicillium kongii* and *Penicillium brasilianum* (Liu et al. 2017c) that were reported from Tibetan Plateau. Azaphilone and isocoumarin derivatives were isolated from the endophytic fungus *Penicillium sclerotiorum* (Arunpanichlert et al. 2010).

Bladt et al. (2013) extracted anticancer and antifungal compounds from species of *Aspergillus, Penicillium* and other filamentous fungi. Citrinin dimers from the halotolerant fungus *Penicillium citrinum* B-57 (Lu et al. 2008), cytotoxic anthranilic acid derivatives from deep sea sediment-derived *Penicillium paneum* SD-44 (Li et al. 2013) and eremophilane sesquiterpenes and diphenyl thioethers from the soil fungus *Penicillium copticola* PSU-RSPG138 (Daengrot et al. 2015) were isolated and identified. Recent studies revealed a broad spectrum of chemicals produced by *Talaromyces*. Analysis of ethyl acetate extract from marine coral-derived species *Talaromyces cellulolyticus* SHJ-3 revealed the presence of a series of chrodrimanin meroterpenoids (verruculide A, chrodrimanin A, chrodrimanin B, chrodrimanin C, chrodrimanin F, chrodrimanin H) and two phenols (6-hydroxymellein (**7**) and *N*-(4-hydroxy-2-methoxyphenyl) acetamide) (Xu et al. 2022a). *Talaromyces* species yield many secondary metabolites, including esters, terpenes, steroids, alkaloids, polyketides, and anthraquinones which exhibit anti-inflammatory, bacteriostatic, and antitumor activities (Lei et al. 2022). Members of *Talaromyces* typically produces a funicone-like group of secondary metabolites (Salvatore et al. 2022). The taxa of the order also produce a diverse spectrum of other chemical compounds and metabolites. Other natural products could be explored by manipulating nutritional or environmental factors.

Other relevant data and future recommendations

Eurotiales have a wide range of effects on our day-to-day lives. Although their identification was challenging earlier because of their morphological similarities, recent taxonomic and nomenclatural changes have helped a lot to improve and stabilize this situation. To propose a new species is critical because it requires a polyphasic data for comparison (Maharachchikumbura et al.

2021a). It becomes more difficult when no specimen material is available for study or a lack of data on the species (many doubtful species described in the late 1800s, called the 'dark ages') (Pitt 1980). Moreover, using low-quality sequence data to describe new species has also raised a concern (Nilsson et al. 2017). Such species must be considered doubtful because these low-quality sequences will make classification and future identification difficult or even impossible. Therefore, it is recommended that the dried specimens and living cultures be properly submitted to recognized repositories to access these in future requirements (Aime et al. 2021). In addition, we also recommend research collaborations among specialized taxonomists to help each other with a second opinion and in the identification of a species.

***Mycocaliciales* Tibell & Wedin, Mycologia 92(3): 579 (2000)**

Subphylum : *Pezizomycotina*
Class : *Eurotiomycetes*
Subclass : *Mycocaliciomycetidae*

Introduction

Mycocaliciales belongs to *Eurotiomycetes* comprised a single family (Wijayawardene et al. 2022a). The taxonomy and phylogeny of *Mycocaliciales* have been the subject of much debate over the years. Molecular studies have suggested that the order is a polyphyletic group. Some members of *Mycocaliciales* have been shown to be more closely related to other lichenized fungi in different orders, such as *Lecanorales* and *Pertusariales,* as well as phylogenetically closely related to *Eurotiales* and *Onygenales* (Tibell & Wedin 2000).

History

The history of *Mycocaliciales* dates back to the late 18th century and the members were previously treated as close to lichenized *Caliciales* group. Vainio (1890) described the generic type *Mycocalicium* which was characterized by the absence of a photobiont and very thin mazaedium. Schmidt (1970) introduced the family *Mycocaliciaceae* to include *Mycocalicium*, *Chaenothecopsis*, *Phaeocalicium*, *Stenocybe*, and *Strongyleuma*. *Mycocaliciaceae* was initially classified as part of the core group of *Caliciales*, along with the families *Caliciaceae* and *Sphinctrinaceae*, based on shared characteristics such as stalked ascomata, dark sclerotized hyphae, and melanized ascospores, forming a monophyletic group (Schmidt 1970). However, later studies revealed that this core group was not monophyletic. *Mycocaliciaceae* differs from *Caliciaceae* in non-lichenized lifestyle, absence of mazaedium, and the spores disperse actively. This distinction was further supported by phylogenetic analyses conducted by Tibell & Wedin (2000). As a result, a new order, *Mycocaliciales*, was established within the *Eurotiomycetes* to accommodate both *Mycocaliciaceae* and *Sphinctrinaceae*. These two families share similarities in their morphology, such as sessile to stalked ascomata, a sclerotized blackish-brown exciple, cylindrical asci, and dark brown ascospores with smooth or ornamented walls. However, *Mycocaliciaceae* species actively disperse their ascospores without forming mazaedium, while *Sphinctrinaceae* species produce ascospores that form a moderately developed mazaedium. *Sphinctrinaceae* was initially established to include the lichenicolous genus *Sphinctrina* that was described by Fries (1828), and later a saprobic genus *Pyrgidium* was added. *Mycocaliciales* was placed in its own subclass *Mycocaliciomycetidae* which formed a distinct clade in *Eurotiomycetes* (Hibbett et al. 2007). Jaklitsch et al. (2016a) synonymized *Sphinctrinaceae* under *Mycocaliciaceae* based on morpho-molecular evidence. Recently, Hyde et al. (2024b), accepted *Mycocaliciales* with a single family, *Mycocaliciaceae*, which includes seven genera: *Brunneocarpos*, *Chaenothecopsis*, *Mycocalicium*, *Phaeocalicium*, *Pyrgidium, Sphinctrina* and *Stenocybe*.

General description

The taxa are mostly reported in the sexual morph and the asexual morph shows ceolomycetous and hyphomycetous states.

Sexual morph: *Ascomata* moderately developed mazaedium, disciform, sessile to stalked. *Excipulum* cupulate, stalk hyphae at least in part sclerotized. *Hamathecium* evanescent or consisting of unbranched to sparingly branched paraphyses, non-amyloid. *Asci* cylindrical, apical tholus sometimes penetrated by narrow canal, unitunicate, non-amyloid. *Ascospores* subglobose to broadly fusiform or ellipsoid, 4–8-spored, after maturity usually accumulating in dark brown masses, non-septate to 1–7 transversely septate, pale to dark brown, non-amyloid. *Spore wall* pigmented, smooth or with an ornamentation formed within the plasmalemma (Vulpinic acid derivatives occur in a few species). Asexual morph: hyphomycetous or coelomycetous. *Conidiomata* pycnidia. *Conidia* bacillar to oblong-ellipsoid, sometimes curved, non-septate, brown (Fig. 113).

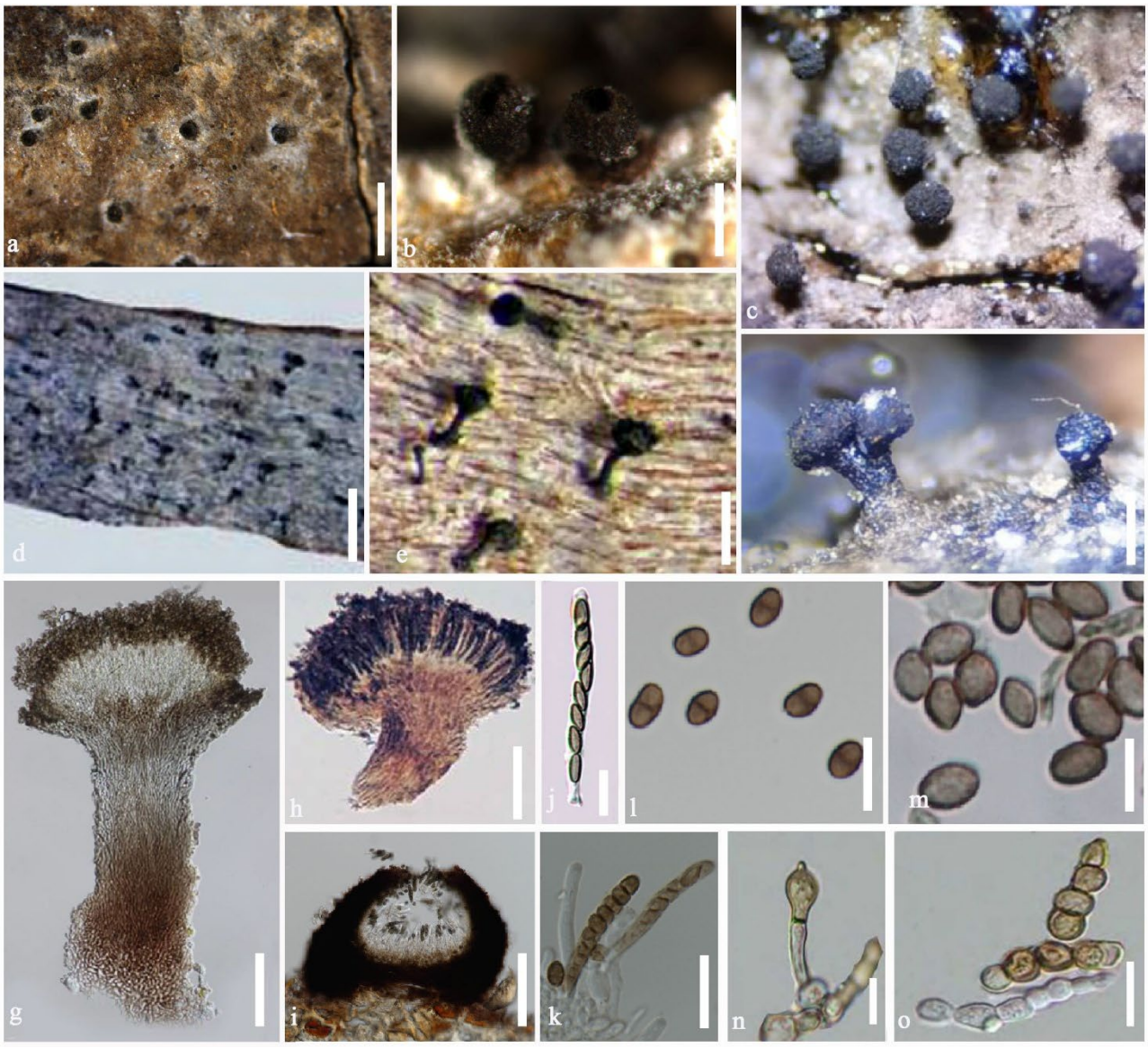


Figure 113 – Sexual and asexual morphs of *Mycocaliciales*. a–f Host substrate (a, b *Pyrgidium* sp., d, e *Mycocalicium* sp., c, f *Chaenothecopsis* sp.). g–j Vertical section through ascoma (g *Chaenothecopsis* sp., h *Mycocalicium* sp., i *Pyrgidium* sp.). j, k Asci (j *Mycocalicium* sp., k *Pyrgidium* sp.). Ascospores (l *Pyrgidium* sp., m *Chaenothecopsis* sp.). n Mature conidiogenous cells with attached conidia. o Conidial chains (n, o *Mycocalicium* sp.). Scale bars: a = 2 mm, b = 500 µm, d = 1000 µm, e = 1500 µm, g = 100 µm, h = 500 µm, i = 100 µm, j–o = 10 µm.

Families included in *Mycocaliciales*

Mycocaliciaceae A.F.W. Schmidt (= *Sphinctrinaceae* M. Choisy)

Evolution

According to Prieto et al. (2021), open ascoma was reported as an ancestor of *Eurotiomycetes* and this feature was even strongly supported for *Mycocaliciomycetidae* in the phylogenetic analysis. Species of *Chaenothecopsis* that grow on angiosperm exudates form a strong monophyletic group, indicating a single origin for this ecological habit. In contrast, species that grow on conifer resin are spread across different parts of the genus, suggesting a longer and more complex evolutionary history. However, resinicolous ecology of *Mycocaliciales* needs further revision.

Justification of order and problems

Mycocaliciales clade has been recovered as a stable, basal lineage within *Eurotiomycetes* in the recent multigene phylogenetic analyses (Prieto et al. 2021). However, several members of the clade still lack molecular data, and some species with available molecular data do not form a monophyletic group. Many morphology-based attempts to resurrect genera have led to overlapping classifications that do not form distinct monophyletic groups (e.g., *Strongyleuma* = *Chaenothecopsis*) (Schmidt 1970, Tibell 1997). To clarify species boundaries and resolve taxonomic uncertainties, it is essential to integrate multiple data sources, including morphological, ecological, and molecular evidence (Tibell 1984, Titov 2006, Tuovila et al. 2013).

Significance

Ecological and economic roles

Among the members of *Mycocaliciales*, *Sphinctrina* and several *Chaenothecopsis* species are reported as lichenicolous fungi, whereas all the members are reported as non-lichenized saprobes on bark, plant exudates and wood and the taxa are reported worldwide (Tibell & Wedin 2000). The largest genus *Chaenothecopsis* accommodates many resinicolous species that inhabit a diverse host range, and some are host-specific, while other species of the genus occur as saprobes, parasites or commensals on lichens and free-living algae, and mainly occur in temperate in the Northern and Southern Hemispheres (Tibell & Wedin 2000).

Chemical diversity

The chemical diversity of *Mycocaliciales* is not well explored. Pulvinic acid derivates are reported in several species (Jaklitsch et al. 2016a).

***Onygenales* Cif. ex Benny & Kimbr. Mycotaxon 12: 8 (1980)**

=*Onygenales* Cif. Atti Ist. Bot. Univ. Pavia, ser. 5, 14: 238 (1957)

Subphylum : *Pezizomycotina*
Class : *Eurotiomycetes*
Subclass : *Eurotiomycetidae*

Introduction

The orders *Arachnomycetales*, *Coryneliales*, *Eurotiales* and *Onygenales*, together with some unclassified taxa, constitute the subclass *Eurotiomycetidae* (Geiser et al. 2006). The order *Onygenales* has undergone several revisions since its establishment. Based on the recent amendments by Kandemir (2022) and Li et al. (2023), *Onygenales* includes ten families (*Ajellomycetaceae*, *Arthrodermataceae*, *Apinisiaceae*, *Ascosphaeraceae*, *Eremascaceae*, *Gymnoascaceae*, *Malbrancheaceae*, *Neogymnomycetaceae*, *Onygenaceae*, *Spiromastigoidaceae*) and several *incertae sedis* clades and more than 51 genera with some *incertae sedis* genera.

Members of *Onygenales* are known for their ecological association with mammals, either via dung or keratin, or via pathogenicity, which can be superficial or systemic (Kandemir 2022). The taxa are distributed worldwide, and keratinophilic, utilizing the early products of keratin decomposition, and usually behave as saprobionts on feathers, horns, hooves, or on soil and dung containing keratin (Doveri et al. 2012). Others are keratinolytic and this ability to degrade keratin often makes them pathogenic to birds, mammals, and humans, causing tricho-, onycho- and dermatomycoses. Others are cellulolytic or chitinoclastic on plant debris, soil and dung (Sugiyama

et al. 2002). The ecology and habitat choices of the species in the *Onygenales* are driven mainly by the keratin and cellulose degradation abilities. Significant ecological traits that determine evolution in *Onygenales* are osmophily, thermophily, cellulolysis, eutrophism, oligotrophism, keratinolysis, and thermal dimorphism (Kandemir 2022).

History

The *Onygenales* is an order of *Ascomycota* originally introduced by Ciferri (1957), while Benny & Kimbrough (1980) formalized the name with a description in Latin, and classified it in *Plectomycetes*. Later, the class *Eurotiomycetes* was proposed to replace the name *Plectomycetes* (Eriksson 1999) and since then *Onygenales* is widely referred to as an order in *Eurotiomycetes*. Von Willdenow (1787) introduced *Lycoperdon equinum* from the hooves of horses as the type species of *Onygenales*. Persoon (1797) reported that *L. equinum* was different from other *Lycoperdon* species, so it was removed as the type species and the genus *Onygena*, commonly referred to as the horn-stalked ball, was established. Unfortunately, the type of material is not known to be preserved (Kandemir 2022). A culture of the neotype specimen is available as CBS 947.70, which stabilizes the nomenclature of the order *Onygenales* (Kandemir 2022).

Upon the introduction of the order, classification of its members was mainly based on the follows: 1) the ascomata, which are variable in morphology, feature structures such as an undifferentiated peridium composed of loosely woven thin-walled hyphae, a reticuloperidium or incompositoperidium that occasionally bears complex appendages, a cleistoperidium or a stipitate stroma; 2) the asci are spherical, with thin, evanescent walls, and are formed freely on the mycelium or within ascomatal peridia; 3) the ascospores are small, single-celled and hyaline or light in color and have various types of ornamentation; 4) the anamorphs are aleurio- or arthroconidia that secede rhexolytically; 5) keratin degradation is shown by several taxa that are associated with the skin of living animal or animal offal such as dung, shed feathers and bones (Sugiyama et al. 2002). The classification of the order *Onygenales* has been controversial, and the number of recognized families has changed several times. Currah (1985) accepted four families in *Onygenales* (*Onygenaceae*, *Arthrodermataceae*, *Myxotrichaceae* and *Gymnoascaceae*), but noted morphological and ecological similarities between *Myxotrichaceae* and some members of *Leotiomycetes*; this was confirmed by later molecular phylogenetic work resulting in its reclassification (Sugiyama et al. 2002, Wang et al. 2006a).

Geiser & LoBuglio (2001) followed Currah's (1985) family-level taxonomy; since then, *Arachnomycetaceae*, *Ajellomycetaceae* and *Nannizziopsiaceae* have been proposed based on phylogenetics (Gibas et al. 2002a, Untereiner et al. 2004, Stchigel et al. 2013). In the Stchigel et al. (2013), nuclear large ribosomal RNA subunit (LSU)-based phylogeny, the *Arachnomycetaceae* did not have strong statistical support in *Onygenales*, leading to the establishment of *Arachnomycetales*. In addition, Stchigel et al. (2013) treated *Ascosphaeraceae* as a family within *Onygenales*, and *Eremascus* as an outgroup to *Onygenales*. However, no multi-locus analysis utilizing a full taxon set of *Onygenales* has been performed, leaving the relationships between these families, as well as their status as monophyletic groups, unclear (Geiser et al. 2015). Until recently, Kandemir (2022) provides a revised overview of the main lines of the taxonomy of *Onygenales*, based on multi-locus analyses of ITS, LSU, TUB2, TEF1, TEF3, RPB1, RPB2, and ribosomal protein 60S L10 (L1) (RP60S) sequences, combined with available data on ecology, physiology, morphology, and genomics. In their study, previously described families, namely, *Arthrodermataceae*, *Ajellomycetaceae*, *Ascosphaeraceae*, *Eremascaceae*, *Gymnoascaceae*, *Onygenaceae* and *Spiromastigoidaceae*, were accepted in *Onygenales*, and introduced two new families, *Malbrancheaceae* and *Neogymnomycetaceae* (Kandemir 2022). Furthermore, several species could not be assigned to any of the defined families (Kandemir 2022). Hyde et al. (2024b) accepted three additional families (*Helicoarthrosporaceae*, *Nannizziopsidaceae* and *Nannizziopsidaceae*) and the count has been increased to 13 families and 11 genera were placed in *incertae sedis*.

General description

In redefining the order *Onygenales*, Benny & Kimbrough (1980) distinguished three families *viz*. *Dendrosphaeraceae*, *Gymnoascaceae* and *Onygenaceae*. In this study, Benny & Kimbrough (1980) described members of *Onygenales* as being frequently keratinophilic, lacking a peridium or having one composed of loose and interwoven hyphae or having glabrous ascomata with or without appendages, ovoid or subclavate asci with eight ascospores, aseptate, hyaline or bright colored ascospores and arthro- or aleurioconidial anamorphs. Currah (1985) reviewed the order *Onygenales* and described the order frequently includes keratinophilic species with sessile or stipitate ascomata, with or without appendages, or sessile, composed of loose, interwoven hyphae (gymnothecium), or naked asci, fruitbodies being absent; asci ovoidal or subclavate, evanescent, containing eight spores; ascospores hyaline or brightly colored; holo- or entero-thallic conidiogenesis, lateral or intercalary; additional septate macroconidia may be present.

To date, the morphological characters of most families under the order *Onygenales* have been stabilized. As described by Currah (1985), the main diagnostic criteria of *Arthrodermataceae* are white, pale yellow or yellowish-brown, globose ascomata with appendages; thin-walled, transparent, subglobose to globose asci; hyaline to pale yellow, smooth, minute, oblate to oblate-discoid or oblate-convex ascospores. In addition, the main diagnostic criteria of *Onygenaceae* are described as follows: sexual states are described with pseudoparenchymatous cleistothecia or elaborate gymnothecia, and asexual morphs are chrysosporium-like or malbranchea-like conidia (Currah 1985). Kandemir (2022) erected the family *Malbrancheaceae* by merging *Auxarthron* and *Malbranchea*, which the main diagnostic criteria of the family *Malbrancheaceae* are mesh-like gymnothecia, well-differentiated thick-walled peridial hyphae with knuckle-joint septal enlargements, punctate ascospores. Currah (1985) and Doveri et al. (2012) described the main diagnostic criteria of *Gymnoascaceae* are: ascomata are mostly yellowish, greenish, reddish or brownish shades, with a gymnoperidium composed of a loose network of hyaline or pigmented hyphae.

Asci globose to ovoid; ascospores are hyaline, yellowish or greenish, spherical, ovoidal or oblate, smooth- and thick-walled, sometimes with equatorial grooves and ridges and/or polar thickenings. Rizzo et al. (2014) described the main diagnostic criteria of *Spiromastigoidaceae* are present, discrete or confluent, brown ascomata covered with orange-brown, curved or twisted appendages; eight-spored, subglobose, ovoid to ellipsoidal asci; and smooth-walled, yellowish to pale brown ascospores (Rizzo et al. 2014).

Sexual morph: *Ascomata* sessile or stipitate, present or absent appendages, or sessile, composed of loose, interwoven hyphae (gymnothecium), or naked asci, fruitbodies being absent. *Asci* ovoidal or subclavate, evanescent, containing eight spores. *Ascospores* hyaline or brightly colored. Asexual morph: Aleurio- or arthroconidia that secede rhexolytically. *Conidiogenesis* holo- or entero-thallic, lateral or intercalary. *Macroconidia* may be present, septate (Figs. 114, 115, 116).

Families included in *Onygenales*

Ajellomycetaceae Untereiner, Scott & Sigler.
Apinisiaceae M. Li, Raza & L. Cai
Arthrodermataceae Locq. ex Currah
Ascosphaeraceae Olive & Spiltoir.
Eremascaceae Engler & Gilg.
Helicoarthrosporaceae Stchigel, Rodr.-Andrade & Cano
Gymnoascaceae Baran.
Malbrancheaceae Kandemir & de Hoog
Nannizziopsidaceae Guarro, Stchigel, Deanna A. Sutton & Cano
Neoarthropsidaceae Torres-Garcia & Gené
Neogymnomycetaceae Kandemir & de Hoog
Onygenaceae Berk.
Spiromastigoidaceae Guarro, Cano & Stchigel.

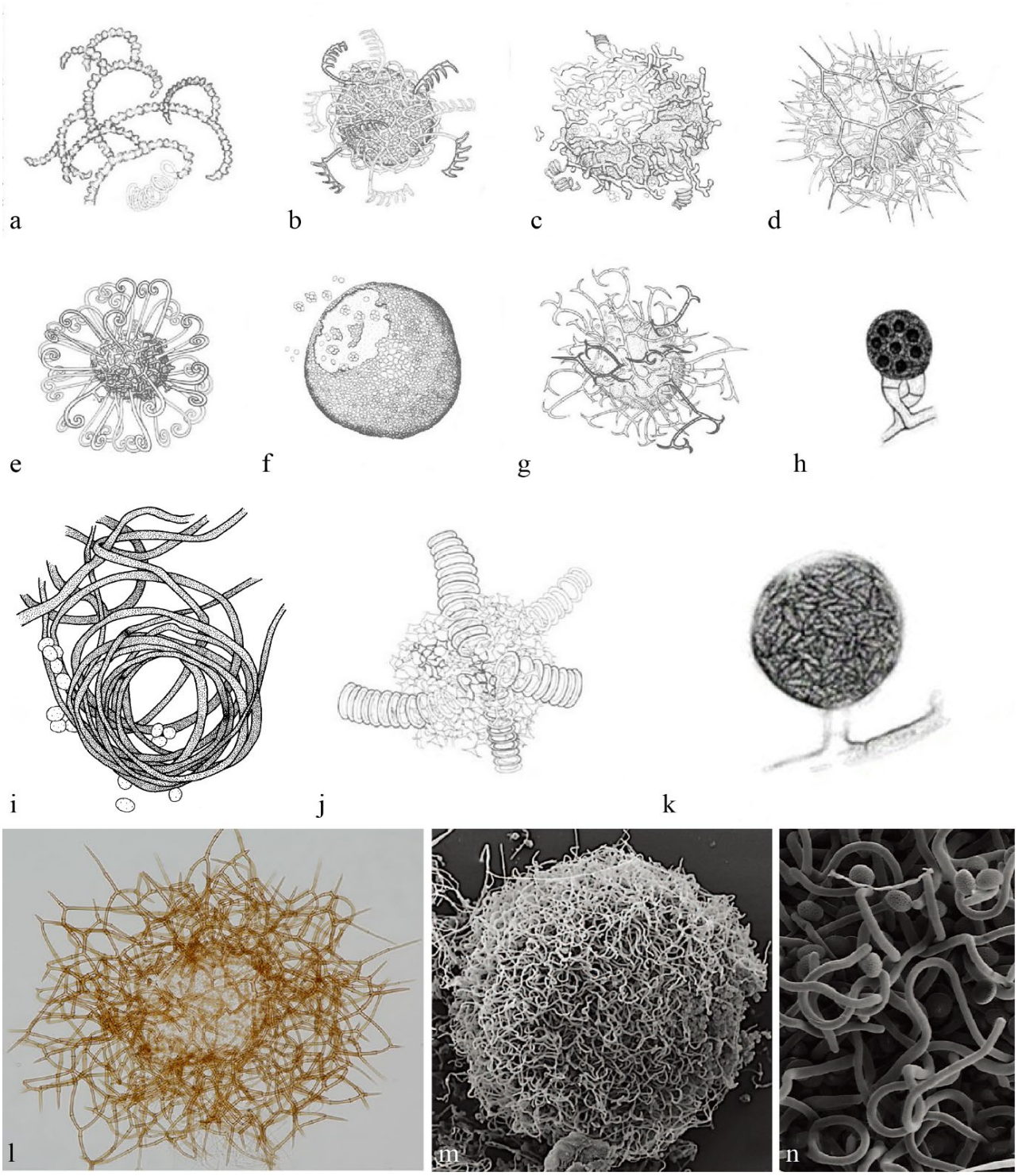


Figure 114 – Ascomata and ascomatal appendages morphology of *Onygenales.* a *Arthroderma* sp. b *Ctenomyces* sp. c *Shanorella* sp. d *Auxarthronopsis* sp. e *Uncinocarpus* sp. f *Aphanoascus* sp. g *Gymnoascus* sp. h *Eremascus* sp. i *Polytolypa* sp. j *Blastomyces* sp. k *Ascosphaera* sp. l *Malbranchea* sp. m, n *Spiromastix* sp. a, b, c, d, e, f, g, j (Currah 1985), h (de Bary 1884), i (Scott et al. 1993), k (David Minter, Whitby), l (Zhang et al. 2021c), m, n (Hirooka et al. 2016).

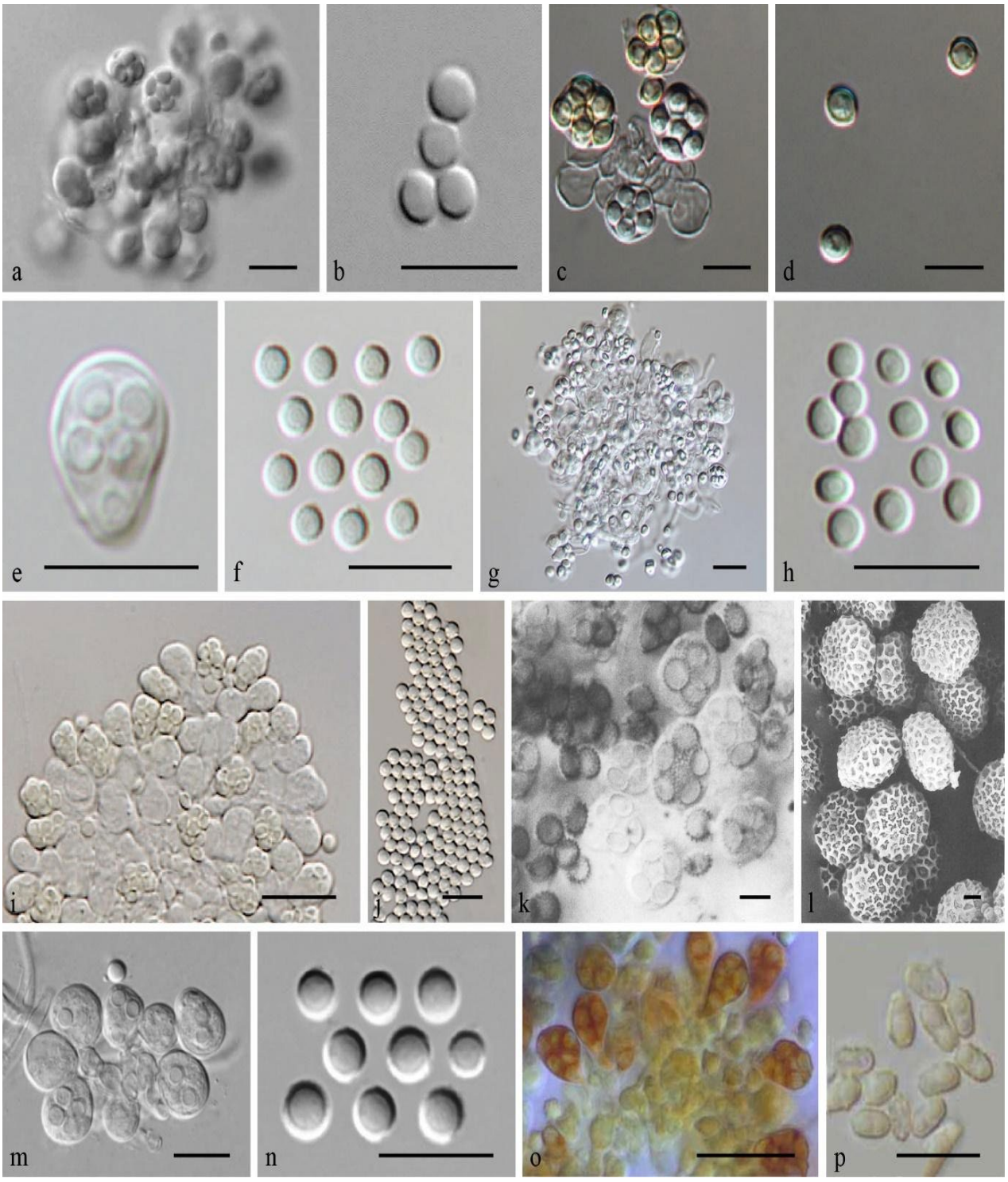


Figure 115 – Asci and ascospores morphology of *Onygenales*. a. b *Arthroderma rodenticum* (adapted from Moulíková et al. 2023). c. d *Gymnascella thermotolerans* (adapted from Zhou et al. 2016). e, f *Malbranchea guangxiense* (adapted from Zhang et al. 2021c). g, h *Auxarthronopsis globiascus* (adapted from Zhang et al. 2021c). i, j *Spiromastigoides sugiyamae* (adapted from Hirooka et al. 2016). k, l *Aphanoascus reticulisporus* (adapted from Cano & Guarro 2002). m, n *Chrysosporium pallidum* (adapted from Zhang et al. 2021c). o, p *Harorepupu Aotearoa* (adapted from Johnston et al. 2015). Scale bars: a–p = 10 μm.

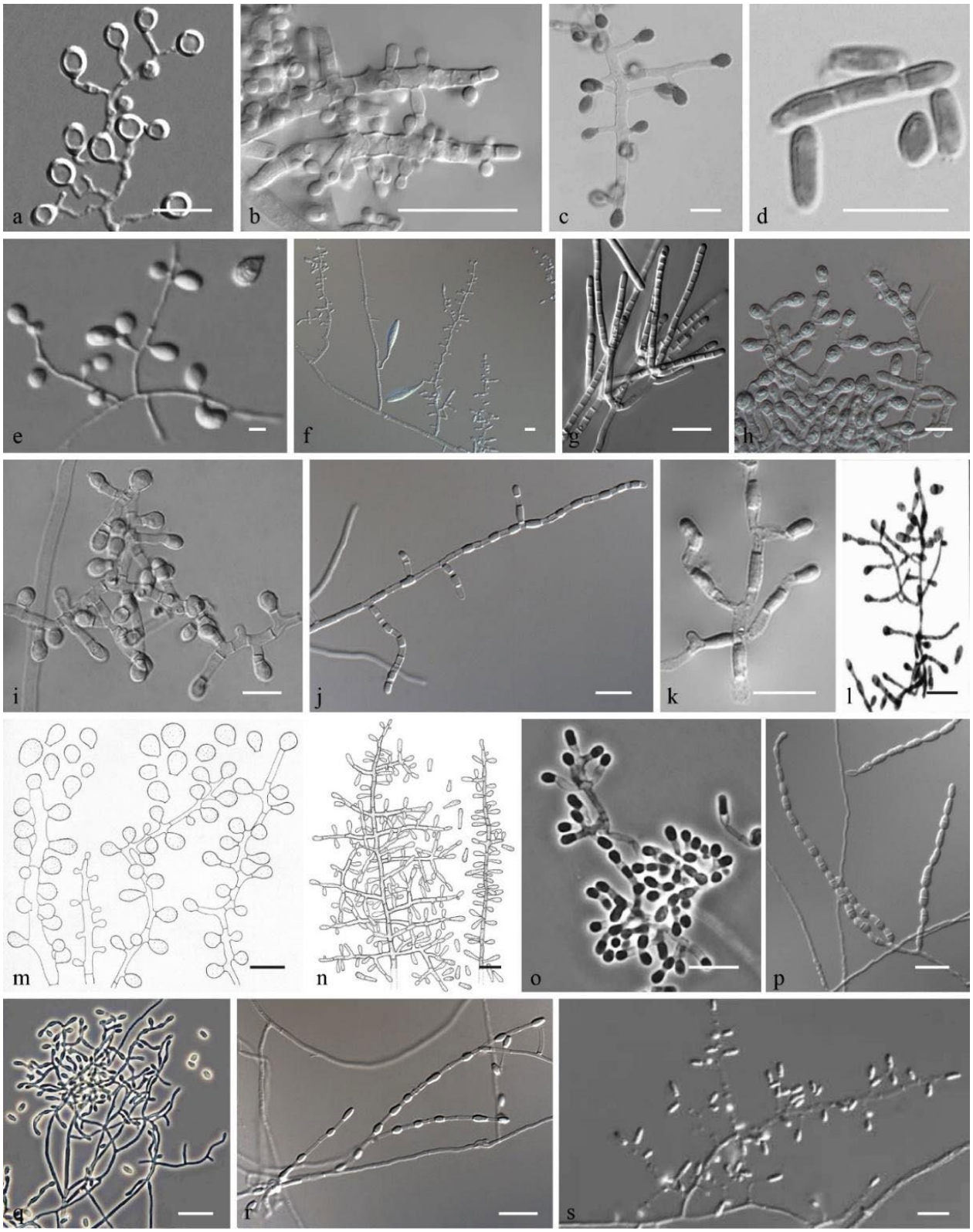


Figure 116 – Asexual morphology of *Onygenales*. a *Emmonsiellopsis coralliformis*. b *Trichophyton benhamiae* var. *luteum*. c *Arthroderma psychrophilum*. d *Arthroderma simile*. e *Ctenomyces obovatus*. f *Nannizzia gypsea*. g *Dactylodendron pluriseptatum*. h *Gymnoascus exasperates*. i *Gymnoascus flavus*. j *Malbranchea stricta*. k *Auxarthronopsis stercicola*. l *Aphanoascus jingzhouense*. m *Chrysosporium sulfureum*. n *Keratinophyton gollerae*. o *Sigleria carmichaelii*. p *Diploöspora rosea*. q *Myotisia cremea*. r *Malbranchea stricta*. s *Nannizziopsis guarroi*. Scale bars: a–s = 10 µm. a (adapted from Jiang et al. 2018); b (adapted from Čmoková et al. 2020); c, d (adapted from Moulíková et al. 2023); e (adapted from Zhang et al. 2019c); f (adapted from Dukik et al. 2020);

g (adapted from Rodríguez-Andrade et al. 2020); h (adapted from Zhang et al. 2017d); i (adapted from Zhang et al. 2021c); j (adapted from Rodríguez-Andrade et al. 2021); k (adapted from Zhang et al. 2021c); l (Zhang et al. 2017d); m (adapted from Van Oorschot 1980); n (adapted from Labuda et al. 2021); o (adapted from Hirooka et al. 2016); p (Tanney et al. 2015); q (adapted from Crous et al. 2017b); r (adapted from Rodríguez-Andrade et al. 2021); s (Stchigel et al. 2013).

Onygenales genera *Incertae sedis*
Amaurascopsis Guarro, Gené & De Vroey
Chrysosporium Corda
Harorepupu P.R. Johnst., H.D.T. Nguyen, D.C. Park & Hirooka
Leucothecium Arx & Samson
Inopinatus J. Brasch, Y. Gräser, K. Voss, K.A. Langen & A. Yurkov
Myotisia Kubátová, M. Kolařík & Hubka
Myriodontium Samson & Polon.
Polytolypa J.A. Scott & Malloch
Pseudoamaurascopsis Torres-Garcia, Dania García & Gené
Shanorella R.K. Benj.
Testudomyces Cano, M. Solé & Guarro

Evolution

Since the establishment of *Onygenales*, it is often assumed that its members all can degrade keratin, but this is not the case. In *Onygenales*, two main ways of feeding are encountered: keratinolytic and cellulolytic. According to the divergence time estimations, *Onygenales* can be considered a relatively recent evolved order (Kandemir 2022, Zhang et al. 2022d). Non-keratinolytic basal families appeared earlier than keratinophilic members of the order, suggesting that cellulolytic and osmophilic abilities might be ancestral characteristics (Kandemir 2022, Zhang et al. 2022d). In contrast, members of *Arthrodermataceae* are characteristically mammal-associated fungi with keratinolytic abilities. Therefore, the degradation of keratin and cellulose may be the main driver of the evolution of this order. In addition, significant ecological traits of *Onygenales* evolution include osmophily, thermophily, cellulolysis, eutrophism, oligotrophism, keratinolysis, and thermal dimorphism (Kandemir 2022). Osmophilia, keratolysis and thermal dimorphism are particularly important, and this may culminate in the emergence of anthropophilic species in the order *Onygenales*.

Justification of order and problems

As mentioned above, the classification of *Onygenales* has been continuously revised and improved since its establishment. With the use of a novel molecular approach, the taxonomy of *Onygenales* is becoming clearer and more stable, but need improvements. Geiser et al. (2006) transferred *Arachnomyces* to *Onygenales* based on multi-locus analyses. Later, *Arachnomyces* was included in *Arachnomycetales* (Gibas et al. 2002a). Due to inconsistencies in the molecular data used, *Spiromastigoides* was first classified in *Spiromastixales* (Rizzo et al. 2014) and later by Johnston et al. (2015) in the family *Spiromastigoidaceae* in *Onygenales*. In addition, Johnston et al. (2015) also noted that *Onygenaceae* and *Gymnoascaceae* were polyphyletic. Stchigel et al. (2013) treated *Nannizziopsidaceae* as a separate family within the *Onygenales*. Stchigel et al. (2017) based on molecular phylogeny classify *Arthrodermataceae*, *Gymnoascaceae*, *Nannizziopsidaceae* and *Onygenaceae* as *Onygenales sensu stricto*.

As with many fungal taxa, a major problem is the absence of interpretable type specimens for numerous taxa in *Onygenales*. Although Kandemir (2022) recently combined multi-locus phylogenetic, ecology, physiology, morphology, and genomics data to provide a more complete overview of *Onygenales*, describing *Arthrodermataceae*, *Ajellomycetaceae*, *Ascosphaeraceae*, *Eremascaceae*, *Gymnoascaceae*, *Onygenaceae* and *Spiromastigoidaceae* as the core families of *Onygenales*, had its limitations. Their molecular data needs to be further refined, and except for ITS and LSU, the data for the remaining loci seem to be relatively scarce for most isolates. As stated by

the authors, their results may be affected by the number of distantly related samples used in the analysis, and taxon sampling effects. In addition, molecular, morphological, and physiological data are insufficient for most species. Thus, there is a lot of work to be done, such as with *Chrysosporium*, *incertae sedis*. It is undeniable that this study is a landmark and important for the taxonomy of *Onygenales*. In the future, as data are updated and refined, continued estimation of the phylogeny and evolutionary processes of members of this order could provide a better understanding of this taxon.

Significance

Ecological and economic roles

According to Kandemir (2022), the ecological preferences of *Onygenales* species can be classified as soil/oligotrophic (soil that contains low nutrition, i.e. sandy soil, cave soil), soil/keratinophilic, dung/agricultural, skin/nail, hair/feather, insect/pollen, osmotic habitats, systemic, plant and other/unknown. Among them, the soil is the main source of *Onygenales* members, which suggests that many of these fungi have the metabolic abilities to synthesize essential amino acids (Kandemir et al. 2022). Soil plays an important role in the evolution of fungi. It harbors many micro- and macro-organisms and provides opportunities for the development of survival and dispersal abilities. Some of these abilities may later evolve as virulence factors when the fungus encounters a new host (Kandemir et al. 2022).

The order *Onygenales* is best known through the keratinolytic species in *Arthrodermataceae* and the dimorphic species in *Ajellomycetaceae*. *Arthrodermataceae* species are mainly isolated from keratinous substrates and are classified as anthropophilic, zoophilic and geophilic (Baert et al. 2020, Dukik et al. 2020). *Ajellomycetaceae* species are also isolated from soil, humans, and other mammals. In the clinical setting, they are referred to as systemic, thermally dimorphic fungi. Unlike members of the *Arthrodermataceae*, those of the *Ajellomycetaceae* are environmental pathogens that return to their environmental niche after infection to complete their life cycle (de Hoog et al. 2018). Another specialized group in *Onygenales* is the reptile-associated fungi classified in *Onygenaceae*. Adaptation to reptile skin requires different mechanisms than those required for mammalian skin, due to differences in keratin structure in the two host groups and body temperature. Bee larvae and pupa are another group of hosts that is being threatened by *Onygenales* species now classified as *Ascosphaeraceae*. In addition, adaptation to environments with high salt or low water contents can be seen in species in different taxonomic groups throughout the order *Onygenales*. Particularly, the families *Eremascaceae*, *Gymnoascaceae* and *Spiromastigoidaceae* include phylogenetically supported clusters of halophilic and xerophilic species (Kandemir et al. 2022).

Chemical diversity

To date, many compounds have been reported from members of the *Onygenales*. Several species in genera *Chrysosporium*, *Spiromastix*, *Malbranchea*, *Polytolypa*, and *Gymnascella* produce secondary metabolites such as polyketides, alkaloids, peptides, lactones, terpenoids, steroids, naphthoquinone, dihydro-naphthoquinone, chryscandin, altersolanols, queenslandon, adenopeptin, α, β-dehydrocurvularin, curvularin, benzolactone, sporandol, Spiromastilactones, vasodilator, anthrasteroid glycosides and acyl amides (Gamble & Gloer 1983, Tsipouras et al. 1997, Hayakawa et al. 1998, Kohno et al. 2001, Yang et al. 2003, Hosoe et al. 2005, Yang et al. 2009, Kumar et al. 2010, Wakana et al. 2014, Hammerschmidt et al. 2015, Niu et al. 2016, Correa et al. 2019). The ability of members of the *Onygenales* to produce such diverse metabolites may be related to their complex and diverse habitats and is the basis for their strong environmental adaptability.

Other relevant data and future recommendations

Increased awareness of the importance of taxon sampling in phylogenetic analyses and increased interest in biodiversity studies will lead to ongoing changes in the taxonomy and nomenclature of the order *Onygenales* (Kandemir et al. 2022). The physiological characteristics of the species and the choice of habitat are closely related. Although *Onygenales* is a recently diverged taxon, it has existed on Earth longer than humans, and at some point, some members encountered

animals and humans. Similar to some other fungi, they either gained new abilities or use their abilities to adapt and survive on these new hosts (Casadevall et al. 2003, Naranjo-Ortiz & Gabaldón 2019).

Almost all families of *Onygenales* have members that can be isolated from the skin and nails, which are capable of causing asymptomatic or symptomatic infections; in addition, some members are capable of growing at 37 °C and causing systemic infections (Kandemir et al. 2022). Since environmental and host changes may lead to the emergence of new fungal pathogens, these pathogens can be currently unknown species or known non-pathogenic species. In addition, these taxa may also change their reproductive patterns to adapt to new hosts. This adaptation may also manifest itself clinically, as when zoophilic species cause acute and inflammatory infections in humans, whereas infections caused by anthropophilic species are chronic and minimally inflammatory.

With the increase in captive wildlife, changes in environmental temperatures, and ongoing human activities involving soil and animals, we will likely be confronted with new fungal pathogens. Although temperature acclimation is not the only criterion for fungal virulence, soil fungi, especially taxa that can grow at 37 °C, may have greater potential because they have the opportunity to select through ongoing interactions with other soil microorganisms. Therefore, the order *Onygenales* continues to deserve close attention (Kandemir et al. 2022).

Phaeomoniellales **K.H. Chen, A.E. Arnold, Gueidan & Lutzoni, Molecular Phylogenetics and Evolution 85: 127 (2015)**

Subphylum : *Pezizomycotina*
Class : *Eurotiomycetes*
Subclass : *Chaetothyriomycetidae*

Introduction

Phaeomoniellales comprises 14 genera and approximately 40 species. It is one of the four orders in the subclass *Chaetothyriomycetidae*, along with *Verrucariales*, *Chaetothyriales*, and *Pyrenulales*, which are part of the economically important class *Eurotiomycetes* (Chen et al. 2015a). The order was named after *Phaeomoniella chlamydospora*, a grapevine pathogen associated with Petri and Esca disease (Crous & Gams 2000). The members of *Phaeomoniellales* exhibit diverse ecological roles, ranging from plant pathogens and endophytes to wood decomposers. Interestingly, this order also includes endolichenic, lichen-associated and lichen-forming fungi (Gueidan et al. 2014a, Chen et al. 2015a).

History

Most members of the *Phaeomoniellales* have been discovered relatively recently. Their inconspicuous and sometimes yeast-like asexual morphology often led to them being discarded or overshadowed by co-isolated fungi (Damm et al. 2010). The genus *Phaeomoniella*, which is a grapevine pathogen and the type genus of *Phaeomoniellales*, was established to distinguish it from *Phaeoacremonium* (Crous & Gams 2000). Subsequently, several species of *Phaeomoniella* with potential pathogenicity on fruit crops were described (Damm et al. 2010, Rossman et al. 2010). *Dolabra* was suggested by Rossman et al. (2010) to be a novel lineage within *Eurotiomycetes*. Later, Gueidan et al. (2014a) proposed using the name *Celotheliales* ad int. derived from *Celothelium*, a lichen-forming genus closely related to *Phaeomoniella*, as the name for this novel lineage. Although *Celothelium* was described the earliest of all fungi in *Phaeomoniellales*, it had limited molecular sequences available, and due to its small size, it was challenging to determine if the sequences originated from the same fungus or from physically nearby fungal materials. Gueidan et al. (2014a) mentioned that some sequences of *Celothelium* showed higher similarity to those of *Pyrenulales*, while others were more similar to *Phaeomoniella*. This uncertainty contributed to potential taxonomic instability and nomenclatural issues. By including various fungal endophytes and endolichenic fungi isolated from asymptomatic plant and lichen tissues, Chen et al. (2015a) described the order *Phaeomoniellales* following *Phaeomoniella chlamydospora*. Crous et al. (2015d) subsequently established several new genera to accommodate species that were provisionally

described under *Phaeomoniella*, including *Aequabiliella*, *Celerioriella*, *Heterophaeomoniella*, *Minutiella*, *Neophaeomoniella*, *Paraphaeomoniella* and *Pseudophaeomoniella*. Generally, the isolation of *Phaeomoniellales* fungi is rare, as evidenced by the fact that the genus *Heterophaeomoniella* has only one known isolate to date (Chen et al. 2022b). The limited number of isolates hinders our understanding of the diversity, evolution, and ecology of this fungal group. In an effort to gather more data on *Phaeomoniellales*. Kraus et al. (2020) utilized spore-trap techniques in a vineyard specifically targeting *Phaeomoniellales*. Sequencing herbarium specimens is likely to reveal fungi belonging to *Phaeomoniellales*. For example, *Paraphaeoisaria* specimens revealed molecular sequences that were nested within *Phaeomoniellales*. Further investigation is necessary to compare the morphology and ecology of *Paraphaeoisaria* with the existing genera of *Phaeomoniellales* (Chen et al. 2022b). Ongoing efforts to isolate endophytes/epiphytes and endolichenic/lichen-associated fungi continue to uncover new isolates of *Phaeomoniellales*, contributing to our expanding knowledge of this fungal group (Lee et al. 2006, Peršoh & Rambold 2012, Lacerda et al. 2018, Bowman & Arnold 2021, Steel et al. 2022).

General description

Sexual morphs have only been observed in *Celothelium*, *Dolabra*, and *Moristroma*. These genera are characterized by blackish, perithecial ascomata. *Celothelium* is a crustose lichen with immersed perithecia that are hemispherical, sometimes flattened or elongated, with or without thallus (Aguirre-Hudson 1991, Aptroot et al. 2008a). *Dolabra* and *Moristroma* have aggregated perithecia, with *Dolabra* found on living tree bark and *Moristroma* on dead trunks (Nordén et al. 2005, Rossman et al. 2010). The morphology of ascospores varies significantly among these three genera. Ascospores of *Celothelium* are filiform and multiseptate, while those of *Dolabra* are aseptate and cylindrical. *Moristroma* produces unicellular, oblong ascospores. In the asexual morphs, conidia can be produced directly on the mycelium or enclosed within pycnidia and acervuli. In most genera of *Phaeomoniellales*, the conidia are hyaline or pigmented, aseptate, smooth, and straight (Crous et al. 2015d). Microconidia and microcyclic conidiation are sometimes observed (Chen et al. 2015a, Damm et al. 2010). However, *Dolabra*, *Xenocylindrosporium*, and *Celothelium* have distinct conidia shapes compared to the rest of the order. The conidia of *Xenocylindrosporium* are curved, tapering to an acutely rounded apex and a truncate base, and they can be aseptate or septate (Crous & Verkley 2009, Spies et al. 2020). *Dolabra* produces long fusiform conidia with up to five septa, featuring a slightly truncated base and a rounded apex (Rossman et al. 2010). Aguirre-Hudson (1991) described *Celothelium* specimens as having conidiomata ranging from pycnidial to stromatic based.
The macroconidia of *Celothelium* are hyaline, aseptate to multiseptate, and filiform. Currently, there is no knowledge of an asexual morph derived from pure cultures of *Celothelium*. If *Celothelium* can be successfully cultured, future investigations into its asexual morphs, coupled with verified molecular data, would significantly advance our understanding of *Phaeomoniellales* (Fig. 117).

Sexual morph: *Ascomata* perithecial, black, aggregated or singular. *Thallus* crustose if present. *Pseudoparaphyses* abundant. *Asci* cylindrical to clavate, or ellipsoid, bitunicate. *Ascospores* oblong to cylindrical, straight or curved, aseptate or multiseptated, hyaline. Asexual morph: *Conidiomata* when present, pycnidial or acervular. *Conidiogenesis* enteroblastic or holoblastic, *Conidia* hyaline or pigmented, oblong-ellipsoidal, or cylindrical, straight or curved, aseptate or multiseptate. Microconidia and chlamydospores sometimes present. Yeast-like budding phenomenon has been reported. Colony surface white, grey, green, orange or pale yellow, sometimes slimy.

Families included in *Phaeomoniellales*

Celotheliaceae Lücking, Aptroot & Sipman (=*Phaeomoniellaceae* P.M. Kirk)

Phaeomoniellales genera *incertae sedis*
Dolabra C. Booth & W.P. Ting
Heterophaeomoniella L. Mostert, C.F.J. Spies, Halleen & Gramaje
Vredendaliella C.F.J. Spies, Moyo, Halleen & L. Mostert

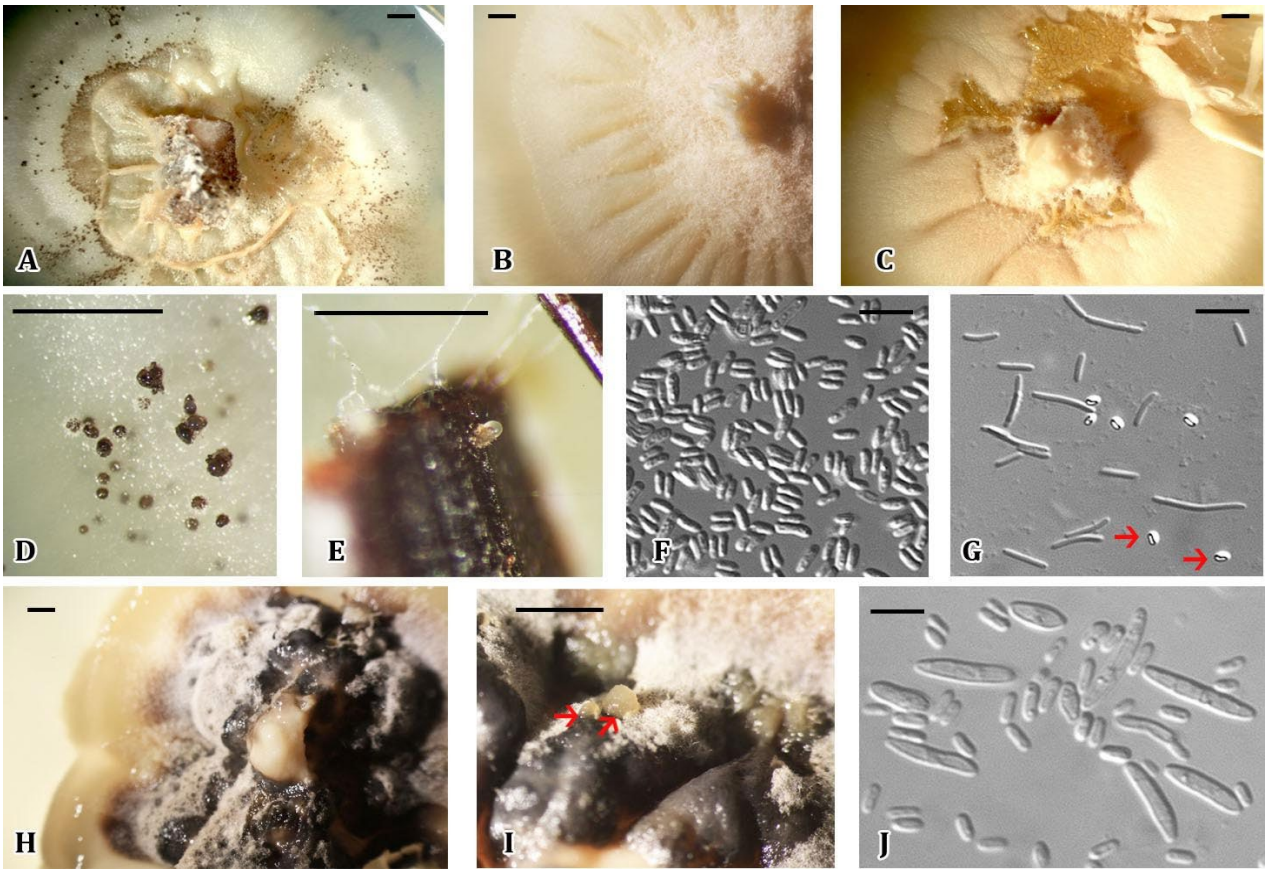


Figure 117 – Morphological and anatomical features of endophytic and endolichenic *Phaeomoniellales* strains. A. AZ0857 (OTU AZ0963) Colony morphology on 2% MEA after 90 days. Colony pale yellow, moist to mucoid, yeast-like, with black dots representing growing pycnidia. B. AZ0993 (OTU AZ0963) – Colony morphology on MEA after 90 days. Colony white to pale yellow, velvet hyphae folded toward the center. C. NC1564 (OTU 4466) – Colony morphology on MEA after 90 days. Colony pale yellow, folded irregularly, with buff region representing exposed sporulating areas. D. AZ0857 (OTU AZ0963) – Black pycnidia. E. 9352 (OTU FL0086) – Pycnidia and conidial masses on pine needle. F. AZ0871 (OTU AZ0963) – Conidia. G. AZ0952 (OTU AZ0963)– Conidia-like structures (red arrows). H. FL0854 (OTU FL0854) – Colony morphology on MEA after 90 days. Pale yellow, blackened from the center, raised, moist but with velvet regions. I. FL0854 (OTU FL0854) – Pycnidia-like structure (red arrows) on the surface. J. FL0854 (OTU FL0854)– Conidia-like structures (the biggest and disformed cells) and conidia (small uniform bacilliform cells). Scale bars: A, B, C, D, H, I = 1mm, E = 0.5 mm, F, G, J = 5 µm. The figure was originally published in Chen et al. 2015a. OTU = Operational Taxonomic Unit, defined in Chen et al. 2015a. OTU AZ0963: Endophytic, OTU 4466: Endophytic, OTU FL0854: Endolichenic, OTU FL0086: Endophytic.

Evolution

Fungi belonging to the *Phaeomoniellales* order exhibit diverse ecological roles. While most known species are associated with living plants as endophytes or plant pathogens, or with dead plants as saprobes, some are associated with lichen or are lichen-forming fungi, such as *Celothelium*. In Chen et al. (2015a), despite lacking strong support, the first split within *Phaeomoniellales* forms a clade composed of *Celothelium* and an endolichenic fungus. It is worth noting that *Celothelium* is characterized by reduced lichen structures (Aptroot et al. 2008a, Gueidan et al. 2014a). These observations suggest that *Phaeomoniellales* might interact with the photobiont of lichen, likely green algae. The diverse ecological roles played by *Phaeomoniellales* make it an ideal model for studying the evolutionary transitions of various features. For example, by studying the endolichenic isolate and the lichen-forming fungi, valuable insights can be gained into how lichen-forming fungi evolved

or were lost in the first place. Looking at the host and trophic switches from plants to lichens or endophytes to pathogens also presents an intriguing research avenue. However, the enigmatic nature of *Phaeomoniellales* poses challenges in their collection and isolation. More sampling efforts, particularly focusing on the understudied lichen-associated and lichen-forming clades, are necessary to obtain a clearer understanding of the evolutionary history of *Phaeomoniellales*.

Justification of order and problems

The members of the *Phaeomoniellales* order share similar asexual morphologies. For instance, their conidia are typically oblong to cylindrical and often hyaline. Yeast-form conidia are also frequently observed. Conidial masses can be found within pycnidia or acervuli, or directly on the mycelium (Aguirre-Hudson 1991, Rossman et al. 2010, Crous et al. 2015d, Chen et al. 2015a). Phylogenetic analyses based on molecular data, whether using a single locus (such as the nuclear ribosomal large subunit) or multiple loci, consistently support *Phaeomoniellales* as a clade sister to a clade containing *Verrucariales* and *Chaetothyriales* (Chen et al. 2015a). The family *Phaeomoniellaceae* was established shortly after the description of *Phaeomoniellales* (Kirk 2015). However, its validity as a name is questionable due to the prior description of *Celotheliaceae* (Kraus et al. 2020). While the clade of *Celothelium* might represent the first split from *Phaeomoniellales*, it is not well-supported by the current data (Chen et al. 2015a). In the literature, researchers have used both family names interchangeably (e.g., *Celotheliaceae*: Kraus et al. 2020, *Phaeomoniellaceae*: van Dyk et al. 2021). As further data becomes available for *Celothelium*, it is possible that additional well-defined lineages will be recognized, potentially leading to the identification of two or more-family names in the future.

Significance

Ecological and economic roles

Several genera within *Phaeomoniellales*, such as *Aequabiliella*, *Phaeomoniella*, *Celerioriella*, *Dolabra*, *Minutiella*, and *Neophaeomoniella*, have been identified as probable pathogens of economically important trees, including plums, grapevines, olives, *Eucalyptus*, rambutan, and lychee (Damm et al. 2010, Rossman et al. 2010, Crous et al. 2015d, Spies et al. 2020, van Dyk et al. 2021). Among them, *Phaeomoniella chlamydospora* is particularly notorious, as it negatively impacts grapevine health in Europe, America, and Africa (Crous & Gams 2000, Abreo et al. 2011, Martín et al. 2012, Gubler et al. 2020). Some species within the genera *Paraphaeomoniella*, *Heterophaeomoniella*, and *Xenocylindrosporium* were isolated from symptomatic or asymptomatic gymnosperms, such as *Encephalartos* and *Pinus* (Lee et al. 2006, Crous & Verkley 2009, Crous et al. 2015d). Additionally, endophytic isolates, especially with gymnosperms, have been reported within *Phaeomoniellales*, although most of these endophytes have not yet been officially described or diagnosed at the species level (Chen et al. 2015a). Certain genera within *Phaeomoniellales* have shown the ability to infect plants with different growth forms or lineages. For instance, *Neophaeomoniella* has primarily been found in angiosperm trees, but *N. niveniae* was isolated from *Nivenia stokoei*, a shrub, and *N. zymoides* has been reported from *Pinus* (Crous et al. 2015d). While most diseases associated with *Phaeomoniellales* occur on tree trunks, several genera have been isolated from leaf spots (Crous & Verkley 2009, Crous et al. 2015d, 2021b).

Members of *Phaeomoniellales* have also been reported in association with unique plants, such as *Xenocylindrosporium* kirstenboschense on *Encephalartos* and *Neophaeomoniella niveniae* on *Nivenia*, both causing leaf spot symptoms (Crous & Verkley 2009, Crous et al. 2015d). Although these two *Phaeomoniellales* species are not known to cause widespread disease, the symptoms they induce warrant further monitoring. The genus *Moristroma* mainly consists of wood-inhabiting fungi, indicating their saprotrophic nature (Nordén et al. 2005). Finally, *Celothelium* encompasses lichen-forming fungi, described to have minimal to zero lichenization, with pyrenocarpous ascomata (Aptroot et al. 2008a, Gueidan et al. 2014a). Overall, *Phaeomoniellales* encompasses a diverse array of trophic modes and host associations, ranging from saprobes, endophytes, plant pathogens,

endolichenic fungi, and lichen-forming fungi. These features make *Phaeomoniellales* an ideal group to study the loss and gain of pathogenicity, and the transition of lichenization processes.

Chemical diversity

Among all members of *Phaeomoniellales*, *Phaeomoniella clamydospora* is the most studied for its chemical properties. In a study by Morales-Cruz et al. (2015), the genomes of three trunk pathogens were analyzed, revealing differences in the expansion of Carbohydrate-Active Enzymes (CAZymes). *Phaeomoniella chlamydospora* exhibited the least expansion of CAZymes among the three genomes. It has been reported that *Phaeomoniella chlamydospora* produces toxins and extracellular enzymes, some of which may contribute to its pathogenicity (Marchi et al. 2001, Andolfi et al. 2011). Little is currently known about the chemical diversity within *Phaeomoniellales*. Given their diverse ecological roles, it is likely that different chemical profiles are present among the various members of this fungal order. Exploring the chemical diversity within this fungal group will shed light on their potential bioactive compounds and their implications in various ecological interactions.

Other relevant data and future recommendations

It is crucial to obtain further isolates for comprehensive studies to unravel the evolutionary relationships and understand the diverse ecological roles and host associations within the order *Phaeomoniellales*. Specifically, obtaining additional information on the lichen-forming *Celothelium*, including morphological and molecular data, would significantly contribute to resolving the relationships between different genera within *Phaeomoniellales* (Chen et al. 2015a). *Phaeomoniellales* may have a wide distribution in nature beyond their known associations with healthy plants and lichens. Systematic sampling approaches, such as spore-trap-based methods and isolation of endophytes/endolichenic fungi, can expand our knowledge of the distribution of *Phaeomoniellales* (U'Ren et al. 2010, Chen et al. 2015a, Kraus et al. 2020). Leveraging the increasing availability of molecular data generated from environmental sampling can help us understand the presence and abundance of *Phaeomoniellales* in different environments, potentially uncovering new ecological roles of these fungi in the ecosystem (Vanga et al. 2022). Additionally, studies investigating the potential symbiotic or commensal relationships between the fungus and its host, beyond the pathogenic fungi, are crucial to understanding the full spectrum of interactions between *Phaeomoniellales* and their hosts. By investigating the genomic characteristics and functional traits of these fungi, we can gain deeper insights into their adaptations, interactions, and potential contributions to their respective ecosystems. In conclusion, a multi-faceted approach involving morphological, molecular, ecological, and genomic studies is necessary to unravel the evolutionary relationships, ecological roles, and host associations within *Phaeomoniellales*.

Pyrenulales **Fink ex D. Hawksw. & O.E. Erikss., Systema Ascomycetum 5(1): 182 (1986)**

Subphylum : *Pezizomycotina*
Class : *Eurotiomycetes*
Subclass : *Chaetothyriomycetidae*

Introduction

Pyrenulales is the one of two lichenized orders in the *Eurotiomycetes*. It comprises ~300 species assigned to 15 genera (Lücking et al. 2017, Wijayawardene et al. 2020).

History

The first species were described in genus *Pyrenula* by Acharius (1803). Later on, several other genera were described that were attributed to the family, of those eventually turned out to belong to the unrelated *Trypetheliales*. Harris (1989) was the first to define the *Pyrenulaceae* and the genus *Pyrenula* in its current sense. Aptroot (1991a) made a world monograph of the family, except for the species of the larger genera, for which a world key was published later (Aptroot 2012). This allowed for the first time for the identification of specimens of this group, and as a result, relatively many additional species were described in the last decade (e.g., Aptroot et al. 2013b, Mendonça et al. 2016).

Around 14 other genera are currently accepted, mostly small genera described recently. An identification key was recently published for all species currently accepted in this family and the similar family *Trypetheliaceae* (Aptroot 2022), in total keying out around 750 species and thus the largest existing key for tropical fungi. In conjunction with this, a four-volume book comprising 2081 pages (Schumm & Aptroot 2022) was published with detailed illustrations of over half of the accepted species, many of which illustrating type specimens.

General description

The order is mostly characterized by the perithecioid ascomata with a clypeus, the simple paraphyses and the distoseptate brown ascospores. Only the two representatives of two genera that are doubtfully included in the order deviate in the ascospores. The taxa within the order are mostly characterized by their ascospores (septation; presence of eusepta in addition to distosepta; granules within the wall; color, size and shape; gelatinous sheath), ascospore ontogeny (Aptroot et al. 2013b), size and shape of the ascoma, ascomata simple, or fused sideways or with fused ostioles, ostiole position (apical, skewed, lateral), presence or absence of pseudocyphellae (actually clusters of calcium oxalate crystals); and secondary chemistry (yellow, orange or red anthraquinones, lichexanthone or nil).

Lichen-forming with trentepohlioid green, or more rarely saprobic; usually on bark, rarely on wood or rock. Sexual morph: *Thallus* usually superficial on the substratum, more rarely immersed, composed of hyphae and trentepohlioid green algae. *Ascomata* perithecia, solitary or aggregated, round, superficially variously colored (by pruina) but usually wall carbonized at least above (clypeus). *Hamathecium* composed of paraphyses. *Asci* often 8-spored, but varying between 1-spored and 8-spored, cylindrical to fusiform or clavate, incompletely bitunicate. *Ascospores* usually ellipsoidal or fusiform, distoseptate, usually some shade of brown, often surrounded by a gelatinous sheath. Asexual morph: coelomycetous. *Conidiomata* frequently present, pycnidial, developing on the same thalli as the perithecia, usually immersed, globose, coriaceous, with a single locule, dark brown to black, ostiolate. *Conidiomata wall* carbonized. *Conidiophores* lining the inner cavity or reduced, septate, simple. *Conidiogenous cells* phialidic, discrete, lageniform, hyaline to pale yellow, smooth, producing microconidia. *Conidia* hyaline, aseptate, usually linear, without appendages (Fig. 118).

Families included in *Pyrenulales*

Pyrenulaceae Rabenh.

Pyrenulales genera *Incertae sedis*
Rhaphidicyrtis Vain.
Xenus Kohlm. & Volkm.-Kohlm.

Evolution

The genus *Pyrenula* is the only large genus in the order and represents the core group. It is invariably lichenized with trentepohlioid algae. Some of the small satellite genera are non-lichenized. Several attempts have been made to reconstruct the phylogeny of the order (Weerakoon et al. 2012, Gueidan et al. 2016, Miranda-González et al. 2022). However, only a small fraction of the accepted species has been sequenced, and representatives of only about half of the genera. The phylogeny shows that there are well-defined clades, but some are inside the large genus *Pyrenula*, and others like *Lithothelium* are even polyphyletic in the current sense. The non-lichenized *Granulopyrenis* clusters as sister group to the core taxa, which may well mean that lichenization originated within the order, in a relatively early period in the evolution of the group. Several characters, including the formation of a mazaedium, occurred several times within the group, apparently at relative late stages of the evolution.

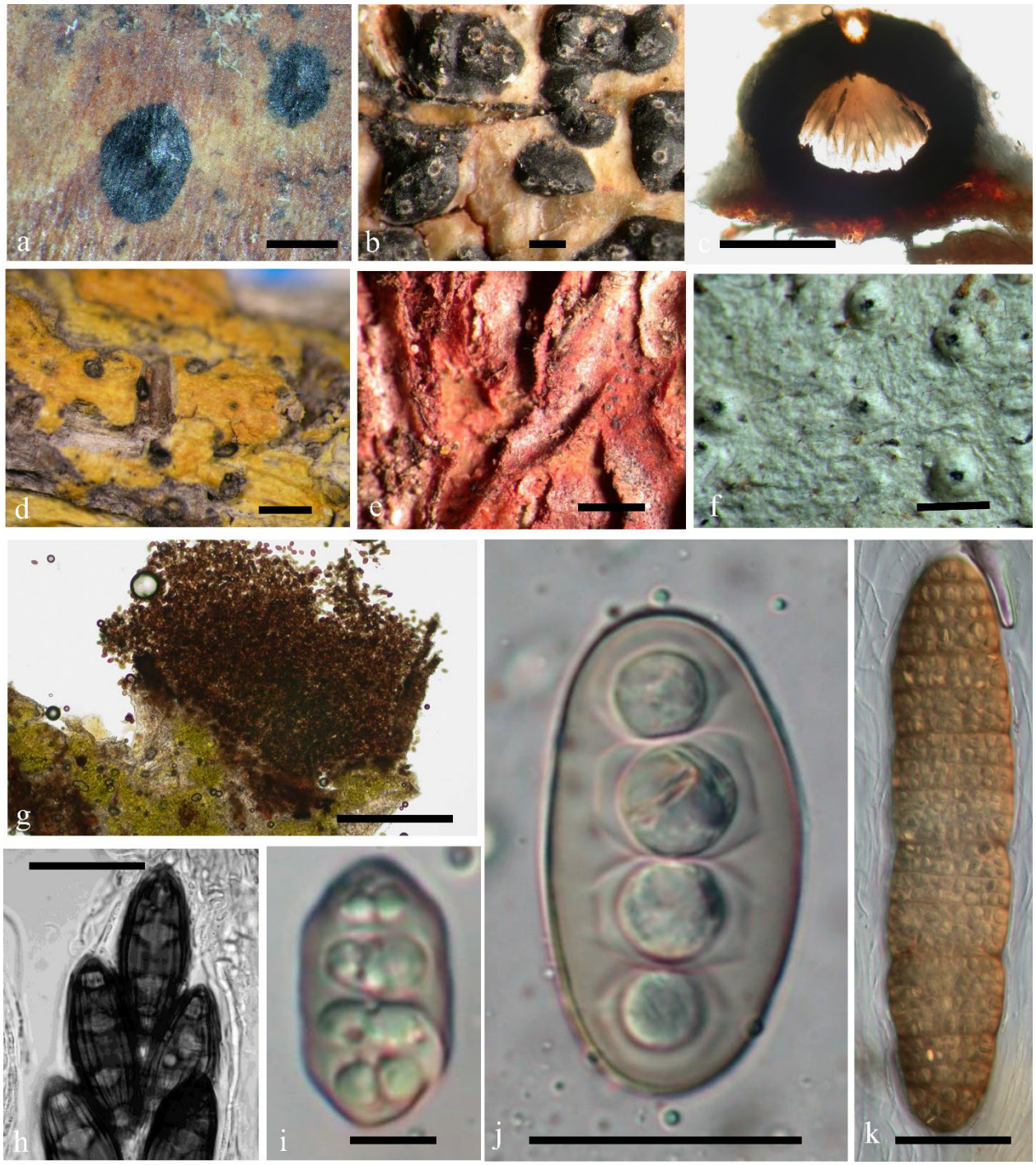


Figure 118 – Morphology of *Pyrenulales.* a Solitary perithecia with a clypeus (*Pyrenula minoides*). b Fused perithecia into a pseudostroma, with separate ostioles (*Pyrenula infraleucotrypa*). c Section through a perithecium without clypeus but with a cleare ostiole, continuous carbonization underneath the hamathecium (*Pyrenula globifera*). d Bright yellow thallus due the anthraquinone parietin (*Pyrenula plicata*). e Bright red thallus due the anthraquinone draculone (*Pyrenula rubronitidula*). f Perithecia that are almost completely covered by thallus (*Pyrenula albonigra*). g Secthion through an ascoma in which discharged spores are ammassing, called a mazaedium (*Mazaediothecium serendipiticum*). h Ascospores with ribs and and internal diamond-shaped distoseptation (*Pyrenula plicata*). i Submuriform distoseptate ascospore (*Pyrenula viridipyrgilla*). j 3-septate distoseptate ascospore (*Pyrenula aggregataspistea*). k Massive muriform ascospore (*Pyrenula monospora*). Scale bars: a, b, d, e, f = 1 mm, c, g = 0.5 mm, h, j, k = 50 µm, i = 10 µm.

Significance

Ecological and economic roles

The taxa are distributed worldwide except for (ant)arctic, alpine and boreal regions, with the highest diversity on bark in the tropics. Most of the species is lichen-forming with trentepohlioid algae.

Chemical diversity

The secondary chemistry in the *Pyrenulales* is not very diverse; most species are devoid of specific substances, quite many contain lichexanthone and a few dozen contain yellow, orange or red anthraquinones (e.g., Mendonça et al. 2016), including draculone.

Sclerococcales Réblová, Unter. & W. Gams, Mycological Progress 16(1): 34 (2016) [2017]

(=*Dactylosporales* Ekanayaka, E.B.G. Jones, Q. Zhao & K.D. Hyde)

Subphylum : *Pezizomycotina*
Class : *Eurotiomycetes*
Subclass : *Sclerococcomycetidae*

Introduction

Sclerococcales comprises >100 accepted species, being *Sclerococcum* the most speciose genus with 95 species. *Sclerococcales* was introduced by Réblová et al. (2017) for a strongly supported clade within the *Eurotiomycetes* (Chen et al. 2015a). *Sclerococcales* comprises a single family, *Dactylosporaceae*, and has been centered in the genus *Sclerococcum*, most of the species of which are teleomorph-based and previously treated in *Dactylospora* (Hafellner 1979). Several studies have reported that other anamorphic fungi belong to the same lineage (Diederich et al. 2013, Pino-Bodas et al. 2017, Réblová et al. 2017). As currently circumscribed, *Sclerococcales* is a heterogeneous assemblage of fungi containing teleomorphic and anamorphic fungi that are symbiotic lichenicolous, fungicolous, hepaticolous, saprotrophic, or gut-associated (Vargas-Asensio et al. 2014). The distribution of taxa within *Sclerococcales* is cosmopolitan, with most occurring on dead wood, lichens, or fungi (Hafellner 1979).

History

The first genus of *Sclerococcales*, *Sclerococcum* was coined for a fungus producing sporodochia on lichen thalli with *Sclerococcum sphaerale* as the type (Fries 1825). The long-established circumscription of *Sclerococcum* remained stable and included anamorphic hyphomycetous fungi producing blackish sporodochia with multicellular conidia. Until recently, a handful of species were placed in it (Hawksworth 1975, 1979, Diederich et al. 2013). In parallel, the teleomorph-based apothecial *Dactylospora* was described with a lichenicolous species, *Dactylospora floerkei*, as the type. *Dactylospora* served for decades to accommodate species producing black apothecia, until Hafellner (1979) defined the genus to include species with asci of which have an apical gelatinous cap instead of an inner amyloid wall thickening. Hafellner (1979) included lichenicolous, fungicolous and saprotrophic species in *Dactylospora*. Diederich et al. (2013) and Pino-Bodas et al. (2017), based nuclear ribosomal and mitochondrial markers, reported that the types of *Sclerococcum* and *Dactylospora*, *Sclerococcum sphaerale* and *Dactylospora parasitica* (Flörke) Arnold (= *D. floerkei*), respectively, belonged to the same clade. Diederich et al. (2018) combined the lichenicolous species of *Dactylospora* in *Sclerococcum* and Olariaga et al. (2019) did so with remaining non-lichenized species. *Sclerococcum*, together with the also apothecioid *Pseudosclerococcum* differing from apothecioid species *Sclerococcum* in having cylindrical hemiamyloid asci and a chalara-like anamorph (Olariaga et al. 2019), form the core of the *Sclerococcales*.

Although evolutionary lineage containing *Sclerococcum* was already recovered by Schoch et al. (2009a) and Chen et al. (2015a), Réblová et al. (2017) was the first that formally recognized it and named it as *Sclerococcales*. Réblová et al. (2017), also discovered that two dematiaceous phialidic

fungi (*Rhopalophora clavispora* and *Fusichalara minuta*) and a third lineage comprising several strains isolated from digestive tracts of beetles, were basal to the *Sclerococcum* clade. Yu et al. (2018) described the new aquatic hyphomycete *Cylindroconidiis aquaticus* and found it to be closely related to *Rhopalophora clavispora* and *Fusichalara minuta*. Provided that molecular sampling among hyphomycetous fungi is poor, more genera are likely to belong to *Sclerococcales*. Although published phylogenies have a well-supported topology, none of the basal lineages has been described as a separate family.

General description

Sexual morphs of *Sclerococcales* are characterized by having black discs of hard consistency. *Sclerococcum martynii* is unusual in that the discs are produced in branched, caespitose stromatic structures (Haelewaters et al. 2022b). Spores that are usually 1-septate to muriform and pigmented. Asci are covered by a gelatinous matter that shows an amyloid or hemiamyloid reaction (Olariaga et al. 2019). Asci are usually non-fissitunicate and lack an endoascal thickening and elongation during discharge (Bellemère & Hafellner 1982), as opposed to the fissitunicate asci in *Pseudosclerococcum* (Olariaga et al. 2019). Asexual morphs of *Sclerococcum* are sporodochial producing multicellular conidia when known, whereas a chalara-like asexual state was described for *Pseudosclerococcum*. Interestingly, only asexual morphs of basal taxa of *Sclerococcales* are known. Asexual morphs of basal taxa are mononematous, unbranched, producing conidia at tips of brown phialides, and assigned to the genera *Cylindroconidiis*, *Fusichalara* and *Rhopalophora* (Réblová et al. 2017, Yu et al. 2018).

Sexual morph: *Thallus* absent, but ascomata growing sometimes on bleached lichen thalli, fungi or liverworts. *Ascomata* apothecial, usually sessile or shortly stalked, clearly stalked o placed on a branched stroma in a *S. martynii* (Wakef.) Haelew. Stallman & Aime, disc-shaped, plane, proper margin usually present. *Hypothecium* hyaline to pigmented. *Excipulum* well developed, usually pigmented, sometimes changing color in KOH. *Hymenium* hyaline to brown, comprising sparingly branched paraphyses and asci. *Paraphyses* usually swollen at the tips. *Epihymenium* usually present, formed by crystallized deposits on paraphyses that do not dissolve in KOH. *Asci* cylindrical to clavate, non fissitunicate or fissitunicate, covered with an amyloid or hemiamyloid gel, eight to multi-spored. *Ascospores* ellipsoid to fusoid, thin-walled to slightly thick-walled, 1-septate to muriform, usually sometimes slightly constricted at the septum, hyaline to dark brown, smooth, warted or striate. Asexual morph: sporodochial or phialidic (Fig. 119).

Families included in *Sclerococcales*

Dactylosporaceae Bellem. & Hafellner (= *Sclerococcaceae* Réblová, Unter. & W. Gams)

Evolution

The ascoma type of the ancestor of the *Eurotiomycetes* was reconstructed as open hence apothecioid by Prieto et al. (2020) and, as only apothecioid ascomata are known within *Sclerococcales*, it is assumed here that its ancestor was also apothecioid. A remarkable fact is that no sexual morphs are known for basal clades of *Sclerococcales*. Within the highly diverse *Eurotiomycetes* with regard to trophic modes (Chen et al. 2015a),), basal lineages of *Sclerococcales* appear to be saprobic due to inhabiting dead wood (Réblová et al. 2017, Yu et al. 2018). Besides a high number of lichenicolous species of *Sclerococcum* that are biotrophic, many species of *Sclerococcum* grow in specific association with liverworts (Zukal 1891, as *Paruephaedria heimerlii*) or fungi (Hafellner 1979) that suggest also a biotrophic/symbiotic life-mode. Species of *Sclerococcum* and *Pseudoscleroccum golindoi*, considered as saprobes, occur typically together with other fungi and it is likely that at least some of them are biotrophic. A remarkable fact is that several *Sclerococcum* species are desiccation tolerant and are occur on seasonally dry lichens of bark of trees (Sarrión et al. 2002). With regard to asci, non-fissitunicate and fissitunicate asci are known in *Sclerococcales* (Olariaga et al. 2019) but the evolution of this trait remains uncertain.

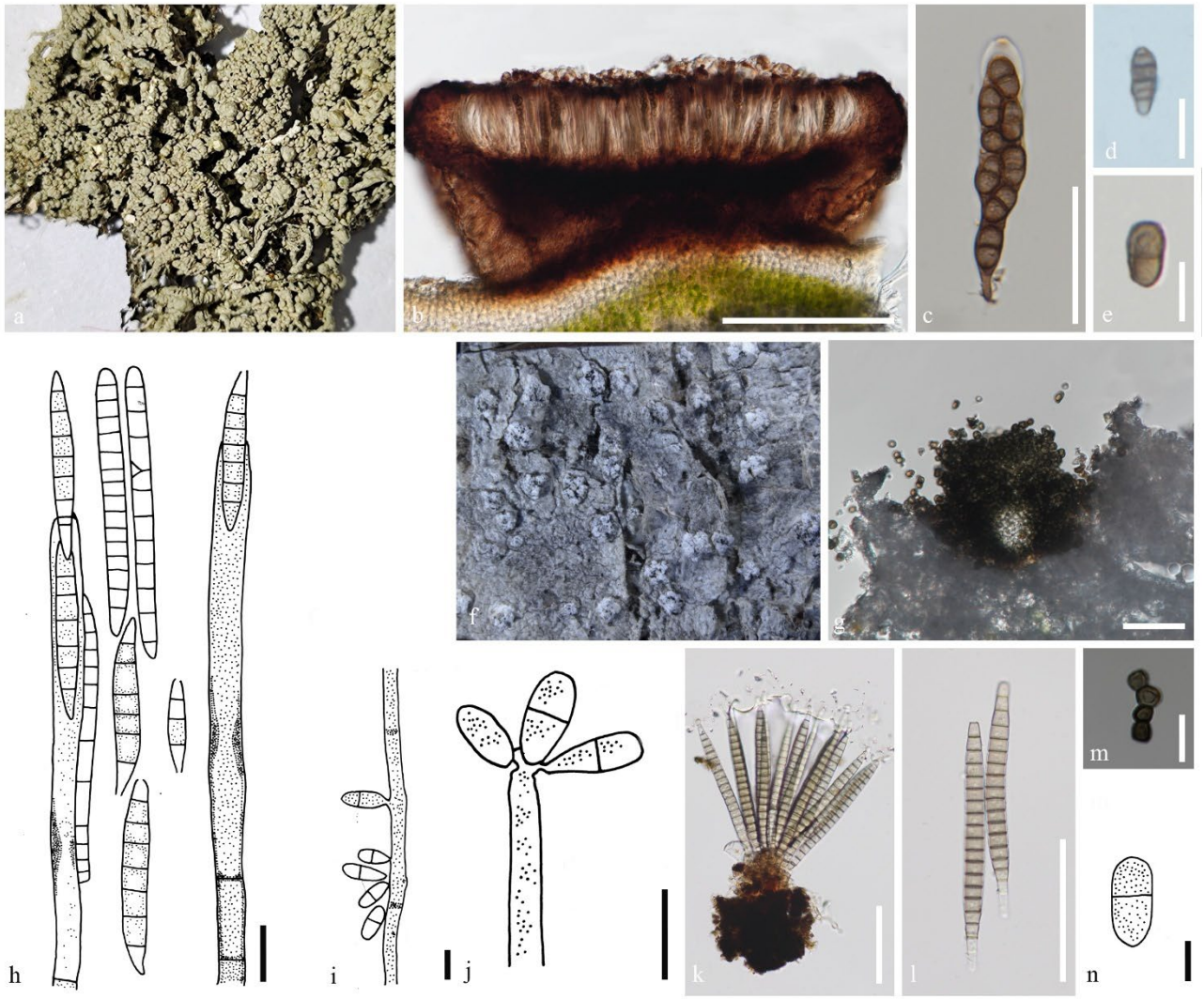


Figure 119 – Sexual and Asexual morphs of *Sclerococcales.* a Morphology of thallus (*Sclerococcum glaucomarioides*). b Sections through ascoma (*Sclerococcum* sp.). c Ascus (*Sclerococcum* sp.). d, e Ascospores (d *Sclerococcum glaucomarioides*, e *Sclerococcum* sp.). f Conidiomata of host surface (*Sclerococcum simplex*). g Sections through Conidioma (*Sclerococcum simplex*). h Phialides and dimorphic conidia (*Fusichalara dimorphospora*). i Conidiogenous cells with pleurogenic conidia. j Conidiogenous cells with acrogenous conidia (i, j *Cylindroconidiis aquaticus*). k Conidiophores bearing conidia (*Pseudobactrodesmium aquaticum*). l Conidia (l *Pseudobactrodesmium aquaticum*, m *Sclerococcum simplex*, n *Cylindroconidiis aquaticus*) (redrawn from Hughes & Nag Raj 1973, drawn from Yu et al. 2018). Scale bars: b = 100 µm, d, e, n = 10 µm, c, g, j = 20 µm, h = 100 µm, i = 25 µm, k, l = 50 µm, m, n = 5 µm.

Justification of order and problems

Sclerococcales is a heterogeneous assemblage of fungi that is phylogenetically well-defined as several studies have recovered it as monophyletic (Réblová et al. 2017, Olariaga et al. 2019, Yu et al. 2018), despite phylogenies being based on a few molecular markers. Taxon sampling within *Sclerococcum*, a homogeneous genus regarding ascal structure and apothecial morphology, is poor. Many undescribed species of saprobic corticolous *Sclerococcum* appear to exist (Olariaga, unpublished) and more hyphomycetous species are likely to be discovered to belong to *Sclerococcales* when molecular data become available.

Significance

Ecological and economic roles

A high number of known species of *Sclerococcales* have specific hosts and inhabit a broad array of ecosystems, such as forest ecosystems, open lands colonized by lichens or stranded driftwood. Most biotrophic species appear to be xerotolerant (Olariaga et al. 2019) and a few marine species are also known (Pang et al. 2014).

Other relevant data and future recommendations

Species of *Sclerococcum* are often overlooked in the field due to their small size. Although lichen-inhabiting species have drawn more attention, non-lichenized members are poorly known especially corticolous saprobic species of *Sclerococcum*. At least five undescribed species that inhabit bark of living trees are known to exist in the Iberian Peninsula (Olariaga et al. in prep), and many more are likely to be discovered on other hosts present in other geographic areas. Critical studies including molecular data are needed to study species with a global distribution and a more comprehensive molecular sampling of species is needed to obtain a better insight on species and generic delimitation.

***Tuberculiformales* Zhi Yuan Zhang & Y.F. Han, Mycosphere 15 (1): 691 (2024)**

Subphylum : *Pezizomycotina*
Class : *Eurotiomycetes*
Subclass : *Sclerococcomycetidae*

Introduction

Tuberculiformales was introduced to accommodate a newly established family *Tuberculiformaceae* that comprises a single genus *Tuberculiforma.* The genus accommodates the type species *Tuberculiforma sinensis, Tuberculiforma catenatus* and some beetle-associated isolates (INBio4503Q, INBio4513J, and INBio4513L) (Zhang et al. 2024d).

History

Tuberculiformales was established based on morphological and molecular evidence and the order recovered a sister clade to *Sclerococcales* in the multigene phylogenetic analyses (SSU, ITS, LSU, and RPB2) (Zhang et al. 2024d). *Sclerococcales* was introduced by Réblová et al. (2017) to accommodate marine, lignicolous species of *Dactylospora*, two species of the lichenicolous genus *Sclerococcum*, and strains of beetle-associated isolates (INBio4503Q, INBio4513J, and INBio4513L). The order was assigned to a newly established subclass *Sclerococcomycetidae* within *Eurotiomycetes*. Zhang et al. (2024d) reported a new species *Tuberculiforma sinensis* from soil in Guizhou Wildlife Park, China. The taxon showed close phylogenetic association with *Anthopsis catenate* and the strains of beetle-associated isolates (INBio4503Q, INBio4513J, and INBio4513L). *Anthopsis* was originally introduced to accommodate the type species *Anthopsis deltoidea* that was isolated from soil in Italy. Later, two species, *A. catenata* and *A. microspore* were added to the genus. Moussa et al. (2017) initially provided the phylogenetic placement within *Chaetothyriales* based on the sequence data from *Anthopsis* species. *Anthopsis catenata* was characterized by inverted phialides producing pale brown, ellipsoidal to subglobose conidia in chains. The sequence data obtained from the type of *Anthopsis catenata* (CBS 492.81) recovered within *Helotiales* but with unresolved phylogenetic position (Moussa et al. 2017). The species was not accounted for in the phylogenetic analyses of Réblová et al. (2017). Previously, Vargas-Asensio et al. (2014) showed that the beetle associated isolates clustered within *Chaetothyriales* based on ITS sequence data (Vargas-Asensio et al. 2014). However, the strain CBS 492.81 formed a close clade to two beetle-associated isolates (INBio4513J, and INBio4513L) in the recent phylogenetic analyses (Zhang et al. 2024d). Further, *Tuberculiforma sinensis* and *Anthopsis catenata* showed the highest molecular identities for their LSU and ITS sequences data and the former differed from the latter in having solitary conidia (Van

Oorschot & de Hoog 1982). Consequently, *A. catenata* was synonymized under *Tuberculiforma* (Zhang et al. 2024d).

General description

The taxa are only reported from the asexual morph. However, the morphological description of the beetle associated isolates is not available (Zhang et al. 2024d) (Fig. 120).

Sexual morph: Not observed. Asexual morph: Refer Zhang et al. (2024d) for updated morphological description.

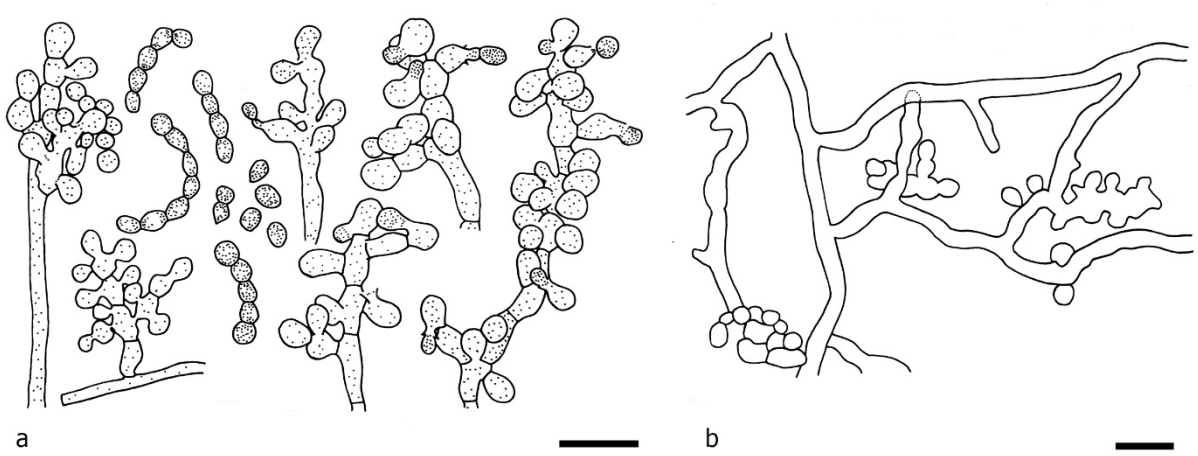


Figure 120 – Asexual morph of *Tuberculiformales.* a Conidiogenous cells and conidia of *Tuberculiforma catenatus* (=*Anthopsis catenate*) (redrawn from Van Oorschot & De Hoog 1982). b Conidiogenous cells and conidia of *Tuberculiforma sinensis* (drawn from Zhang et al. 2024d). Scale bars: a, b = 10 μm.

Families included in *Tuberculiformales*

Tuberculiformaceae Zhi Yuan Zhang & Y.F. Han

Justification of order and problems

Based on the phylogenetic analyses, the order formed a distinct clade with strong support which included the new isolates of *Tuberculiforma sinensis* (CGMCC 3.25512, ZY 22.047, ZY 22.048, and ZY22.049), *T. catenate* (CBS 492.81) and three beetle-associated isolates (INBio4503Q, INBio4513J, and INBio4513L). The author also highlighted the absence of *Anthopsis catenata* from the analyses of Réblová et al. (2017). However, the phylogenetic investigation conducted for *Anthopsis* in the same year by Moussa et al. (2017) found that *Anthopsis sensu stricto* was clustered in *Chaetothyriales*, while *T. catenate* (*A. catenate*) was considered as a member of *Helotiales*. Thus, incorporating all the members of *Anthopsis* along with the members of *Tuberculiformales* and the recollection and reinvestigation of beetle-associated fungi is also important to study the potential relationship between the members of *Eurotiomycetes*.

Significance

Ecological and economic roles

Tuberculiforma sinensis and *T. catenate* were reported from soil from China (Zhang et al. 2024d) and Germany (Van Oorschot & De Hoog 1982) respectively. The beetle-associated isolates were obtained from Costa Rica (Vargas-Asensio et al. 2014).

Chemical diversity

No relevant studies are available regarding the chemical diversity of the members of *Tuberculiformales.*

Verrucariales **Mattick ex D. Hawksw. & O.E. Erikss., Systema Ascomycetum 5(1): 183 (1986)**

Subphylum : *Pezizomycotina*
Class : *Eurotiomycetes*
Subclass : *Chaetothyriomycetidae*

Introduction

Verrucariales is an order in *Ascomycota* which comprises over 1,000 species assigned to more than 60 genera. Members of this order are ecologically diverse, with species colonizing many different substrates (rock, soil, wood, mosses, lichens while growth on wood and less common) and living in various habitats (on arid and exposed rock surfaces, on permanently immersed boulders in streams, on rocky shores in the intertidal zone). They are found at different latitudes, from the tropics to the polar regions (Gueidan et al. 2007, 2008, Holger et al. 2008, Muggia et al. 2010, Wang et al. 2014b). Although most of the *Verrucariales* are lichenised, the family *Sarcopyreniaceae* consists of 11 species of lichenicolous (lichen-dwelling) fungi (Diederich et al. 2018). Currently, almost all genera belonging to *Verrucariales* are included in *Verrucariaceae* (Eriksson 2006). *Verrucariaceae* is the third-largest family of lichen-forming fungi in *Ascomycota* (Gueidan et al. 2007). The order also represents *Verrucaria*, one of the most speciose lichenized (lichen-forming) genera (Lücking et al. 2017). *Verrucariales*, was introduced by Hawksworth & Eriksson (1986), belongs to the subclass *Chaetothyriomycetidae* of *Eurotiomycetes*. It was traditionally considered as a monophyletic group; however, many species in *Verrucariaceae* (i.e. *Verrucaria*, *Staurothele*, *Thelidium*, and *Polyblastia*) are polyphyletic and have mixed evolutionary origin and *Verrucaria* was defined using symplesiomorphic character states (such as crustose thallus and simple ascospores) (Gueidan et al. 2007). *Verrucariales* presently comprises three families *viz*. *Adelococcaceae*, *Sarcopyreniaceae*, and *Verrucariaceae*. Phylogenetic analysis suggested that *Verrucariales* has a sister relationship to the *Chaetothyriales*, an order of non-lichenised fungi and that the divergence between the lichenized *Verrucariales* and non-lichenized *Chaetothyriales* occurred about 131 MYA (Gueidan et al. 2007, 2008).

Adelococcaceae was described by Triebel (1993), Fee (1824), which presently includes three genera with *Adelococcus* as the type (Theissen & Sydow 1918). The taxa of *Adelococcaceae* are characterized by asci verrucarialean, not fissitunicate, ventricose to broadly cylindrical, shortly stipitate, with apically enlarged ascal wall without an ocular chamber (Nash et al. 2004). *Sarcopyreniaceae* was introduced by Navarro-Rosinés et al. (1998) with one genus, namely *Sarcopyrenia*. *Sarcopyreniaceae* is one of the few families composed entirely of lichenicolous fungi (Diederich et al. 2018). *Verrucariaceae* was introduced by Eschweiler (1824), taxa were distributed between two taxonomic ranks intended as names of orders, the *Dermatocarpeae* and the *Verrucariae*, based on thallus structure.

History

Some genera now classified in the *Verrucariaceae* were considered by past authors to be distinctive enough to warrant inclusion in their own family. These historical family names are considered synonymous with *Verrucariaceae* (Pérez-Ortega et al. 2010): *Endocarpaceae* Fée ex Zenker (1828), *Dermatocarpaceae* Stizenb. (1862), *Glomerillaceae* Norman (1868), *Endopyreniaceae* Zahlbr. (1898), *Mastodiaceae* Zahlbr. (1908), *Pyrenothamniaceae* Zahlbr. (1898), *Thelidiaceae* Walt.Watson (1929), *Bagliettoaceae* Servít (1954) and *Staurotheleaceae* Servít (1954).

During the past two decades, Eschweiler (1824) attempted to classify genera of *Verrucariaceae*. For these taxa, he created two 'cohors' *Verrucariae* and *Dermatocarpeae*, based mainly on the structure of the thallus. He attributed the crustose taxa to the *Verrucariae* and the squamulose and foliose taxa to the *Dermatocarpeae*. Unfortunately, Eschweiler (1824) also included many non-related genera within these two groups. In 1827, Zenker validated the family *Verrucariaceae* (at the time called *Verrucariae*), in which he included the genus *Verrucaria* and some other unrelated crustose taxa. This author also separated the squamulose and foliose taxa from the crustose *Verrucariae*, and placed them within *Endocarpa*. It was only almost one century later that the first

extensive monographic work on the family *Verrucariaceae* was published (Zschacke 1913, 1914, 1918, 1921, 1924, 1927). In 1933–1934, Zschacke recognized the two families *Verrucariaceae* and *Dermatocarpaceae* following Zahlbruckner (1921–1922) in an earlier publication. Servít worked on the *Verrucariaceae* in the late 1940s and 1950s (Servít 1946, 1950a, b, 1952, 1953, 1954), and published a classification for the entire group in 1955. In this work, he also considered the family *Dermatocarpaceae* as a separate group, and recognized four additional families (*Staurothelaceae*, *Microglaenaceae*, *Pyrenidiaceae* and *Bagliettoaceae*). However, two of these families are currently recognized in other orders as synonyms (*Microglaenaceae* is a synonym of *Thelenellaceae* and *Pyrenidiaceae* is a synonym of *Dacampiaceae* and the validity of the two other families has always been questioned, and excluded from subsequent classifications (Jahns 1973). The scarcity of additional morphological characters available for proposing a new generic system prevented the proposal of important changes in the classification. It is only recently, with the development of molecular techniques, that a new set of data became available for assessing the generic circumscription and the relevance of morphological characters in classifying species from this family.

It is only recently, with the development of molecular techniques, that a new set of data became available for assessing the generic circumscription and the relevance of morphological characters in classifying species from this family. The first molecular studies to include molecular data on *Verrucariaceae* aimed at finding the phylogenetic placement of high-rank taxa within the ascomycetes (Lutzoni et al. 2001, 2004, Liu & Hall 2004, Lumbsch et al. 2005b, Geiser et al. 2006, Spatafora et al. 2006), and showed that *Verrucariales* was sister to an order of non-lichenized fungi, the *Chaetothyriales*. Other molecular studies have mostly addressed phylogenetic relationships at the infrageneric level (Heiðmarsson 2003, Amtoft et al. 2008 for *Dermatocarpon*), and two molecular phylogenetic studies have presented that have challenged the traditional morphology based generic delimitation of this family (Gueidan et al. 2007). They confirmed that spore septation cannot be used as the main generic character by showing that none of the crustose genera *Verrucaria* (simple spores), *Polyblastia* (muriform spores), and *Thelidium* (transversally pauci- to multiseptate spores) were monophyletic. Moreover, a squamulose thallus was shown to have evolved from a crustose thallus several times independently in this family, and hymenial algae were also acquired in distantly related groups (Gueidan et al. 2007).

General description

Morphologically, species within *Verrucariaceae* are characterized by perithecial ascomata, bitunicate asci (Janex-Favre 1971) with a dehiscence occurring by gelatinization of the apical part of the outer ascus wall (Grube 1999), a hamathecium formed by periphyses located in the upper part of the ostiolar collar and short pseudoparaphyses located below and in the ostiolar collar (Janex-Favre 1971), the lack, at least at maturity, of long interascal sterile hyphae which separate them from the *Adelococcaceae*, in which long interascal sterile hyphae are persistent (Triebel 1993) and a blue reaction of the hymenial gel to potassium-iodine (Henssen & Jahns 1974). Traditionally, three main morphological characters were used to define genera within this family (Zahlbruckner 1921-1922, Zschacke 1933-1934): spore septation, thallus structure and the presence or absence of algae in the hymenium. However, this generic delimitation has been considered artificial by many authors (Servit 1946, Fröberg 1989, Nimis 1998, Poelt & Hinteregger 1993, Halda 2003). One of the major issues was the use of spore septation to circumscribe genera within this family. For example, the occasional appearance of longitudinal septa in some spores in specimens with otherwise only transverse septa (pauciseptate muriform spores) led to a great deal of confusion in attributing these specimens to a genus. In some cases, spore septation varies within species (e.g., Orange 1991) and is, therefore, also potentially problematic at the generic level. Similarly, thallus structure and the presence of hymenial algae were believed to be of limited use as synapomorphies, because of possible convergent evolution. Currently, almost all genera belonging to *Verrucariales* are included in *Verrucariaceae* (Eriksson 2006). Two other genera, also included in *Verrucariales* and characterized by their long and persistent interascal elements (paraphysoids according to Triebel 1993) in addition to their short

pseudoparaphyses, and by their lichenicolous habits, are classified in the second family of this order, *Adelococcaceae*.

Sexual morph: *Thallus* usually crustose, sometimes foliose or squamulose. *Ascomata* perithecioid, sessile or immersed in the thallus or substrate. *Ascomata* superficial, ostiolate, spherical, ellipsoid or ovate with walls of *textura angularis*, *intricata* or *epidermoidea* in surface view. *Hemathecium*, evanescent. *Pruinose* present or absent. *Hymenium* brown, free of alga. *Pseudoparaphyses* short, vertical, filament-like. *Paraphyses* sometimes swollen at the tips. *Hypothecium* hyaline to pigmented. *Excipulum* well or poorly developed, hyaline to pale brown. *Asci* fasciculate, clavate, broadly clavate or fusiform, stalked, with 8 biseriate or irregularly arranged ascospores, evanescent. *Ascospores* brown at maturity, usually fusiform, elongate ovate to ovate, with an apical or sub-apical germ pore. Asexual morph: *Pycnidia* (Figs. 121, 122).

Families included in *Verrucariales*

Adelococcaceae Triebel
Sarcopyreniaceae Nav.-Ros. & Cl.Roux
Verrucariaceae Zenker

Verrucariales genera *incertae sedis*
Botryolepraria Canals, Hern.-Mar. Gómez-Bolea & Llimona
Gemmaspora D. Hawksw. & Halici
Kalbiana Henssen
Merismatium Zopf

Evolution

In the classifications of Servıt (1955), Zahlbruckner (1921–1922), and Zschacke (1933–1934), taxa within *Verrucariales* were mainly circumscribed based on thallus structure, ascospore morphology, and the presence or absence of hymenial algae. Ancestral state reconstructions suggest *Verrucariales* as one of the independent ascomycete groups where lichenisation has evolved on a hostile rock surface that might have favored this shift to a symbiotic lifestyle (Lutzoni et al. 2001, James et al. 2006).

Justification of order and problems

Verrucariales and *Chaetothyriales* were strongly supported as sister groups in many studies (Lutzoni et al. 2001, 2004, Lumbsch et al. 2005b), even if these two orders are extremely disparate ecologically. Among the accepted families by Servıt (1955), two families are currently recognized in other orders as synonyms (*Microglaenaceae* is a synonym of *Thelenellaceae*, and *Pyrenidiaceae* is a synonym of *Dacampiaceae*) and the validity of the two other families has always been questioned(Henssen & Jahns 1973, Poelt 1973), and excluded. Although Servıt (1955) accepted the separation of the families *Verrucariaceae* and *Dermatocarpaceae* based on thallus morphology, previously he suggested the limitations of this character (Servıt 1946). Because the generic delimitation within *Verrucariaceae* is mainly based on ascospore septation and thallus structure, molecular data and a broad taxon sampling with multiple genes were needed to assess the current morphology-based classification and phylogenetic relationship within this family. Consequently, several molecular studies have been carried out on members of this family, either at the infrageneric level or in the context of large-scale molecular phylogenies (e.g., Lutzoni et al. 2001, 2004, Lumbsch et al. 2002, 2004b, 2005b, Liu & Hall 2004, Del Prado et al. 2006, Geiser et al. 2006, James et al. 2006, Spatafora et al. 2006, Gueidan et al. 2007, Muggia et al. 2010).

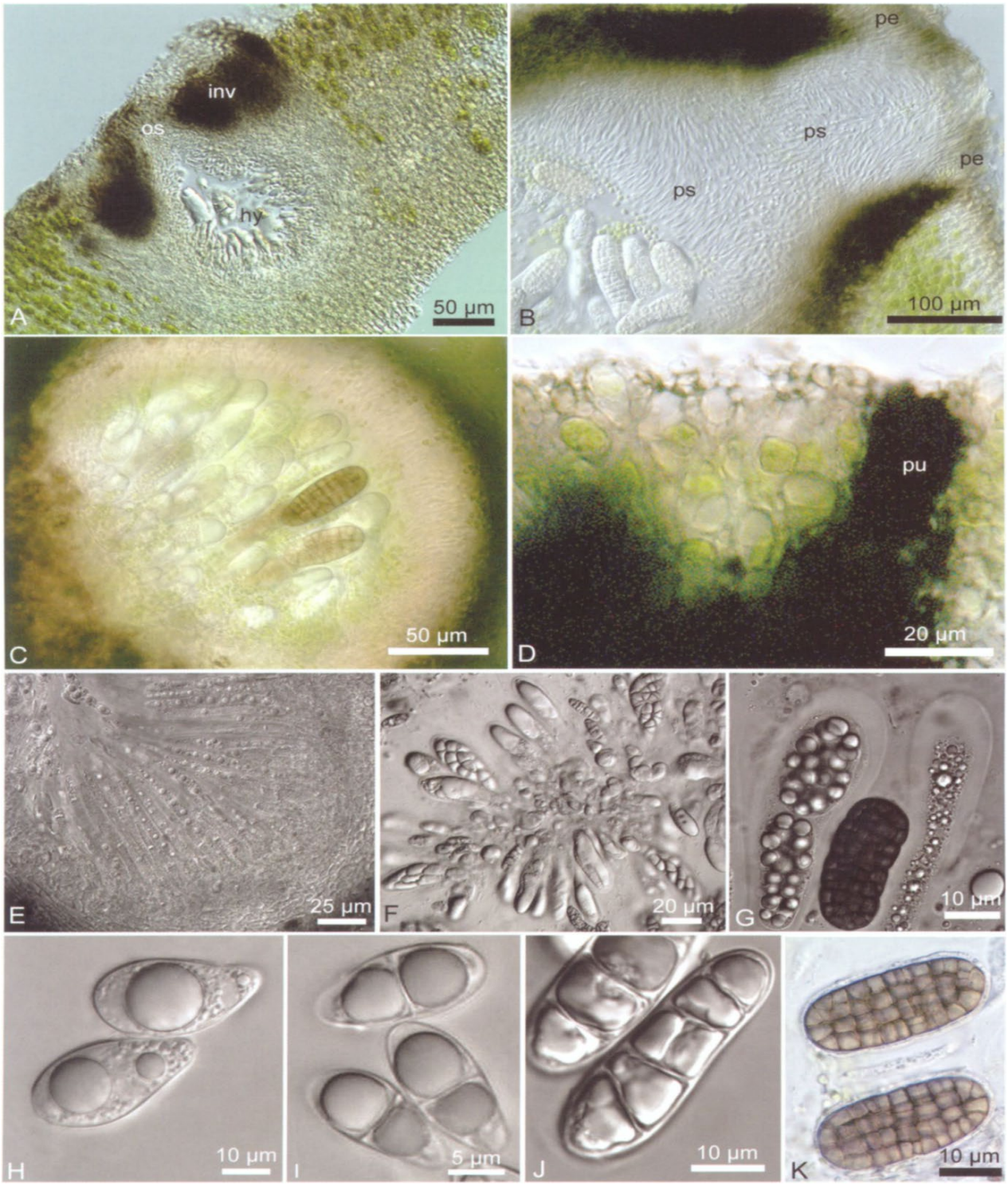


Figure 121 – Main anatomical characters of species in *Verrucariaceae*. A Cross-section of a perithecium of *Wahlenbergiella mucosa* showing an apical involucrellum (hy: hymenium; inv: involucrellum; os: ostiole). B Cross section of the ostiole of a perithecium of *Endocarpon adscendens* showing the short pseudoparaphyses (ps) and the per iphyses (pe). C Cross-section of the perithecium of *Staurothele areolata* showing small photobiont cells in the hymenium. D Cross-section of the thallus of *Hydropunctaria maura* showing a black punctum (pu). E Cross-section of a perithecium of *Placidium arboreum* showing cylindrical and uniseriate asci. F Squash mount of the hymenium of *Polyblastia viridescens* showing clavate and biseriate asci. G Thick bitunicate ascus wall in *Endocarpon pusillum*. H Simple spores in *Verrucaria hochstetteri*. I Transversally uniseptate spores in *Placidiopsis cinerscens*. J Transversally multiseptate spores in *Thelidium* sp. K Brown muriform spores in *Staurothele frustulenta* (adapted from Gueidan et al. 2008).

This rock-dwelling ancestor most likely relied on sparse nutrients provided by the winds or rain. It is possible that where unicellular free-living algae could survive on rock surfaces (mainly the northerly outcrops, which are less exposed to the sun), ancestral lineages of rock-inhabiting fungi were able to evolve symbiotic relationships with photosynthetic microorganisms to ensure a more constant source of carbohydrates. This ability to develop symbiotic interactions with unicellular free-living algae might have allowed some rock-inhabiting fungal lineages to evolve lichenisation, such as the *Verrucariales* (Gueidan et al. 2008). Character states that were used to define the genus *Verrucaria*, such as the crustose thallus, the absence of hymenial algae or the simple ascospore, are symplesiomorphic, and therefore several non-related lineages were retained within *Verrucariaceae* (Gueidan et al. 2007).

Significance

Ecological and economic roles

Most taxa of *Verrucariaceae* occur in rocks and soil, while the growth on wood, bark, and leaves is less common. Several species are components of biological soil crusts and contribute to the formation and stabilization of soil, such as the members of *Endocarpon* and *Catapyrenium* (Belnap et al. 2001). Several *Verrucariaceae* genera consist entirely of lichenicolous (lichen-dwelling) fungi: *Bellemerella*, *Clauzadella*, *Haleomyces*, *Halospora*, *Norrlinia*, *Phaeospora*, *Telogalla*. Lichenicolous fungi occur in other genera to a lesser extent. Some genera, including *Heteroplacidium*, *Placidiopsis*, *Placocarpus*, *Placopyrenium*, *Thelidium*, *Verrucaria*, and *Verruculopsis* contain lichenicolous lichens (Diederich et al. 2018). Crustose *Verrucariaceae* species are often under-represented in local or national checklists due to their typical habitat on rocks and their inconspicuousness. There are several algal genera that are known to become photobiont partners with *Verrucariaceae* mycobionts. This kind of association is mainly influenced by bioclimatic factors, geography, and habitats. The *Verrucariaceae* is the only mostly lichen-forming family to have photobiont associations with yellow-green algae (class *Xanthophyceae*, genus *Heterococcus*). Known green algal associates include members of the class *Trebouxiophyceae* (genera *Asterochloris*, *Auxenochlorella*, *Chlorella*, *Chloroidium*, *Diplosphaeria*, *Elliptochloris*, *Myrmecia*, *Pseudostichococcus*, *Trebouxia*, and *Trochiscia*) (Malavasi et al. 2022). Several species (i.e. *Clavascidium lacinulatum*, *C. sinense*, *Placidium nitidulum*, *P. nigrum*, *P. varium*, and *Heteroplacidium* spp.) have been reported from arid and semi-arid regions that indicates their tolerance to extreme conditions such as solar radiation, aridity and oligotrophy, with important ecological functions, such as sand fixation by rhizines or lower surface and carbon fixations by photosynthesis (Knudsen et al. 2014, Zhang et al. 2022c). Although most species are terrestrial, there are some semi-aquatic species, with representatives from both fresh and saltwater (Jaklitsch et al. 2013); some of these species (e.g., *Hydropunctaria* spp. *Mastodia* spp. *Verrucaria* spp. and *Wahlenbergiella* spp.) are used as bioindicators of coastal water pollution (Nokes et al. 2022). There are a few species in *Verrucariaceae* that have important economic significance. An example of a lichen in this family that has been used in traditional medicine is *Dermatocarpon miniatum* (Ullah et al. 2021).

Chemical diversity

A few *Verrucariales* taxa are associated with a wide range of chemical production. A species in the family *Verrucariaceae* (i.e. *Endocarpon pusillum)* produce secondary metabolites such as two new described naphthoquinone and isoindolin-1-one and other known compounds including endocarpin B, (-)-regiolone, ferulic acid, alternaphenol B, lumichrome, indole-3-acetic acid, veratric acid, monodictyphenone, cephalanone F, and alternaphenol B (Rundong et al. 2022). However, these chemical substances are not exclusive to *Verrucariaceae*. This indicates a close sister-group relationship between these families, but the quantity of chemicals can vary. Mycosporine-like amino acids (MAAs), including (mycosporine glutamicol, mycosporine glutaminol), were quantified in fresh and preserved material of the chlorolichen *Dermatocarpon luridum* (*Verrucariaceae*) (Chollet Krugler et al. 2019).

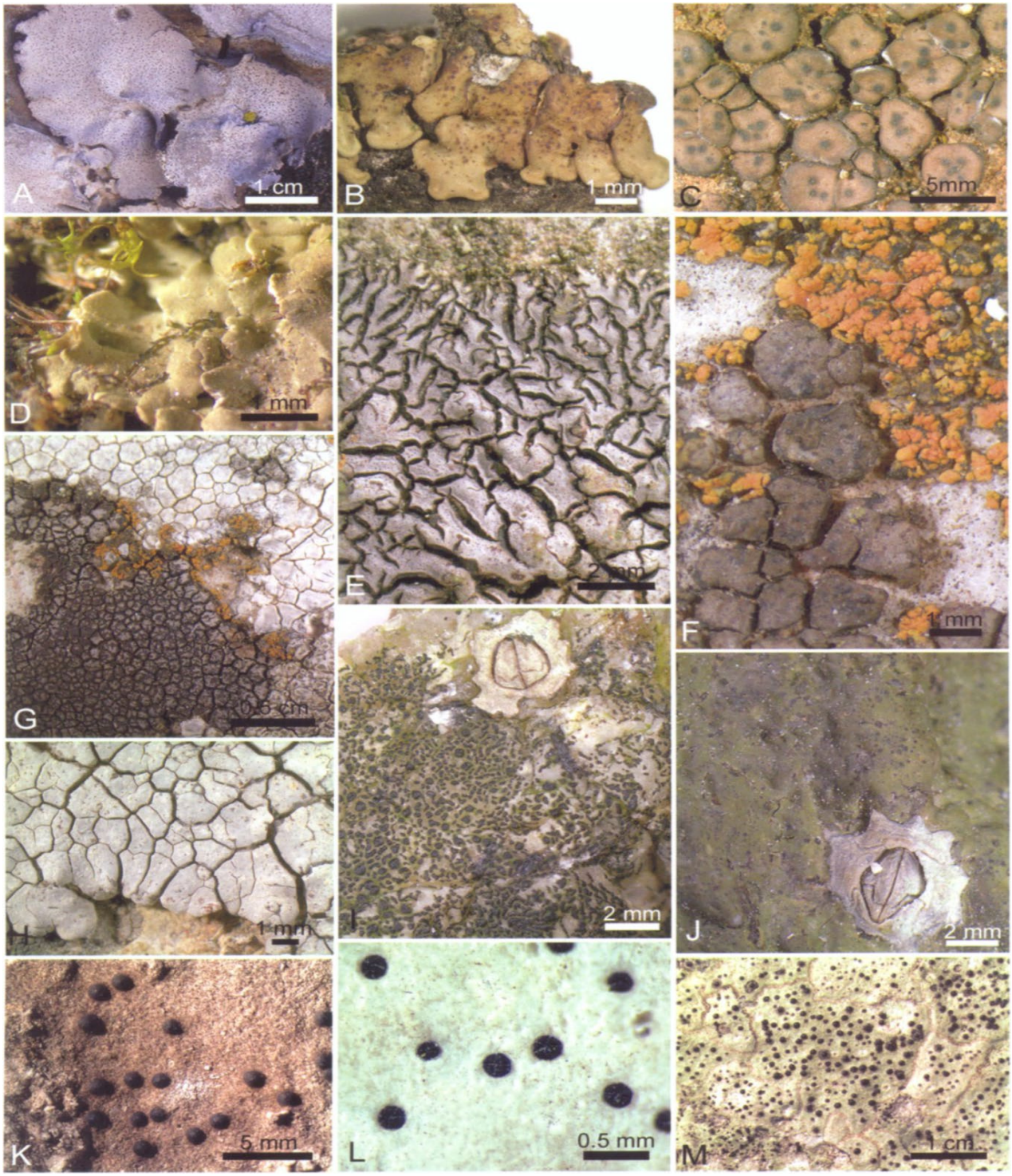


Figure 122 – Main habits of species of *Verrucariaceae*. A Foliose umbilicate thallus of *Dermatocarpon*. B Squamulose and corticolous species *Placidium arboreum*. C Squamulose and terricolous species *Placidium umbrinum*. D Small squamulose thallus for *Catapyrenium daedaleum*. E Crustose placodioid species *Placopyrenium bucekii*. F Crustose species *Verrucula granulosaria*, parasitic on *Caloplaca granulosa*. G Crustose species *Placopyrenium fuscellum*, parasitic on *Aspicilia calcarean*. H Crustose epilithic species *Placocarpus schaereri*. I Marine species *Wahlenbergiella striatula*. J Marine species *Wahlenbergiella mucosa*. K Semiendolithic species *Verrucaria weddellii*. L Endolithic species *Bagliettoa baldensis*, with radially-split involucrellum. M Crustose endolithic species *Parabagliettoa cyanea*, with superficial perithecia.

Other relevant data and future recommendations

Despite their ecological roles and production of secondary metabolites, *Verrucariales* taxa are often influenced by high soil water conditions or excessive water addition regulation patterns and changes in soil pH (Zhang et al. 2016c, 2018a). It has been proposed that *Atla* genus may serve as pioneer organisms and first colonize and dominate glaciers and soils (Zhang et al. 2016c). Co-culture experiments using the fungus *Endocarpon pusillum* and its algal partner allowed the functional identification of genes involved in the nitrogen and carbon transfer between both symbionts, and three lectins without signal peptide domains were found to be essential for the symbiotic recognition in the lichen (Wang et al. 2014b). So far, many species have been overlooked and many verrucarialean fungi are yet to be described (e.g., Habib et al. 2023, Khalid & Zulfiqar 2023). Morphological studies and molecular phylogenetic analyses now suggest that further studies are required for a better taxonomic resolution of *Verrucariaceae* (Gueidan et al. 2007). Several genera were recently described or resurrected, and others were re-circumscribed (Saini et al. 2021, Zhang et al. 2022c). Savić et al. (2008) have shown that morphological features traditionally used for characterizing the genera *Polyblastia*, *Thelidium*, *Staurothele* and *Verrucaria*, such as spore septation and color, occurrence of hymenial photobionts, involucrellum structure, and substrate preference, are only partially consistent with supported clades, and thus are not always reliable for characterizing natural groups, so that these genera, as currently delimited, are non-monophyletic. Because the generic delimitation within *Verrucariaceae* is mainly based on ascospore septation and thallus structure, molecular data are needed to assess the current morphology-based classification. Despite their importance in bio-deterioration, the taxonomy of the calcicolous endolithic lichen genus *Bagliettoa* is problematic, mostly because of difficult identifications and unsettled species concepts. A few taxonomic changes were proposed to reconcile the morphology-based classification with the molecular phylogeny (*Endocarpon diffractellum*, *Heteroplacidium fusculum* and *Bagliettoa marmorea*) (Gueidan et al. 2007). The genus *Bagliettoa* is in need of further revision (Yuzon et al. 2014).

***Geoglossomycetes* Zheng Wang, C.L. Schoch & Spatafora, Persoonia 22: 131 (2009)**
***Geoglossales* Zheng Wang, C.L. Schoch & Spatafora, Persoonia 22: 131 (2009)**

Subphylum : *Pezizomycotina*
Class : *Geoglossomycetes*

Introduction

The class *Geoglossomycetes* is quite limited in number of species diversity (Silva & Fortuna 2020) and the name "*Geoglossales*" is derived from the Greek words "geo" (earth) and "glossa" (tongue), which appropriately characterize the shape of their fruiting bodies. The members of this family are commonly referred to as earth tongues (Arauzo & Iglesias 2014). Corda (1838b), established *Geoglossaceae* to include species of ascomycetes that are terrestrial, stipitate, claviform, or capitate, typically dark or blackish, with gymnocarpic development, inoperculate asci with spores ranging from long elliptical to cylindrical or claviform, typically multi-septate and sooty in color when mature (Aouali 2021).

The ascocarps of the majority of Geoglossaceae species are typically diminutive, dark in color, and club-shaped, with a height ranging from 2 cm to 5 cm. It is known that other types of fungi can parasitize ascomata (Seeler 1943). Earth tongues are among the most common *Ascomycota*, especially in temperate regions where they grow on a variety of substrates (Hustad et al. 2011, Wang et al. 2011). They are also referred to as "grassland fungi," a name coined to designate species that thrive in waxcap grasslands and belong to a taxonomically varied collection of species that appear to be ecologically linked (Nitare 1988, McHugh et al. 2001). According to Hustad et al. (2013), large, dark brown or black ascoma is a distinguishing feature of *Geoglossomycetes* fungi. Ascomata frequently emerge from the soil or detritus, allowing them to be readily identified in their natural habitat. Additionally, they can be found growing on decaying wood or plant matter (Rossman et al. 1999).

History

The history of *Geoglossales* is intricately intertwined with the history of mycology. Since Persoon (1794a) first identified *Geoglossum*, earth tongues have been a focus of mycological research since they are one of the most extensively dispersed genera of fungi on the planet (Hustad et al. 2011). This group of fungi was classified based on their shared characteristics, such as the elongated, tongue-like fruiting bodies (ascomata). Together with the research of other mycologists, the work of Hennings improved the comprehension of the diversity and distribution of *Geoglossales*. The previous definition of *Geoglossaceae sensu lato* included six genera and 48 species (Kirk et al. 2008b). Early molecular evidence using ribosomal DNA suggested that *Geoglossaceae sensu lato* was not a monophyletic group, and the hyaline-spored genera (*Leotia*, *Microglossum* and *Spathularia*) were not related to the darker-spored genera (*Geoglossum* and *Trichoglossum*) (Pfister & Kimbrough 2000, Wang et al. 2006b). Initially, *Geoglossales* and *Geoglossaceae* were treated as members of *Leotiomycetes* (Korf 1973, Spooner 1987). Later, Schoch et al. (2009c) established *Geoglossomycetes* for this order based on a six-gene phylogenetic analysis. Kirk et al. (2008b) and Schoch et al. (2009c) classified *Geoglossales* into six genera which included nearly 50 species. Different molecular studies (Arauzo & Iglesias 2014, Fedosova et al. 2018) have demonstrated that the *Geoglossaceae* is currently undergoing significant alterations. *Microglossum* was previously included in *Geoglossaceae*, and is now excluded because of molecular evidence (Sandnes 2006, Schoch et al. 2009c) and *Sabuloglossum*, *Glutinoglossum* and *Nothomitra* were later included by Hustad et al. (2011, 2013). *Geoglossomycetes*, was proposed by Schoch et al. (2009c) for a clade that includes species of *Geoglossum*, *Sarcoleotia*, and *Trichoglossum* and holds the most basal position within the superclass *Leotiomyceta*. Research conducted by Fedosova et al. (2018), added 13 *Glutinoglossum* species, of which seven are known from Europe. Arauzo & Iglesias (2014) added *Leucoglossum* and *Hemileucoglossum* to *Geoglossaceae*. Presently, *Geoglossales* accommodates a single family *Geoglossaceae* with seven genera and two genera (*Nothomitra* and *Sarcoleotia*) are accepted under *Geoglossomycetes* genera *incertae sedis* (Hyde et al. 2024b).

General description

Geoglossomycetes is a small group with limited genera and thus the same interpretation can be made for the order *Geoglossales* (Silva & Fortuna 2020). Ohenoja (1995) studied *Geoglossales* and concluded that saprobic fungi thrive in meadows, pastures and prairies, as well as along rivers, roads, and swamps. *Geoglossaceae* consists of terrestrial, clavate, stipitate, or capitate, gymnocarpic black ascomycetes with inoperculate asci and typically elliptical, septate, clavate or cylindric ascospores (Silva & Fortuna 2020). Upon maturation, these fungi are typically dark and resemble charcoal (Arauzo & Iglesias 2014). Due to the sporadic appearance of fruiting bodies, Kučera & Lizoň (2012) assert that it is virtually impossible to assess the abundance of geoglossaceous species. The taxa of *Geoglossales* show diversified morphological characters. *Geoglossum* is considered to be the most diverse genus followed by *Trichoglossum* (Dasgupta et al. 2022). Boudier (1885) distinguished the genus *Trichoglossum* from *Geoglossum* based on the presence of setae in the ascoma, which occur both in the stem and ascogenous portion of the plant, giving it a velvety appearance. The fruit bodies of *Geoglossum* are typically dry to sticky or gelatinous (especially in wet conditions), club-shaped and brown to black in color. The hymenium (spore-bearing surface) is restricted to the club-shaped upper portion of the fruit body (Kučera & Lizoň 2012). The surface of stipes can be smooth, squamulose (covered in microscopic scales), or, in certain cases, covered with tufts of tiny hairs, long and cylindrical. The asci have a club-like structure, are inoperculate (have no cap or lid), and often have eight ascospores which range from club-shaped to fusiform to slightly cylindrical, septate and aseptate and brown to hyaline (Silva & Fortuna 2020). Asci and paraphyses coexist, and in some species, the paraphyses are found on the stipes, dispersed or gathered into little tufts or scales. In several species, they form a continuous gelatinous coating that is spread out across the stipe surface (Mains 1954). *Trichoglossum* taxa are mostly known as hairy earth tongues and distinguished by their black or dark brown club-shaped apothecia, amyloid asci, inoperculate, hymenial setae (present on both sterile and ascogenous positions), apically twisted or bent, septate paraphyses, and fusoid

and septate ascospores. On the spore-bearing surface minute filaments known as setae are present (Jaklitsch et al. 2016a).

Sexual morph: *Ascomata* usually capitate, stipitate, and dispersed, gregarious. *Stipe* cylindrical, black, smooth, furfuraceous. *Ascigerous portion* capitate, club-shaped to pileate, indistinguishable from the stipe. *Hymenium* surface black, continues with stipe during the early stages of development. *Paraphyses* filiform. *Asci* clavate, inoperculate, thin-walled structure, typically 8-spored, elongate, dark-brown to blackish, hyaline. *Ascospores* septate (Figs. 123, 124). Asexual morph: Asexual stages are unknown in the majority of taxa within this order (Schumacher & Sivertsen 1987).

Families included in *Geoglossales*

Geoglossaceae Corda

Geoglossales genera *incertae sedis*
Nothomitra Maas Geest.
Sarcoleotia S. Ito & S. Imai

Evolution

Considering the sheer number of ascomycete species and the diversity of their morphologies and life forms, the substitution rate heterogeneity across their phylogeny is likely to be quite pronounced, even at the class level. Several studies have suggested that the *Geoglossaceae* are distinct from other helotialean fungi, with paraphyses with dark pigmentation and dark ascospores with multiple septa considered to be distinguishing characteristics (Wang et al. 2006b). Several authors indicated the association of *Geoglossomycetes* with bryophytes and the presence of ectomycorrhizal or ericoid mycorrhizal lifestyles in *Geoglossomycetes*. However, no reliable informations are available regarding their root colonization (Imai 1941, Nitare 1982, Schumacher & Sivertsen 1987, Jumpponen et al. 1997, Wang et al. 2011). Thus, their lifestyle is largely unknown (Baba et al. 2021). A good example is *Sarcoleotia globosa* which has been mentioned to be associated with numerous plant species such as *Alnus*, *Cassiope*, *Cornus*, *Empetrum*, *Juniperus*, *Linnaea*, *Luetkea*, *Phyllodoce*, *Pinus* and *Salix*. In a recent study conducted by Thoen et al. (2019), *S. globosa* has been detected as an ectomycorrhizal fungus of the alpine bistort (*Bistorta vivipara: Polygonaceae*), which was also investigated using a culture-independent technique. Baba et al. (2021) discovered *Sarcoleotia globosa* in the soil of an ornamental *Erica* pot. The authors also observed the germination of its ascospores on plain agar, and conducted a study by collecting isolates from horticultural and natural environments in Japan and analyze their phylogeny and root colonizing ability. Their phylogenetic analysis based on ITS sequences revealed that the collected samples were segregated into three strongly supported clades based on the host plant, and all tested strains formed hyphal coils in vital rhizodermal cells of *Vaccinum virgatum* seedlings, which resembled those of ericoid mycorrhizae.

Justification of order and problems

The taxa of *Geoglossaceae*, were initially considered as helotialean fungi under *Ascomycota*. Scientists have primarily directed their attention toward studying the morphological characteristics of these organisms and conducting taxonomical analyses in order to elucidate their phylogenetic relationships. Research suggested the separation of *Geoglossaceae* from other helotialean fungi was based on the presence of paraphyses with dark pigments and dark ascospores containing several septa, which were considered to be distinctive characteristics defining this group (Lutzoni et al. 2004). In *Geoglossum* and *Trichoglossum*, paraphyses (or comparable structures) cover the stipe surface and obstruct the fertile margin of the hymenium, and this characteristic is not observed in other inoperculate ascomycetes (Spooner 1987, Ekanayaka et al. 2017b). Similar to *Geoglossum*, *Sarcoleotia globosa* has pileate-like apothecia that initially have hymenium that are continuous with the stipe until they separate to create a fruit body like a pileate (Schumacher & Sivertsen 1987). The distinct hymenium margin of *Thuemenidium*, *Microglossum*, and *Bryoglossum* species supports the molecular evidence that these genera should be separated from the *Geoglossaceae*.

Geoglossomycetes were grouped closely with *Pezizomycetes*, *Orbiliomycetes*, and other early lichenized ascomycetes in the molecular phylogenetic study. This grouping obtained moderate to strong support from different sets of genes (Schoch et al. 2009c). There is a widespread belief that earth tongues are related to bryophytes, however, there is no concrete proof available. *Geoglossum*, *Trichoglossum*, and *Sarcoleotia* are the three major genera from which about 50 species (Kirk et al. 2008b) have been recorded; nevertheless, the relationships between these species are poorly understood.

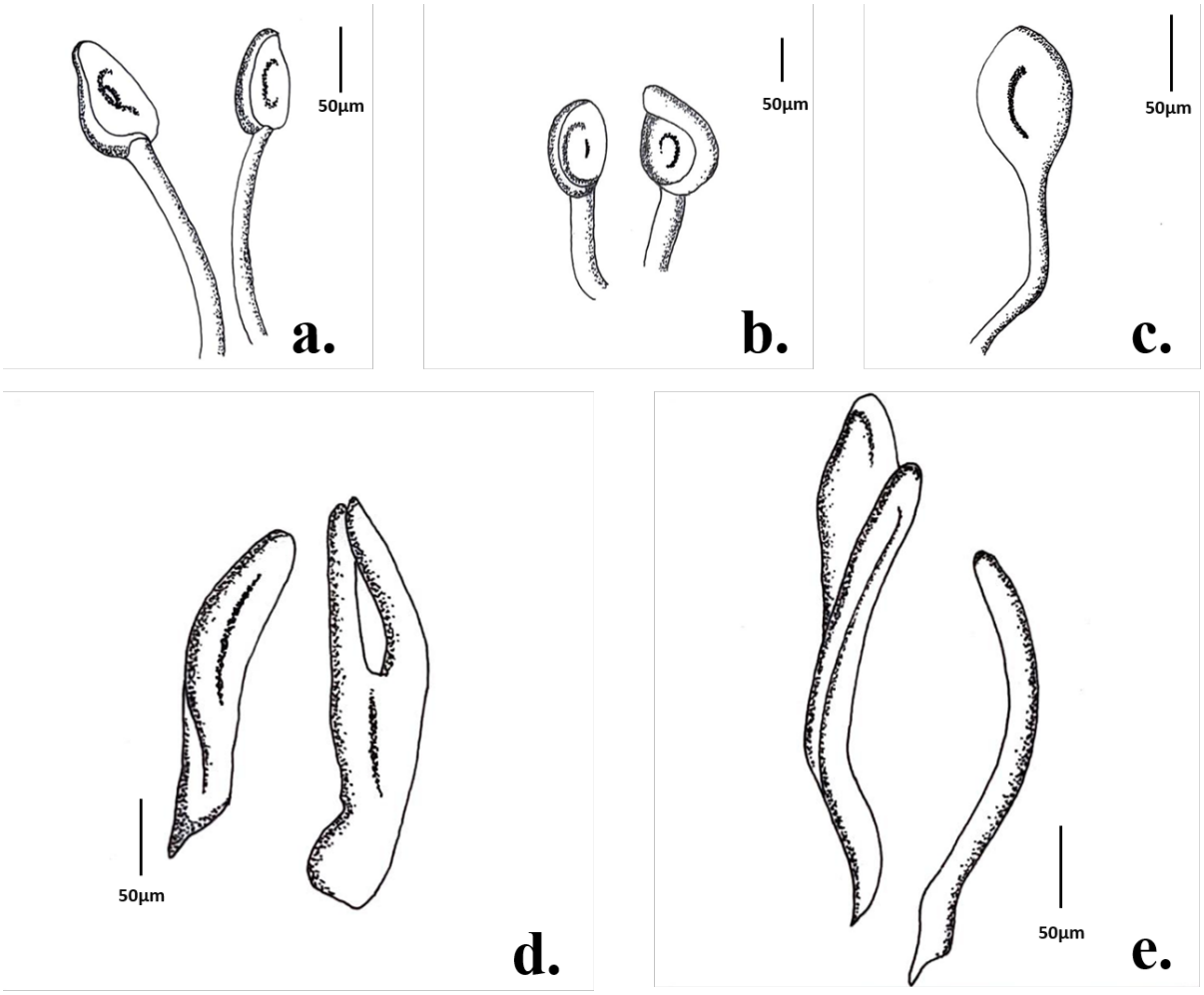


Figure 123 – Fruiting bodies of *Geoglossales*. a Fruit body of *Trichoglossum hirsutum* (Redrawn from Aouali 2021). b Ascomata of *Trichoglossum benghalense* (Redrawn from Chakraborty et al. 2022). c Ascomata of *Geoglossum fallax* (Redrawn from Silva and Fortuna 2020). d Fruit body of *Geoglossum barlae* (Redrawn from Aouali 2021). e Ascomata of *Glutinoglossum glutinosum* Unpublished photographs).

Significance

Ecological and economic roles

Although earth tongue fungi have a worldwide distribution, most species were described from North America and southwest China. *Trichoglossum* diversity in Asia includes Indian species; however, only three Indian species have been reported as of yet. *Trichoglossum rasum* was reported from India (Prabhugaonkar & Pratibha 2017) and *T. tetrasporum* was reported from Northeast region, West Tripura of India (Debnath et al. 2019), and recently *T. benghalense* has been reported from lower Gangetic plane of West Bengal, India (Chakraborty et al. 2022). *Glutinoglossum glutinosum* found in northern Africa, Asia, Europe, and North America, indicating its widespread distribution in the Northern Hemisphere (Hustad & Miller 2015) and in the United Kingdom and the species has

been used as an indicator of medium-quality grassland (Hurford & Schneider 2007). As degraders of persistent organic substances such as keratin and lignin, ascomycetes play a crucial role in nutrient cycling. Additionally, many ascomycetes participate in symbiotic associations including mycorrhizae and lichens (Beimforde et al. 2014). Ma et al. (2022) recently isolated a few bioactive compounds from *Geoglossum fallax*, suggesting that there may be future opportunities in the pharmaceutical industry, despite the fact that the economic significance of earth tongue has not yet been fully explored.

Chemical diversity

The exploration of chemical diversity within *Geoglossales* has largely remained unexplored. Only a recent study conducted by Ma et al. (2022), revealed the presence of two carboxamides *viz*. geoglamides A and B which are characterized by the presence of rare long chain fatty amides containing a 4-oxo-1,4-dihydropyridine moiety in *Geoglossum fallax*. *Geoglamides* A exhibited cytotoxic activity against human MCF-7 cells with an IC50 value of 25.9 ± 0.51 µM, whereas geoglamides B exhibited mild pancreatic lipase inhibition activity. One rare C6-C5 type meroterpenoid *viz*. geoglol A was obtained from this mushroom. Along with these carboxamides *Geoglossum fallax*, also produces seven known metabolites.

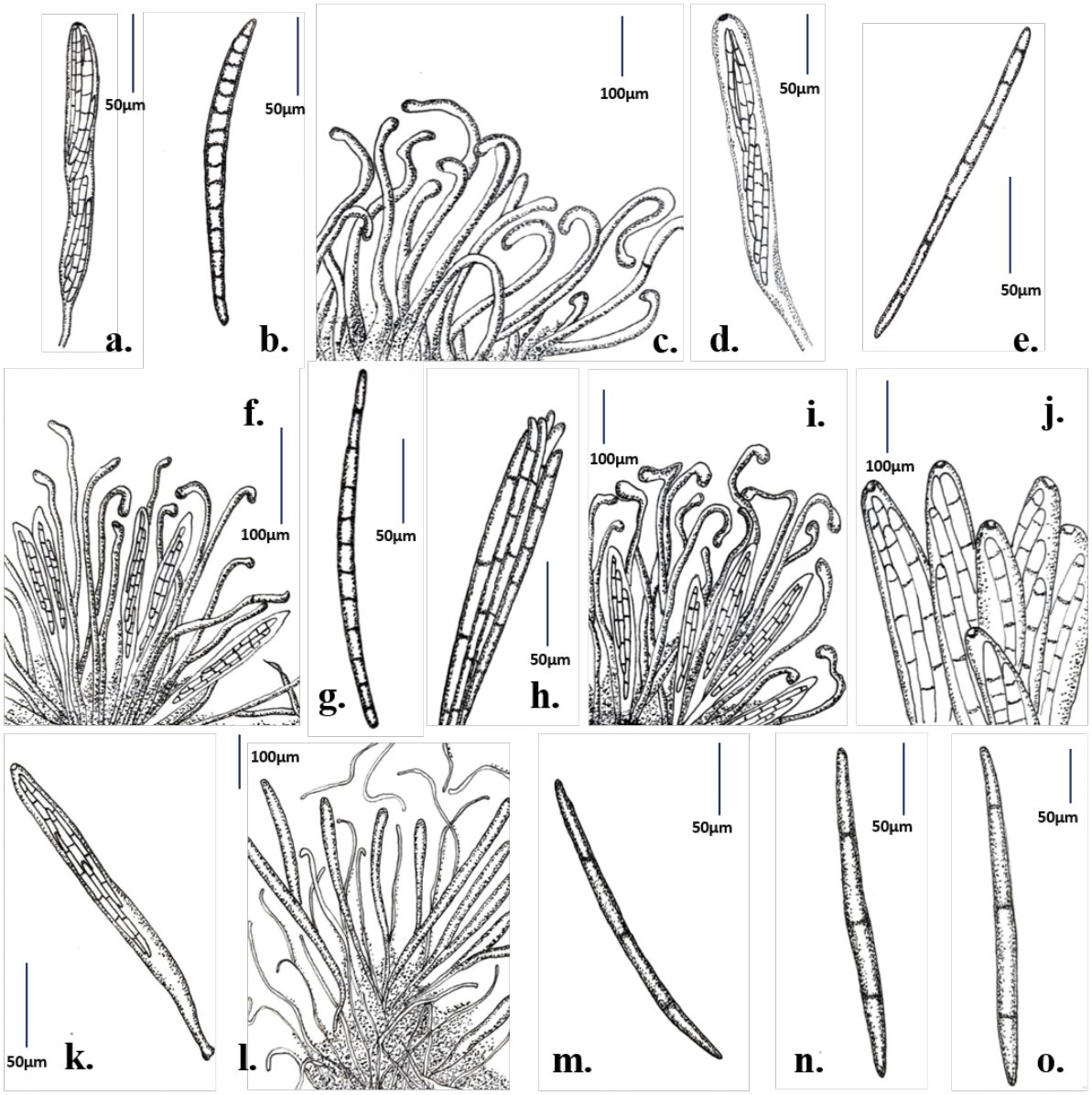


Figure 124 – Asci, paraphyses and ascospores of *Geoglossales*. (a–c) *Trichoglossum hirsutum* (Redrawn from Aouali 2021). a Ascus with ascospores. b Ascospores. c Paraphyses. d–f *Trichoglossum benghalense* (Redrawn from Chakraborty et al. 2022). d Ascus with ascospores. e Ascospores. f Septate unbranched paraphyses. g–h *Geoglossum fallax* (Redrawn from Silva & Fortuna 2020). g Ascospores. h Ascus. i–k *Geoglossum barlae* (Redrawn from Aouali 2021). i Asci and paraphyses. j–k Ascus with ascospores. l–o *Glutinoglossum glutinosum* (Unpublished photographs). l Asci and paraphyses. m–o Ascospores.

Other relevant data and future recommendations

Several species of *Geoglossum* are deemed important for conservation, and numerous species appear on the Regional Red Lists of several European nations. *Geoglossum* members are typical components of Europe's imperilled waxcap grassland habitat. In Estonia, *G. arenarium* is designated as vulnerable while *G. atropurpureum* and *G. atrovirens* are listed as critically endangered (Parmasto 2009). In Switzerland, *G. cookeanum* is listed as an endangered species (Senn-Irlet et al. 2007). *G. difforme* is reported as critically endangered and endangered in Denmark and Sweden, respectively (Pihlgren et al. 2010). In Sweden, *G. hakelieri* is listed as vulnerable. In Denmark, *G. littorale* is designated as critically endangered, and in Sweden as endangered. In Sweden, *G. uliginosum* is listed as critically endangered (Senn-Irlet et al. 2007). Thus, conservation measures may be required to preserve the populations of earth tongue mushrooms as they are rare or endangered. Their distribution, habitat needs, and potential dangers may all be the subject of future research. Several hypotheses were made about its edibility too. Although black earth tongue species are not typically edible (Arora 1986), McIlvaine & Macadam (1912) believed they are delectable (McIlvaine & Macadam 1912). Further investigation could focus on their nutrient characteristics, flavour profiles, and potential culinary uses.

***Laboulbeniomycetes* Engl., in Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1: vi (1897)**
***Laboulbeniales* Lindau, Die Natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten 1 (1): 491 (1897)**

Subphylum : *Pezizomycotina*
Class : *Laboulbeniomycetes*
Subclass : *Laboulbeniomycetidae*

Introduction

The order *Laboulbeniales* is placed within *Laboulbeniomycetes*, a class that currently consists of five clades, i.e. the three described orders *Herpomycetales*, *Laboulbeniales*, and *Pyxidiophorales*, as well as the informal *Chantransiopsis* and *Laboulbeniopsis* clades (Haelewaters et al. 2021a). *Laboulbeniales* rely on their host for spore transmission through direct contact between the hosts (De Kesel 1995). Uniquely among fungi, hyphae are never produced at any point in the life cycle, and no asexual reproduction is known for the order (Haelewaters et al. 2019c, 2021a). *Laboulbeniales* form a microscopic 3D structure called a thallus, which develops from mitotic divisions of two-celled ascospores. These thalli exhibit determinate growth and can be found either solitary or in bristle-like bunches on the host (Blackwell et al. 2020). A mature thallus consists of a receptacle, the “core” of the thallus from which all other parts develop and that attaches to the host with a single foot (superficially attached) or a haustorium (penetrating the host’s cuticle); the perithecium (or multiple perithecia) producing the ascospores, which are discharged through an ostiole at the perithecial tip; and one or more, often branch-like appendages that are either fertile (carrying antheridia that produce spermatia) or sterile (with thus-far unknown function) (Fig. 125).

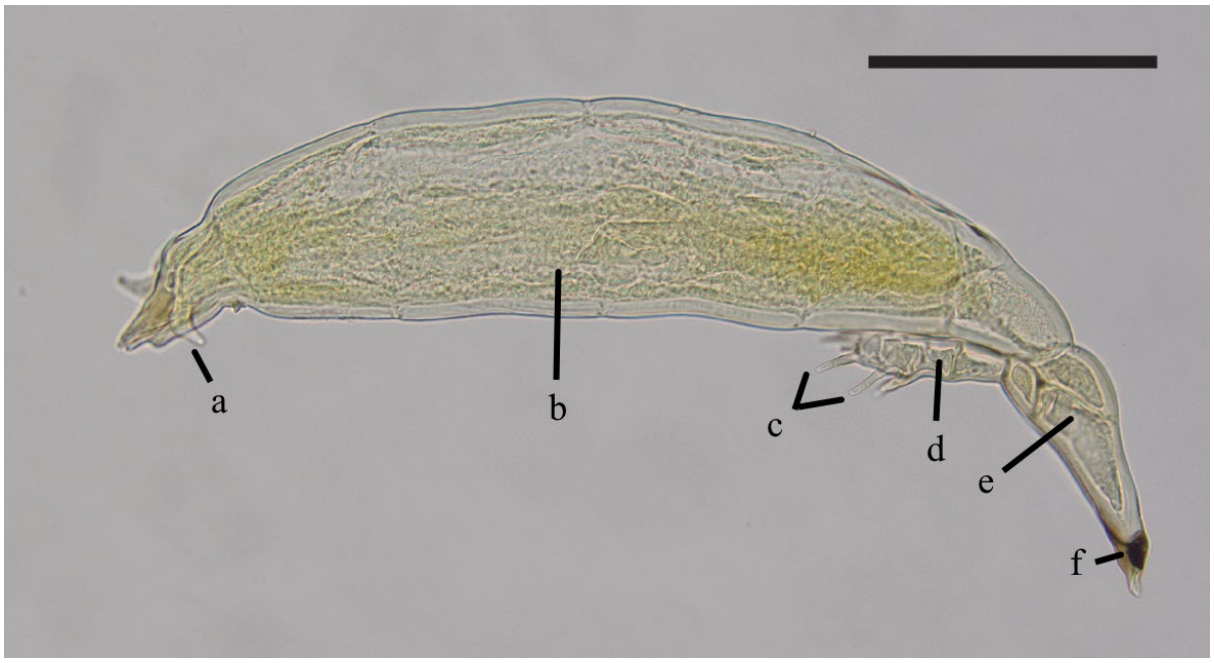


Figure 125 – A typical thallus of *Laboulbeniales*. *Hesperomyces harmoniae* Haelew. & De Kesel (described in Haelewaters et al. 2022b). Indicated are a Perithecial tip with lobes. b Perithecium. c Single antheridia with flask-shaped necks. d Appendage. e receptacle. f Haustorium. Scale bar = 100 μm.

Contrary to *Herpomycetales*, the other order of thallus-forming *Laboulbeniomycetes*, *Laboulbeniales* have radiated widely, counting 146 genera and 2,379 described species that can be found on arthropod hosts in three subphyla: *Chelicerata*, *Hexapoda*, and *Myriapoda* (Weir & Hammond 1997, Senanayake et al. 2023, Haelewaters et al. 2024). However, the currently known species diversity in the order is likely only scratching the surface of the actual diversity, as the true total global diversity of *Laboulbeniales* has been estimated to be around 40,000 species (Weir & Hammond 1997) and recent work has analyzed the severity of this species knowledge gap or Linnean shortfall (Haelewaters et al. 2024). The majority of known species of *Laboulbeniales* can be found on *Coleoptera* and *Diptera* (Weir & Hammond 1997, Haelewaters et al. 2021a).

Most *Laboulbeniales* exhibit a relatively high degree of host-specificity; they are restricted to a limited number of host taxa belonging to the same genus (e.g., Szentiványi et al. 2018). Some species previously considered to have a wide host range and a large geographic distribution, have been shown to be complexes of multiple species based on molecular phylogenetic data in combination with ecology (host association), morphology, and geography (Haelewaters et al. 2018, 2019b, 2022b, Van Caenegem et al. 2023b).

The degree of host-specificity has been suggested to be linked to the presence or absence of a rhizoidal structure called the haustorium, which penetrates the host's integument and thus comes into contact with host-specific physical and chemical defenses (Haelewaters et al. 2022a). Specificity can be established on other levels as well. In some species, thalli of certain taxa are confined to precise positions on the host cuticle, such as legs, wings, or elytra (Benjamin & Shanor 1952, Goldmann & Weir 2012, Haelewaters & Pfister 2019, Van Caengem et al. 2023a). This phenomenon is generally referred to as position specificity and is oftentimes observed in co-occurrence with morphological variation, as different morphotypes of a single phylogenetic species can be restricted to a specific place on the body of the host (Goldmann et al. 2013, Haelewaters & Pfister 2019, Van Caenegem et al. 2023a). Also, cryptic diversity may be frequent in this order, as more studies are recently unveiling evidence for the existence of cryptic species "hidden" in species complexes, e.g., in *Arthorhynchus* (Haelewaters et al. 2020a) and *Hesperomyces* (Haelewaters et al. 2018, 2022b).



Figure 126 – Representative examples of *Laboulbeniomycetes* and their arthropod hosts. a, b, d–l. *Laboulbeniales*. c, m *Herpomycetales*. n *Pyxidiophorales*. a *Hesperomyces harmoniae* on *Harmonia axyridis* (*Coleoptera*, *Coccinellidae*). b *Rickia wasmanni* on *Myrmica sabuleti* (*Hymenoptera*, *Formicidae*). c *Herpomyces chaetophilus* on a mouthpart of *Periplaneta americana* (*Blattodea*, *Blattidae*). d *Gloeandromyces nycteribiidanum* on *Megistopoda proxima* (*Diptera*, *Streblidae*). e *Laboulbenia calathi* on a leg of *Calathus melanocephalus* (*Coleoptera*, *Carabidae*). f *Laboulbenia flagellata sensu lato* from *Carabidae* sp. (*Coleoptera*). g *Hesperomyces harmoniae* from *Harmonia axyridis* (*Coleoptera*, *Coccinellidae*). h *Rhachomyces anophthalmi* from *Anophthalmus ravasinii* subsp. *ravasinii* (*Coleoptera*, *Carabidae*). i *Gloeandromyces nycteribiidarum* from *Trichobius*

yunkeri (*Diptera*, *Streblidae*). j *Rhachomyces philontinus* from *Philonthus varians* (*Coleoptera*, *Staphylinidae*). k *Laboulbenia filifera* from *Anisodactylus kirbyi* (*Coleoptera*, *Carabidae*). l *Teratomyces* sp. 1 from *Heterothops* sp. (*Coleoptera*, *Staphylinidae*). m *Herpomyces stylopygae* from *Blatta orientalis* (*Blattodea*, *Blattidae*). n *Pyxidiophora corallisetosa*, a perithecium with typical peridial hairs pointed upwards and often apically bifurcated, in cotton blue (Photos: a, c, e. André De Kesel; b. Theodoor Heijerman; d, g–m. Danny Haelewaters; f. Walter P. Pfliegler; n. Michał Gorczak) Scale bars: a–n = 50 µm.

History

Laboulbeniales were first observed in the 1840s by the French entomologist Joseph Alexandre Laboulbène (1825-1898) (Haelewaters et al. 2021b). The unique combination of distinct features of these fungi has made the assignment of *Laboulbeniales* to a known group of organisms complicated, resulting in the first few years of discovery being quite tumultuous (Haelewaters et al. 2021a). An early observer of *Laboulbeniales* mistook the minute thalli for parasitic plants, whereas a contemporary misinterpreted his findings of bat fly-associated *Laboulbeniales* as acanthocephalan worms. Extremely influential was the opinion of Roland Thaxter (1858–1932). He not only recognized *Laboulbeniales* as fungi but also placed them in the phylum *Ascomycota* (Blackwell et al. 2020). Throughout the early 20th century, Thaxter singlehandedly described 100s of species in his works (1183 of the species he described are currently valid, i.e. roughly 50% of currently known species), notably through his five-volume "Contribution towards a monograph of the *Laboulbeniaceae*" (Thaxter 1896, 1931). Many of Thaxter's descriptions and observations remain indispensable in the current day and age.

General description

The entire lifecycle of *Laboulbeniales* takes place on the exoskeleton of the host (de Groot et al. 2020). The two-celled ascospores are released from early deliquescent asci; perithecia are filled with ascospores. Ascospores have limited survival capacities once discharged into the environment (De Kesel 1995). A sticky ascospore will adhere to the integument of a typical host, on which through subsequent mitotic divisions a resilient, 3D structure of determinate growth, a thallus, is produced. The thallus is attached to the host exoskeleton with a foot cell and usually consists of a receptacle with appendages carrying one or multiple perithecia and antheridia (De Kesel 1995). In the majority of known species, the interaction between the thallus and the host is non-penetrative, but members from 13 out of the 146 known genera possess a haustorium (Tragust et al. 2016). This rhizoidal appendage is used to puncture the integument and make contact with the haemocoel, to extract nutrients from the host (adapted from Haelewaters et al. 2022a) (Fig. 126).

Families included in *Laboulbeniales*

Ceratomycetaceae S. Colla
Euceratomycetaceae I.I. Tav.
Laboulbeniaceae G. Winter

Evolution

Fossil evidence of arthropod–*Laboulbeniales* associations is scarce. Thus far, only two fossil species have been described, both associated with insects enclosed in amber: *Stigmatomyces succini* from a stalk-eyed fly in Bitterfeld amber, aged 25.3–23.8 million years old (Rossi et al. 2005) and *Columnomyces electri* from the cholevine beetle *Proptomaphaginus alleni* in Dominican amber, aged 15–20 million years old (Perreau et al. 2021). The second species presented a remarkable opportunity to gain insight into a longstanding coevolution, as current species of *Columnomyces* are associated with beetles belonging to the genus *Proptomaphaginus*. The diversification of *Laboulbeniales* is estimated at 110.78 MYA, based on a molecular clock analysis by Haelewaters et al. (2019c).

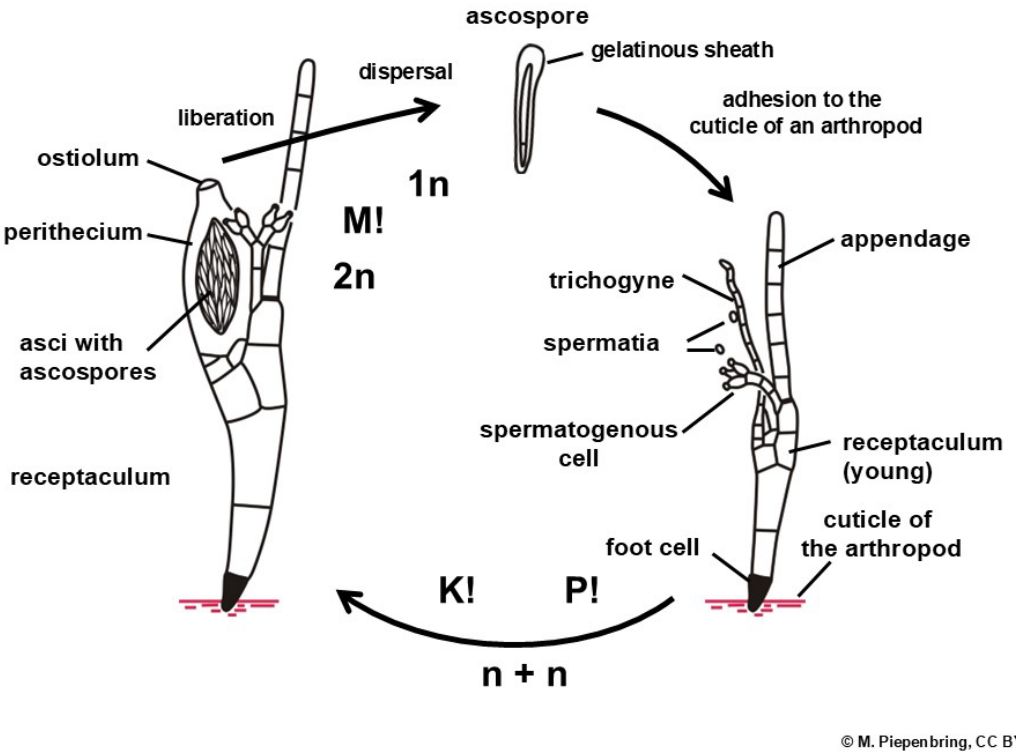


Figure 127 – Sexual and asexual life cycles of *Laboulbeniales* (From Mycological teaching diagrams by Meike Piepenbring (2023)). Abbreviations: **1n** = haploid, **2n** = diploid, **P!** = plasmogamy, **K!** = karyogamy, **M!** = meiosis.

The precise evolutionary origin of *Laboulbeniomycetes* remains a point of debate. Blackwell et al. (2020) highlighted how several distinct theories surrounding this topic have surfaced over the course of the 20th century. Among these, one of the most obdurate theories was the Floridean Hypothesis, first developed by Karsten (1869). Entirely based on morphological convergence between numerous prominent features, this hypothesis explored how *Laboulbeniomycetes* could potentially have been derived from a lineage of red algae. However, towards the end of the 20th century, this theory was ultimately disproven as DNA-based studies, such as Kwok et al. (1986), offered insights into evolutionary relationships between fungi and red algae, allowing us to look beyond superficial similarities. With molecular-based studies of *Laboulbeniomycetes* having emerged only very recently, numerous phylogenetic relationships within the class require robust investigations. Based on SSU sequences regrouping 65 taxa, Goldmann & Weir (2018) demonstrated that *Laboulbeniomycetes* is a monophyletic group within *Ascomycota* and closely related to *Sordariomycetes*, confirming the previous placement of the *Laboulbeniales–Pyxidiophora* clade within *Ascomycota* (Weir & Blackwell 2001). The uncertain placement of the genus *Herpomyces* was later resolved by Haelewaters et al. (2019c) via the introduction of the new order *Herpomycetales* supported by a three-locus phylogeny. Despite those recently undertaken efforts, deeper nodes remain unresolved and the sister group of *Laboulbeniomycetes* is to be discovered (Blackwell et al. 2020, Haelewaters et al. 2021b).

Significance

Ecological and economic roles

Fungi belonging to the order *Laboulbeniales* are obligate ectobionts of arthropods. While some are true biotrophs (Haelewaters et al. 2020b), others may even provide some benefits to their host, such as protection against entomopathogenic fungi (e.g., Konrad et al. 2015). Kaishian et al. (2022) suggested that *Laboulbeniales* may occupy a wide range on the symbiosis spectrum.

Chemical diversity

The chemical diversity of the *Laboulbeniales* has been largely overlooked. It has been observed that most species of this order synthesize melanin in their cell walls, particularly in the foot. This specific pigment accumulation has been suggested to be involved in host penetration mechanisms (Weir & Beakes 1996). This blackish pigment provides rigidity, meanwhile interfering with PCR amplification (Haelewaters et al. 2015). Recently, however, Van Caenegem & Haelewaters (2024) suggested that melanin alone is not sufficient to inhibit PCR, so that other molecules, such as phenols and proteins, could be responsible for PCR interference. Some insect hosts produce chemical compounds to inhibit the development of fungal parasites; however, the ability of *Laboulbeniales* to develop on host integument suggests that they have succeeded in breaking the host chemical arsenal, such as that one of the metapleural gland of ants (Santamaria & Espadaler 2015). Differential chemical composition of the parasite growing substrate (i.e. host body parts) may influence the development of ascospores and subsequent thalli maturation (Riddick & Schaefer 2005), suggesting molecules produced by *Laboulbeniales* to fight against host chemical defenses vary across species. The non-homogenous distribution of thalli on host bodies between species and populations has been suggested to be in part the result of different cuticle chemical profiles for *Myrmica* ants infected by *Rickia wasmannii* (Haelewaters et al. 2019a).

Herpomycetales Haelew. & Pfister, Index Fungorum 382: 1 (2018)

Subphylum : *Pezizomycotina*
Class : *Laboulbeniomycetes*
Subclass : *Laboulbeniomycetidae*

Introduction

Closely resembling *Laboulbeniales* in their obligately ectoparasitic lifestyle and gross thallus morphology, members of *Herpomycetales* have until recently been grouped within the order *Laboulbeniales* (Blackwell et al. 2020, Haelewaters et al. 2021b). *Laboulbeniales* have radiated widely among a multitude of hosts in three of the major arthropod subphyla, whereas *Herpomycetales* are exclusively found on *Blattodea* (cockroaches).

History

Only recently *Herpomycetales* have been recognized as a stand-alone order within the class *Laboulbeniomycetes*. This order comprises a single genus, *Herpomyces* (Thaxter 1902), which currently counts 27 species (Gutierrez et al. 2020). The genus was placed in a tribe, *Herpomycetineae* (Thaxter 1908), and subsequently a suborder, *Herpomycetineae* (Tavares 1981). Since Tavares' classification system, a sister relationship between *Herpomyces* and other *Laboulbeniales* was speculated and later confirmed by molecular data. The first study presenting a molecular phylogeny including *Herpomyces* was Goldmann & Weir (2018), with a single SSU sequence of *H. stylopygae* that was retrieved in an unresolved position outside the *Laboulbeniales* clade. Based on the phylogenetic reconstruction of a three-locus dataset, in combination with morphological, developmental, and host data, Haelewaters et al. (2019c) erected the order *Herpomycetales*.

General description

Similar to *Laboulbeniales*, no asexual stadia or hyphal growth are known for members of *Herpomycetales*. Thalli develop directly on the host from a sticky, two-celled ascospore that adheres to the integument and, through subsequent mitotic divisions initially gives rise to a four-celled primary axis, and eventually, a perithecium (Haelewaters et al. 2019c). The asci are always eight-spored (versus four-spored in *Laboulbeniales*) and the ascospore has two cells that are equal in size (versus unequal in *Laboulbeniales* due to the septum being positioned near one end of the ascospore) (Richards & Smith 1955a, Haelewaters et al. 2019c). Species of *Herpomycetales* are dioecious, with female thalli developing secondary receptacles from the suprabasal cell, which could supposedly play a role in nutrient uptake from the host. These secondary axes produce perithecia and have been

observed to connect directly with the integument of the host (Haelewaters et al. 2019c). The perithecia are multi-tiered and possess double wall layers, but whereas in *Laboulbeniales* this structure arises from the perithecial basal cells, in *Herpomycetales* the inner wall only starts at the fourth or fifth tier of the outer perithecial wall. The rows of the outer wall consist of numerous cells that are equal in height (adapted from Haelewaters et al. 2019c, Fig. 126).

Families included in *Herpomycetales*

Herpomycetaceae I.I. Tav.

Evolution

The diversification of extant species of *Herpomycetales* is estimated at 63.65 MYA (Haelewaters et al. 2019c). Since *Laboulbeniales* and *Herpomycetales* do not form a monophyletic clade, the thallus morphology may have appeared independently in the evolution of these orders (Haelewaters et al. 2019c). No fossil species of *Herpomycetales* are known.

Significance

Ecological and economic roles

Given their association with *Blattodea*, the distribution of *Herpomyces* species is heavily affected by human activities (Gutierrez et al. 2020). Wang et al. (2016c) hypothesized that *Herpomyces chaetophilus* was introduced in the USA with its cockroach host *Periplaneta americana*, a non-native in North America. Pfliegler et al. (2018) demonstrated that half of the known species of *Herpomyces* are spread by their globally invasive host species and through the international pet trade.

Chemical diversity

Histochemical investigations of Richards (1954) on *H. stylopygae* pointed out the presence of a basal darkening "shield", also later reported by Richards & Smith (1955b), which is thought to undergo a sclerotization process similar to the one occurring in the host cuticle. This phenomenon is not necessarily present in other *Herpomyces* species as *H. ectobiae* shows no such sclerotization process. Richards (1954) similarly reported that *Herpomyces* showed positive reactions to the presence of chitin and proteins and that other histochemical reactions suggest the presence of other chemical components to be characterized.

***Pyxidiophorales* P.F. Cannon, Ainsworth & Bisby's Dictionary of the Fungi, Edn 9 (Wallingford): xi (2001)**

Subphylum : *Pezizomycotina*
Class : *Laboulbeniomycetes*
Subclass : *Laboulbeniomycetidae*

Introduction

Pyxidiophorales is an order of fungi in *Laboulbeniomycetes*. Fungi in this order are characterized by perithecial, often long-necked ascomata and arthropod-mediated dispersal of ascospores. Unlike *Laboulbeniales* and *Herpomycetales*, *Pyxidiophorales* do not form a reduced few-celled thallus but produce an undetermined hyphal mycelium from which the perithecia arise. They can be found in many different habitats: on dung, decaying plant material, submerged wood, in bark beetle galleries, and on the sporocarps of other fungi (Haelewaters et al. 2021b). While many species were originally described as saprotrophic, a few species are confirmed mycoparasites and some can only be grown in mixed culture with other species, suggesting that most *Pyxidiophorales* might be mycoparasitic (Kirschner 2003, Jacobs et al. 2005).

History

Pyxidiophora asterophora, the type species of the order was described and illustrated in detail (Tulasne 1860) as *Hypomyces asterophorus* on *Asterophora lycoperdoides*, an agaric species that grows on old *Russula* sporocarps. *Hypomyces asterophorus* was later transferred to the separate

genus *Pyxidiophora*, but considered a member of *Hypocreaceae* or *Hypomycetaceae* depending on the taxonomic views of the author (Lundqvist 1980). The species was then largely forgotten and only rarely recorded or mentioned as an example of hyperparasite. At the end of the 19th century, the nectrioid genus *Treleasia* was described (Spegazzini 1896) and over a decade later another – *Copranophilus* (Spegazzini 1909), yet the similarity of these species to *Pyxidiophora* was not discussed. Saccardo & Saccardo (1906) established the genus *Mycorhynchus*, for a pycnidial fungus with a long neck and elongated uniseptate conidia. In the following decades, multiple new species of *Mycorhynchus* were described by other authors, which were successful in observing early deliquescent asci and started to treat the genus as belonging to true pyrenomycetes (Breton & Faurel 1967, Hawksworth & Webster 1977).

During their investigations on insect-associated fungi, researchers in the early 20th century discovered and described minute few-celled, asexually reproducing organisms that were soon dubbed "Thaxteriolae" in reference to the genus *Thaxteriola* and Roland Thaxter who described some of them (Thaxter 1920, Lundqvist 1980, Haelewaters et al. 2021b). Later similar structures were also observed on mites associated with bark beetles and other insects (Majewski & Wiśniewski 1978).

Lundqvist (1980) recognized that *Mycorhynchus* is similar to the until that time monotypic *Pyxidiophora*. He observed that some species of *Mycorhynchus* have a dark spot on one end that resembles the melanized holdfast of *Thaxteriolae* and after examining the most recent collections of *Acariniola* proposed that these are, in fact, ascospores produced by perithecial fungi. Through literature and the examination of type material, he was also able to synonymize *Mycorhynchus* as well as several other genera of nectrioid or hypocrealean pyrenomycetes like *Ascolanthus*, *Copranophilus* and *Treleasia* with *Pyxidiophora*.

Lundqvist's (1980) research paved the way for the investigation of Blackwell & Malloch (1989b, 1990), who studied in detail the life cycles of a few species of *Pyxidiophora*. They described both bark beetle-associated and coprophilous species, finding in both an adaptation of *Pyxidiophora* ascospores for dispersal via phoretic mites. Additionally, *Pyxidiophora* was proposed as a missing link between *Laboulbeniales* and other ascomycetes (Blackwell & Malloch 1989a), a hypothesis that was later supported by molecular data and led to the recognition of *Pyxidiophorales* in *Laboulbeniomycetes* (Weir & Blackwell 2001, Haelewaters et al. 2021b).

General description

Sexual morph: *Pyxidiophorales* are characterized by forming a flask-shaped perithecium with pseudoparenchymatic peridium constructed of round, oval to irregularly angular cells and long necks (rostrum) constructed of parallel, narrow, elongated cells. Some species can be stromatic with hyaline, yellowish, or ochraceous stroma (Lundqvist 1980). In certain species, the perithecial neck can be very long, up to 80% of total perithecium length. Perithecial ostioles are without an apical apparatus (Lundqvist 1980). The peridium and perithecial neck can be setose in some species (e.g., *P. corallisetosa*, *P. spinulo-rostrata*). Perithecia are hyaline to subhyaline, rarely strongly melanized (*P. badiorostris*) (Doveri & Coué 2006).

Asci are early deliquescent with various numbers of ascospores (generally 2–7 spored) (Hawksworth & Webster 1977, Lundqvist 1980). In many species, asci have not been observed. Ascospores are two-celled, uniseptate, fusiform, usually with one end more obtuse, and often enveloped in mucilaginous sheath. Ascospores might form a dark, melanized spot or foot on their obtuse end. Such spots might develop both after or before the discharge of ascospores from the perithecium. Matured, released spores can further divide into 3–4-celled structures (Hawksworth & Webster 1977), rarely more-celled forms (Blackwell & Malloch 1989b). Ascospores released from the perithecium can sometimes form a droplet on the perithecial ostiole that can stick as a whole to a passing arthropod host.

Mycorhynchidium is the only cleistothecial genus in the order. It has nonetheless been suggested that structures interpreted as cleistothecia in the original description might be young and undeveloped perithecia (Haelewaters et al. 2021b).

Dispersal ascospore-derived asexual morph: *Pyxidiophorales* ascospores divide into a few-celled thallus and produce secondary, asexual spores after release from the perithecium, usually after attachment to a phoretic host. Secondary spores can be produced exogenously on short conidiophores or budding directly from the thallus (e.g., *P. spinuliformis*) or endogenously (e.g., *Endosporella* spp.).

Phialidic hyphal asexual morph: Asexual morphs of *Pyxidiophorales* are most often *Chalara*-like with conidium formation inside phialides or *Gabarnaudia*-like with conidium formation at the tips of phialides (Haelewaters et al. 2021b). Synnematic forms can also be present as shown by Blackwell & Malloch (1989b). Some species such as *Gliocephalis hyalina* and the recently transferred *P. hyalina* are known only from their asexual state (Jacobs et al. 2005, Wu & Diao 2023). The genus *Pleurocatena*, characterized by setose conidiophores, was also described as an asexual genus, but later a sexual morph was described (Gams & Arnold 2007). Despite differences in conidiogenesis and conidiophore morphology, most *Pyxidiophorales* conidia are cylindrical, truncate, and sometimes rounded at one end giving them a bullet-like shape (Haelewaters et al. 2021b). Budding, round, yeast-like conidia have been observed in one species of *Pyxidiophora* (Blackwell & Malloch 1989b). Thick-walled, hyaline chlamydospores were described for *Pleurocatena brevior* only (Gams & Arnold 2007).

Families included in *Pyxidiophorales*

Pyxidiophoraceae Arnold

Evolution

The evolution of *Pyxidiophorales* is discussed in the context of relationship with *Herpomycetales* and *Laboulbeniales*. They have been considered as a link between those thallus-forming *Laboulbeniomycetes* and the rest of *Ascomycota* (Blackwell & Malloch 1989a, Weir & Blackwell 2001), but little emphasis is put on the group's evolution itself. *Laboulbeniomycetes* are thought to be sister group to *Sordariomycetes* (Haelewaters et al. 2019c, 2021a) and *Pyxidiophorales* is the most basal clade in the class. *Pyxidiophorales* share many characters with typical *Sordariomycetes* (hyphae, multiple anamorphs, most perithecium anatomy) and some with *Laboulbeniales* and *Herpomycetales* (ascospore and ascus form, arthropod-related dispersal). Most contemporary researchers view the evolution of *Laboulbeniales* and *Herpomycetales* as events of trait loss (e.g., loss of asexual reproduction) and shortening of a life cycle only to arthropod hosts that started with pyxidiophora-like ancestors (Blackwell et al. 2020; Haelewaters et al. 2021b).

Justification of order and problems

The order *Pyxidiophorales* was erected by Kirk et al. (2001) based on morphological and molecular arguments by Blackwell & Malloch (1989a) and Weir & Blackwell (2001). Similarity of ascospores of *Pyxidiophora* and *Laboulbeniales*, especially the formation of black area of attachment to the host in developed spores, led to the idea that *Pyxidiophora* can be considered a missing link between *Herpomycetales* and *Laboulbeniales* and the rest of *Ascomycota*. This also suggested that *Pyxidiophora* should not be placed in *Hypocreales*, where it was thought to belong in the opinion of previous authors (e.g., Arnold 1972). Later, first molecular data were used as a proof for phylogenetic relationship of *Laboulbeniales* and *Pyxidiophora* as sister groups (Weir & Blackwell 2001), which led to the elevation of the previously erected family *Pyxidiophoraceae* (Arnold 1972, Lundqvist 1980) to the rank of order. The order *Pyxidiophorales* was also supported as a clade separated from both *Laboulbeniales* and *Herpomycetales* (Haelewaters et al. 2019c). It was also found as a separate group from the informal *Chantransiopsis* clade, which includes the genera *Chantransiopsis*, *Subbaromyces* and *Tetrameronycha* (Goldmann & Weir 2018, Blackwell et al. 2020).

The monotypic genus *Laboulbeniopsis* groups as a sister clade to *Pyxidiophora* in two phylogenetic studies that included sequences of *Laboulbeniopsis* (Henk et al. 2003, Blackwell et al. 2020). This might suggest that this genus belongs to *Pyxidiophorales* or is closely related to them. However, due to a lack of in-depth research on both *Laboulbeniopsis* and *Pyxidiophorales*, none of the previously mentioned authors decided to change the taxonomic position of this genus, and thus it is to date regarded as an informal clade. The many validly published names for ascospore-derived

asexual morphs (*Amphoropsis*, *Myriapodophila*, *Thaxteriola*) that are not connected with any sexual morph or hyphal asexual morph present taxonomic problems. While Lundqvist (1980) and Blackwell & Malloch (1990) presented strong support for including those taxa in *Pyxidiophoraceae*, we know them only in very specific, few-celled form and the life cycle studies that would allow for their valid synonymy with other names are extremely laborious and time-consuming. Another important gap of knowledge in taxonomy of *Pyxidiophorales* is limited morphological, distributional, and ecological data available for most species. Many species of *Pyxidiophora*, and nearly all taxa established for ascospore-derived anamorphs, were described in the protologue, and have never been recorded since (Lundqvist 1980, Blackwell et al. 2020).

Significance

Ecological and economic roles

Little is known about the ecological role of most *Pyxidiophorales*. Since some of the species are confirmed as contact mycoparasites, this mode of life is sometimes generalized for all members of the group. *Pyxidiophora hyalina* (= *Chalara hyalina*) was described as a parasite of nematode cysts, suggesting that other members of the group might also share this life mode (Morgan-Jones et al. 1984, Wu & Diao 2023). Because *Pyxidiophorales* are rarely recorded, their ecological impact in natural ecosystems cannot be properly assessed (Haelewaters et al. 2021b). Two species, *viz*. *Gliocephalis hyalina* and *P*. *lundqvisti*, were isolated from stored wheat grains leading to the hypothesis that some *Pyxidiophorales* might be parasites of important crop pathogens and thus could have biocontrol potential (Corlett 1986, Jacobs et al. 2005). Similarly, *Pyxidiophora hyalina* could be tested for biocontrol potential against the nematode *Heterodera glycines*, from which it was isolated (Morgan-Jones et al. 1984).

Other relevant data and future recommendations

Analyzing environmental DNA from metabarcoding and metagenomic studies could offer a possibility of a fast increase in our knowledge of the distribution and ecology of *Pyxidiophorales* (Haelewaters et al. 2021b). Increased sampling and obtaining sequence data for molecular phylogenetic studies would be necessary for elucidating the position of *Pyxidiophorales* in relation to thallus-forming *Laboulbeniomycetes* and other *Ascomycota*. Establishing novel cultures of *Pyxidiophorales* would allow for life cycle and biology research (e.g., interactions with putative hosts) as well as investigating secondary metabolites.

***Lecanoromycetes* O.E. Erikss. & Winka, Myconet 1(1): 7 (1997)**
***Acarosporales* V. Reeb, Lutzoni & Cl. Roux, Mycological Research 111(5): 528 (2007)**

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Acarosporomycetidae*

Introduction

Acarosporales accommodates two families, *Acarosporaceae* and *Eigleraceae,* with one recently introduced genus *Vanderaaea* whose familial placement remains uncertain (Wijayawardene et al. 2022a). The phylogenetically closely related taxa of *Acarosporaceae* exhibit considerable variation in types of asci, hamathecium and secondary chemistry (Reeb et al. 2004). *Acarosporaceae* was established for lichenized species characterized by irregular discs and polyspored asci (Zahlbruckner 1907). The family initially included five genera including, *Acarospora*, *Glypholecia*, *Maronea*, *Biatorella* and *Thelocarpon*. The polyspored asci with more than 100 spores were formed by meiosis followed by several mitoses and this character was used as a distinct feature to identify *Acarosporaceae* (Ozenda & Clauzade 1970, Golubkova 1988, Hafellner 1995). However, a few species such as *Acarospora macrospora*, *A*. *oligospora*, *A*. *placodiiformis*, and *Glypholecia scabra* possess fewer than 100 spores per ascus yet were included within *Acarosporaceae* based on various other morphological characteristics. Various authors used different characters to circumscribe the family including thallus development (Golubkova 1988), apothecium structure (Elenkin 1911a,

Dodge 1973), ascus structure (Hafellner 1995), or ontogeny of the apothecium (Vězda 1978). It was estimated more than 400 species can be accommodated in *Acarosporaceae* (Magnusson 1929, 1935). Poelt (1973) accepted nine genera in *Acarosporaceae* and Eriksson & Hawksworth (1991b) accepted eleven genera with *Thelocarpaceae* are regarded as an earlier synonym. Hafellner (1995) accepted *Acarospora sensu stricto*, *Glyphopeltis*, *Sarcogyne*, *Polysporina* and *Lithoglypha*. *Eigleraceae* was erected by Hafellner (1984) to accommodate a species previously placed in *Aspicilia* or *Lecanora*.

History

Initially, all the lichenized species exhibiting polyspored asci with more than 100 spores were placed in *Acarosporaceae* based on the assumption that polyspored asci originated once during the evolution of lichenized Ascomycetes. However, this hypothesis has been questioned by many authors due to the morphological and anatomical variation observed among species of *Acarosporaceae sensu lato*. Consequently, several members were transferred to other families. Polyspored asci have also been observed in the order *Lecanorales*, leading to the hypothesis that true polyspory may have evolved multiple times during the evolution of lichenized ascomycetes (Reeb et al. 2004).

Both *Acarosporaceae* and *Hymeneliaceae* were included within the suborder *Acarosporineae*. The suborder was invalidly proposed by Poelt (1973) and was later validated by Rambold & Triebel (1992). The phylogenetic analysis conducted by Reeb et al. (2004) found that a representative species of *Hymeneliaceae* and *Ionaspis lacustris* nested within the *Ostropomycetidae* and suggested excluding the family and invalidating the suborder. The heterogeneity of the *Acarosporaceae sensu auct*. was noticed by Poelt & Vězda (1981), including the generic type *Acarospora*. Hafellner (1993, 1995) re-assessed the family and suggested a new family concept based on a shared ascus-type without amyloid structures and an inamyloid or weakly amyloid tholus. *Acarosporaceae* formed a clade outside of *Lecanorales sensu stricto,* and later phylogenetic studies also revealed the distance relationship, but the family fell within the *Lecanoromycetes* (Reeb et al 2004, Wedin et al 2005b, Schoch et al 2009a, Bendiksby & Timdal 2013). Reeb et al. (2004) excluded this family from *Lecanorales* and placed it in a newly established subclass *Acarosporomycetidae*. The subclass was also recognized in the previous phylogenetic analysis conducted by Miadlikowska & Lutzoni (2004). Hibbett et al. (2007) established *Acarosporales* in the subclass *Acarosporomycetidae*.

Westberg et al. (2015) accepted *Acarospora*, *Glypholecia*, *Myriospora*, *Pleopsidium*, *Polysporina*, *Sarcogyne*, *Thelocarpella* and *Timdalia* based on phylogeny with two genera *Caeruleum* and *Lithoglypha* were also presumed to belong within *Acarosporaceae* which lack molecular data. Based on the huge taxon sampling with the sequences from the type *Eiglera flavida*, the placement of *Eiglera* and *Eigleraceae* under *Acarosporales* was confirmed (Miadlikowska et al. 2014). *Vanderaaea* was recently established by Crous et al. (2021a) to accommodate *V. ammophilae* which was reported from dead leaves of *Ammophila arenaria* from the Netherlands. The taxon was mainly characterized by sporodochia with curved, 0–1-septate conidia. The genus was treated under *Acarosporales* genus *incertae sedis* in Wijayawardene et al. (2022a) who also accepted both *Acarosporaceae* and *Eigleraceae* within *Acarosporales*.

General description

The taxa are characterized by immersed or sessile, disciform or perithecioid ascomata, chlorococcoid photobionts, a hyaline, annulate true exciple, inamyloid hymenium, moderately to poorly branched, septate, anastomosing paraphyses, unitunicate, lecanoralean, inamyloid or with slightly amyloid tholi asci, and more than 100 ascospores per ascus with hyaline, small, aseptate, non-halonate ascospores (Reeb et al. 2004). *Acarospora*, *Myriospora*, *Pleopsidium* and *Timdalia* have ascomata with margins that contain green algae (the apothecia are referred to as lecanorine, pseudolecanorine, or more often cryptolecanorine) whereas *Lithoglypha*, *Polysporina* and *Sarcogyne* have algal-free lecideine ascomata often with carbonized margins and/or discs (Westberg et al. 2015). However, the presence or absence of green algae in the ascoma margin varies within a single species (Westberg et al. 2015). *Acarospora* differs from *Polysporina* and *Sarcogyne* in lecanorine ascomata and the latter two genera have lecideine ascomata (Westberg et al. 2015).

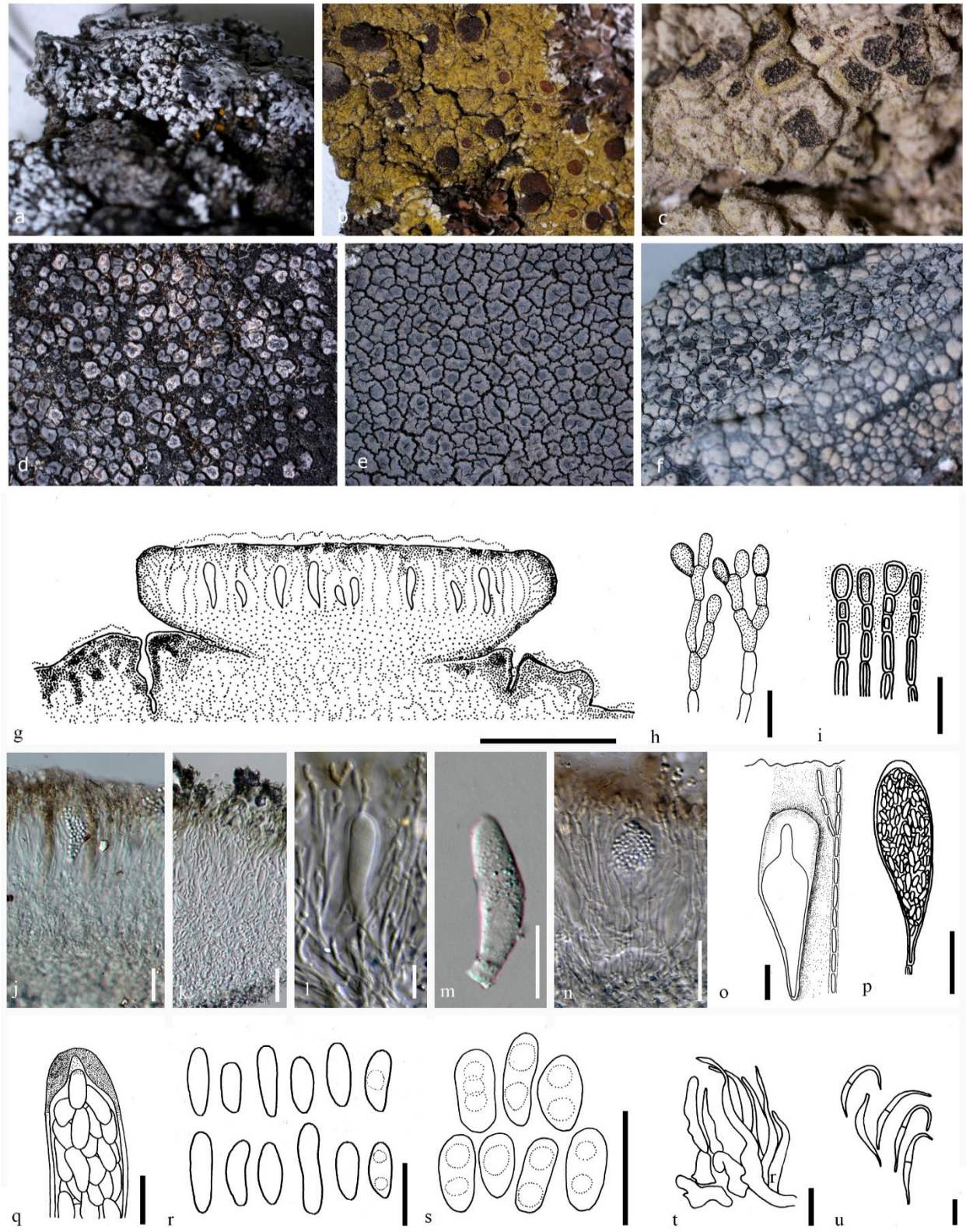


Figure 128 – Sexual and asexual morphology of *Acarosparales*. a–f Thallus morphology (*Acarosparales* sp.). g Vertical section through ascomata (*Sarcogyne sekikaica*). h–k Paraphyses (h Distel cells of paraphyses of *Sarcogyne sekikaica*, i *Sarcogyne iridana*, j, k *Acarosporales* sp.). l–p Ascus and paraphyses (l–n *Acarosporales* sp., o *Lithoglypha aggregata*). p Ascus (*Sarcogyne iridana*). q Apex of submature ascus showing amyloid reaction of the tholus (*Sarcogyne sekikaica*). r, s Ascospores (r *Sarcogyne iridana*, s *Sarcogyne sekikaica*). t Conidiogenous cells giving rise to conidia (*Vanderaaea ammophilae*). u Conidia (*Vanderaaea ammophilae*) (redrawn from Brusse 1988, McCarthy & Kantvilas 2013, McCarthy & Elix 2014, drawn from Crous et al. 2021a). Scale bars: Scale bars: g = 200 µm, h, i = 10 µm, j–n, p = 20 µm, m = 10 µm, q, r, t, u = 10 µm, s = 5 µm.

Sexual morph: *Thallus* crustose, squamulose, rarely foliose-umbilicate. *Photobiont* chlorococcoid. *Ascomata* immersed or sessile, apothecia (cryptolecanorine, lecanorine, or lecideine, more rarely biatorine or pseudolecanorine), rarely perithecia. *Paraphyses* (in *sensu lato*) moderately or slightly branched-anastomosed. *Asci* bitunicate, functionally unitunicate, inamyloid or slightly amyloid tholus, presence of ocular chamber. *Ascospores* generally more than 100 per ascus, simple and colorless, without halo. Asexual morph: *Conidiomata* sporodochial, round, erumpent, green-brown, giving rise to a mucoid conidial mass. *Conidiophores* reduced to conidiogenous cells formed on a stroma of pale brown pseudoparenchymatal cells, smooth, ampulliform to subglobose, proliferating holoblastically. *Conidia* solitary, hyaline, smooth, 0–1-septate, fusoid, flexuously curved, apical cell developing into a long flexuous apical appendage with subobtuse tip, basal cell tapering towards a truncate hilum (Fig. 128).

Families included in *Acarosporales*

Acarosporaceae Zahlbr.
Eigleraceae Hafellner

Acarosporales genus *Incertae sedis*
Vanderaaea Crous

Evolution

Acarosporaceae was considered as among the earliest lichenized members which split from the rest of the *Lecanoromycetes* and appeared in the late Carboniferous-early Permian but among the most recent groups to diverge (upper Cretaceous) (Prieto & Wedin 2013). The strongly black pigmented (carbonized or melanized) ascomata have independently arisen several times in the evolution of the *Acarosporomycetidae* and the carbonization seems to be a derived character that has appeared several times during the evolution of the *Acarosporomycetidae* (Westberg et al. 2015).

Justification of order and problems

Important diagnostic features are the multi-spored asci with the crustose habit. A majority of species are found on acidic to basic siliceous rock or soil. Phylogeny and morphology are not always congruent, with characters such as carbonization of the ascomata (used to distinguish *Polysporina* and *Sarcogyne* from *Acarospora*) appearing to have evolved on several occasions (Westberg et al. 2015). Taxonomic remodeling of the genera has yet to be completed, but it is unlikely that they will be morphologically coherent. Wider species sampling for phylogenetic analyses is also needed.

Significance

Ecological and economic roles

Members of *Acarosporaceae* reported in all continents on exposed rocks and soil and their ability to survive under highly mineralized rocks and low-pH habitats show adaptations to extreme environments (Wedin et al. 2009a). Some representatives of *Acarospora smaragdula* complex are known to accumulate substantial amounts of potentially toxic metals, including iron and copper, resulting in populations with highly divergent coloration and morphology (Wedin et al. 2009a).

Chemical diversity

The chemical diversity of *Acarosporales* is not well explored. Norstictic acid is reported in *Acarospora smaragdula sensu stricto* (Wedin et al. 2009a).

***Baeomycetales* Lumbsch, Huhndorf & Lutzoni, Mycological Research 111(5): 529 (2007)**

(= *Arctomiales* S. Stenroos, Miądl. & Lutzoni; *Hymeneliales* S. Stenroos, Miądl. & Lutzoni; = *Trapeliales* B.P. Hodk. & Lendemer)

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Ostropomycetidae*

Introduction

This lichenized order *Baeomycetales* was introduced to accommodate species with chlorococcoid photobiont, sessile or rarely stalked, disciform ascomata, hyaline or pigmented, annulate or cupulate exciple, inamyloid hymenium, moderately to richly branched, septate paraphyses, unitunicate, inamyloid or with slightly amyloid tholi, 8-spored asci and hyaline, aseptate or transseptate, halonate or non-halonate ascospores (Hibbett et al. 2007). The generic concept of *Baeomycetaceae* has changed over time. Initially, *Baeomycetaceae* was erected for *Baeomyces* (Dumortier 1829). Reinke (1895) treated *Baeomyces* under *Lecideaceae*. Later, Zahlbruckner (1903-1907, 1926) treated it under *Cladoniaceae*. Lamb (1954) considered that *Lecanorales* is the ancestor of *Baeomycetaceae* and considered *Baeomyces* to be equally related to *Cladonia* and stated that *Baeomyces* represents an intermediate condition between the *Lecideaceae* and the *Cladoniaceae*. The taxonomy of familial and ordinal concepts of *Baeomycetales* has also undergone several changes with the advent of molecular data, which led to the inclusion of eight families within the order.

History

Kauff & Lutzoni (2002) proposed an elevation of the *Baeomycetaceae* (represented in their tree by *Baeomyces placophyllus*) to the order level (*Baeomycetales*) in the *Ostropomycetidae*. *Baeomycetaceae* was earlier placed in *Helotiales* (Chadefaud 1960, Rambold et al. 1993) and *Lecanorales* but was rejected by later studies (Kauff & Lutzoni 2002, Miadlikowska et al. 2006). Kauff & Lutzoni (2002) initially proposed *Baeomycetales* because, in their study, *Baeomyces placophyllus* cladded within *Ostropomycetidae* and rejected placement in *Helotiales*. This is also supported by the study of Miadlikowska et al. (2006). *Baeomycetales* was introduced by Hibbett et al. (2007) within *Ostropomycetidae* and the order formed a close phylogenetic association with *Agyriales*, *Ostropales* and *Pertusariales* in the phylogeny. *Trapeliales* was established to accommodate *Trapeliaceae* (Hodkinson & Lendemer 2011) and the authors accepted only *Anamylopsoraceae* and *Baeomycetaceae* within *Baeomycetales*. Miadlikowska et al. (2014) accepted *Anamylopsoraceae* and *Baeomycetaceae* within *Baeomycetales*. However, they questioned the placement of *Anamylopsoraceae* within *Baeomycetales* because of the weak support obtained for *Anamylopsora* in the study of Lumbsch & Lindemuth (2001).

Further, *Baeomycetales* formed a close phylogenetic clade to *Arctomiales*, *Hymeneliales*, *Ostropales* and *Trapeliales* (Miadlikowska et al. 2014) within *Ostropomycetidae*. Based on the phylogenetic analyses, Resl et al. (2015) recognized *Arctomiaceae*, *Hymeneliaceae*, *Trapeliaceae* and *Xylographaceae* within *Baeomycetales*. Based on temporal band approach, *Arctomiales*, *Hymeneliales* and *Trapeliales* were synonymized under *Baeomycetales* and accepted seven families including *Arctomiaceae*, *Arthrorhaphidaceae*, *Baeomycetaceae*, *Cameroniaceae*, *Hymeneliaceae*, *Protothelenellaceae*, *Trapeliaceae* and *Xylographaceae* under *Baeomycetales* (Kraichak et al. 2018b). *Cameroniaceae* is the only family which was introduced in the past decades (Lumbsch et al. 2012) to accommodate a monotypic genus *Cameronia*. However, the inclusion of *Arctomiales* and *Trapeliales* in *Baeomycetales* was not supported in the phylogenetic analysis conducted by Magain et al. (2020).

General description

Arctomiaceae is the only family of the *Ostropomycetidae* which associates with cyanobacteria (*Nostocales*) whereas other species are associated with chlorococcoid as a photobiont partner.

Sexual morph: *Ascomata* sessile or rarely stalked, disciform. *True exciple* hyaline or pigmented, annulate or cupulate. *Hymenium* non-amyloid. *Paraphyses* moderately to richly branched, septate. *Asci* unitunicate, inamyloid or with slightly amyloid tholi, 8-spored. *Ascospores* hyaline, aseptate or trans-septate, halonate or non-halonate. Asexual morph: *Conidiomata* pycnidia, globose, immersed to surficial and ±adnate, with conidiogenous. *Conidia* filiform (Fig. 129).

Families included in *Baeomycetales*

Arctomiaceae Th. Fr.

Arthrorhaphidaceae Poelt & Hafellner

Baeomycetaceae Dumort.
Cameroniaceae Kantvilas & Lumbsch
Hymeneliaceae Körb.
Protothelenellaceae Vězda, H. Mayrhofer & Poelt (= *Thrombiaceae* Poelt & Vězda ex J.C. David
Trapeliaceae M. Choisy ex Hertel
Xylographaceae Tuck.

Evolution

Baeomycetaceae with *Icmadophilaceae* were previously placed in the non-lichenized order *Helotiales,* considering the independent evolution of lichenizations which were later transferred to other orders (Chadefaud 1960, Rambold et al. 1993). However, the absence of a photobiont partner in *Xylographa constricta* in the predominantly lichenized order showed the delichenization during the evolution which is reported as a saprobe (Spribille et al. 2016).

Justification of order and problems

The order was recently delimited by Kraichak et al. (2018b) based on the temporal band approach. However, the inclusion of *Arctomiales* and *Trapeliales* in *Baeomycetales* was not supported in the phylogenetic analysis conducted by Magain et al. (2020). Thus, broad taxon sampling with reinvestigation of this order is recommended. Several new genera, including *Brianiopsis*, *Farkasiella*, *Gallowayiopsis*, *Kleopowiella*, *Trapegintarasia*, *Trapejamesia*, and *Xyloelixia* were added to *Trapeliaceae* and *Xylographaceae* based on morphological and molecular analyses. However, the phylogeny of the total species diversity of these two families was not analyzed, even though many studies were conducted recently (Kondratyuk et al. 2022). The phylogenetic position of several genera also remains uncertain, which needs further recollections to resolve the taxonomy of *Baeomycetales*.

Significance

Ecological and economic roles

The taxa are reported in both corticolous and saxicolous habitats as well as soil and the taxa are reported worldwide (Spribille et al. 2016). Several lichenicolous fungi are reported in *Baeomyces* (Ihlen 1998, Diederich et al. 2018, Zhurbenko & Ohmura 2020). The members are primarily reported as lichenized. The non-lichenized saprobic fungus *Xylographa constricta* appears to squeeze the wood fibres and raise them into small heaps (Spribille et al. 2016).

Chemical diversity

The chemical tests revealed several substances in the recently introduced genera. Gyrophoric acid (major), 5-O-methylhiascic acid (minor or trace), or 5-O-methylhiascic acid (major) and gyrophoric acid are reported in *Gallowayiopsis*. Stictic acid, or, stictic and ± norstictic acids, or norstictic acid, as well as aliphatic (fatty) acids are detected in *Brianiopsis*. In *Kleopowiella*, gyrophoric acid, or gyrophoric acid (major) and 5-Omethylhiascic acid minor are reported. 5-O-methylhiascic acid (major), 5-methoxtlecanoric acid (major or minor), gyrophoric acid (minor), hiascic acid (minor or trace), lecanoric acid (minor) and orsellinic acid (minor) are reported in *Trapegintarasia*. Confriesiic acid (major or trace), friesiic acid (minor or major) and 1–3 unidentified fatty acid(s) (major) are detected in *Xyloelixia* (Kondratyuk et al. 2022). Ahti (1982) reported that *Baeomycetaceae* species primarily produce 8-orcinol depsidones of the stictic acid complex.



Figure 129 – Morphology of *Baeomycetales*. Thallus morphology of *Baeomycetales* (a *Ainoa* sp., b–d *Anamylopsora* sp., e–f, h, i *Baeomycetales* sp., g *Placopsis* sp.). k, l Vertical sections through ascomata (k, l *Baeomycetales* sp.). m, n Paraphyses (m *Baeomycetales* sp. n *Xylographa lagoi*). o, p Ascus (o *Baeomycetales* sp., p *Xylographa lagoi*). q, r Ascospores (q *Steinera* sp., r *Xylographa lagoi*). (drawn from Spribille et al. 2014, Magain et al. 2020). Scale bars: k = 500 µm, l, m, o = 20 µm, n, p = 5 µm, q = 10 µm, r = 2.5 µm.

Caliciales **Bessey, University of Nebraska Studies 7: 299 (1907)**

Subphylum : *Pezizomycotina*

Class : *Lecanoromycetes*
Subclass : *Lecanoromycetidae*

Introduction

Caliciales is the fifth largest lichenized order in *Ascomycota* which comprises over 1200 species assigned to 55 genera. The order also represents *Buellia*, one of the most speciose lichenized genera (Lücking et al. 2017). *Caliciales* which was introduced by Fries (1817) belongs to the class *Lecanoromycetes*. The passive spore dispersal which found in calicioid fungi is considered as an unusual feature among lichenized taxa (Tibell 1984). *Caliciales* was traditionally considered as a monophyletic group. However, the monophyletic nature of this order became contentious at the end of 19th century (Henssen & Jahns 1973, Schmidt 1970). Advanced molecular studies in the 20th century have led to numerous changes in the classification of *Caliciales* (Tibell & Wedin 2000, Miadlikowska et al. 2006, Gaya et al. 2012). Thus, *Caliciales* presently comprises two families, namely *Caliciaceae* and *Physciaceae*, which can be separated based on multigene phylogenetic analyses as well as phenotypic characters (Gaya et al. 2012, Prieto et al. 2013, Lücking et al. 2017, Prieto & Wedin 2017, Andrade et al. 2020, Wijayawardene et al. 2017a, 2018, 2020). *Caliciaceae* was described by Fee (1824) which presently includes 36 genera with *Calicium* as the type (Lücking et al. 2017). The type genus was introduced by Persoon (1794a). The taxa of *Caliciaceae* are characterized by thin-walled and evanescent prototunicate asci, whereas ascus and spore structures have been primarily used to characterize *Physciaceae* (Lohtander et al. 2000). *Physciaceae* was introduced by Zahlbruckner (1926) with three genera, *viz*. *Anaptychia*, *Physcia* and *Pyxine* and the family presently comprises 19 genera (Lücking et al. 2017). The members of *Caliciales* are mainly lichenized while several genera encompass lichenicolous species i.e. *Acolium*, *Amandinea*, *Buellia*, *Caliciella*, *Calicium*, *Dimelaena*, *Diplotomma*, *Endohyalina*, *Monerolechia*, *Rinodina* and *Tetramelas* (Diederich et al. 2018). The taxa are distributed worldwide with most occurring on bark, wood, rock, soil, basaltic lava flows and man-made concrete in undisturbed primary forests as well as urban areas (Rikkinen 2003b, Puntillo & Puntillo 2009, Temu et al. 2019, Molins et al. 2020).

History

Studies on calicioid fungi commenced when mycological research first started and was represented by a heterogeneous assemblage of taxa which have a mazaedium (Prieto et al. 2013). However, several taxa of *Eurotiomycetes* and *Leotiomycetes* that produce mazaedia or mazaedia-like structures have not been treated in *Caliciales sensu lato* due to ascus morphology which lack prototunicate asci (Prieto et al. 2013). The studies on calicioid fungi started with the introduction of two calicioid genera, *Calicium* and *Sphaerophorus* (Persoon 1794a). Acharius (1803, 1814, 1815, 1816b, 1817a) described *Cyphelium* and *Coniocybe* and placed in 'Plantae Calicioidea' with *Calicium* and *Sphaerophorus*. Subsequently, Fee (1824) referred 'Plantae Calicioidea' as 'Coniocarpi' and recognized two families namely, *Caliciaceae* and *Sphaerophoraceae*. Nylander (1862, 1863, 1876) introduced a few species in *Caliciales*. Vainio (1890) provided a significant work on this order and reported 14 species with several non-lichenized genera such as *Chaenothecopsis*, *Microcalicium*, *Strongylopsis* and *Strongyleuma*. Tibell (1982) accepted 26 species with five new species from Costa Rica. Henssen & Jahns (1973) and Schmidt (1970) stated the heterogeneous assemblage of this order based on the investigation of mycocaliciaceous material which had an active spore dispersal mechanism with non-lichenized lifestyle. Hence, Schmidt (1970) established *Mycocaliciaceae* for non-lichenized calicioid genera. Tibell (1984) provided a detailed study on *Caliciales* and supported the non-monophyletic nature of this order based on morphological, chemical, and ultrastructural evidence with phenetic and cladistic analyses. He concluded that *Caliciaceae*, *Mycocaliciaceae* and *Sphinctrinace* are monophyletic which form the core group of *Caliciales*, while five more families and eight tentatively assigned genera were assumed as polyphyletic lineages (Prieto et al. 2013). Tibell & Wedin (2000) established a new order *Mycocaliciales* to include the non-lichenized families *Mycocaliciaceae* and *Sphinctrinaceae* based

on the phylogenetic analysis of the SSU gene region together with morphology. This order was further assigned to a new subclass *Mycocaliciomycetidae* in *Eurotiomycetes* (Hibbett et al. 2007).

Miadlikowska et al. (2006) accepted both *Caliciaceae* and *Physciaceae* under the suborder *Physciineae* in *Teloschistales* based on the phylogenetic analysis. This suborder was originally introduced by Henssen & Jahns (1974) for *Physciaceae*. Wedin & Grube (2002) suggested to combine both families under the name *Physciaceae*. Wedin et al. (2000a) noted the close phylogenetic relationship of these two families with *Lecanorales*. However, the study of Miadlikowska et al. (2006) was accepted in subsequent studies (Hibbett et al. 2007, Lumbsch & Huhndorf 2007, Kirk et al. 2008a). Gaya et al. (2012) accepted *Caliciaceae* and *Physciaceae* under *Caliciales* based on multigene phylogenetic analysis and this classification has been accepted in recent studies (Prieto et al. 2013, Lücking et al. 2017, Prieto & Wedin 2017, Wijayawardene et al. 2017a, 2018, 2020, 2022a).

General description

Calicioid lichens are also called as 'pin lichens' or 'stubble lichens' with regard to their morphology (Tibell 2003). *Caliciaceae* includes mazaediate genera and non-mazaediate genera with Bacidia-type asci, whereas *Physciaceae* includes Lecanora-type asci (Wedin et al. 2000, Miadlikowska et al. 2006, 2014, Gaya et al. 2012, Prieto & Wedin 2017). The mazaedium is an accumulation of spores covering the ascomatal surface formed by an early disintegration of the asci when semi-mature spores are released to mature in a loose mass. The color of the mazaedium depends on the spore pigmentation and is dispersed passively (Tibell 1984, Prieto et al. 2013, Prieto & Wedin 2017). Calicioid taxa form apothecial ascomata which are stalked or sessile to immersed on various thallus structures which are crustose, foliose, or fruticose (Middelborg & Mattsson 1987, Elix 2009, Helms et al. 2003). *Dirinaria* and *Pyxine* form micro-foliose structures (Andrade et al. 2020). In mazaediate taxa, the asci are prototunicate and dissolve before the spores reach maturity (Ekanayaka et al. 2017a). The shape of the ascomata can vary and mostly form disc-shaped ascomata (Tibell 1996a, Printzen 2010). *Chlorococcoid*, *Trebouxia* and *Trentepohlia* are commonly found as photobionts, but they differ with genus as well as species (Tibell 1996a, Hoffmann & Van Landuyt 1997, Dahlkild et al. 2001, Helms et al. 2003, Elix 2009).

A strongly melanized excipulum is observed in *Caliciaceae* and several genera of *Physciaceae* and is absent in apothecia that are embedded in the thallus. However, the presence of strongly melanized excipulum is also found in several families of *Lecanorales*. Thus, it is not considered as a distinctive character within *Caliciales* (Wedin et al. 2000a). Asci can be clavate or cylindrical and ascospores are mostly ellipsoidal and range from 1-septate to multi-septate and sometimes sub-muriform or muriform (Tibell 1996a, Wedin et al. 2000a). The ascospores of *Caliciaceae* and *Physciaceae* are mostly identical (Wedin et al. 2000a). Internal wall thickenings in the ascospores were widely used for generic delineation of *Physciaceae* (Poelt 1965, Hafellner et al. 1979, Mayrhofer 1982). However, later studies stated that wall thickenings may change during spore ontogeny (Scheidegger 1988, 1993, Scheidegger & Ruef 1988). In addition, ascospore color, size, septation and ornamentations were used in the species delineation of *Caliciales* (Tibell 1996a). However, Helms et al. (2013) stated that ascus type and hypothecial pigmentation provide a better resolution for *Physciaceae*. The asexual morph is reported in several genera of *Caliciales* which produce soridia or isidia (Sheard 1982, Elix et al. 2009, Zachariah et al. 2019). Umbilicaria-type pycnidia is observed in *Buellia*, *Dermatiscum*, *Physcia*, *Physconia* and *Santessonia*. The type of pycnidia and conidiophores supports the close association with *Lecanorales* (Wedin et al. 2000a). Scheidegger (1993) stated that conidial type gives better generic resolution than ascospore morphology.

Sexual morph: *Thallus* crustose, foliose and fruticose. *Prothallus* present or absent. *Ascomata* apothecial, stalked to sessile, mostly disc-shaped, concave to plane, proper margin present or absent. *Mazaedium* present or absent. *Pruinose* present or absent. *Hypothecium* hyaline to pigmented. *Excipulum* well or poorly developed, mostly strongly melanized. *Hymenium* inspersed with oil droplets or not, hyaline to brown, comprising sparingly branched or unbranched paraphyses and asci.

Paraphyses sometimes swollen at the tips. *Epihymenium* present or absent. *Asci* cylindrical to clavate, prototunicate or non-prototunicate, Bacidia-type or *Lecanora*-type, amyloid or non-amyloid, eight to multi-spored. *Ascospores* ellipsoid to oblong, with or without distinct wall thickenings, 1-septate to muriform, sometimes slightly constricted at the septum, hyaline to dark brown, mostly ornamented. Asexual morph: *Soridia*, *Isidia*, *Lobules* or *Pycnidia* (Figs. 130, 131, 132).

Families included in *Caliciales*

Caliciaceae Chevall.
Physciaceae Zahlbr.

Evolution

Commensalistic or parasitic species have presumably derived through de-lichenization in *Caliciales* (Wedin & Tibell 1997). The mazaedium and passive spore dispersal were assumed to have evolved independently in the polyphyletic group of Tibell's (1984) classification which have later been transferred to several classes such as *Arthoniomycetes*, *Coniocybomycetes*, *Eurotiomycetes*, *Lecanoromycetes* and *Leotiomycetes* based on phylogenetic analyses (Prieto et al. 2013). The evanescent asci, with passive spore dispersal, and the development of a mazaedium, are a secondary reduction from a non prototunicate ascus with an apical dehiscence apparatus and active spore dispersal. They have occurred several times independently within *Caliciaceae* (Tibell 2003, Gaya et al. 2012, Wedin et al, 2000a). In the study of Helms et al. (2003), all monophyletic lineages with non-crustose growth exhibited uniform ascospore types indicating a higher evolutionary age of ascospore types than foliose growth habit.

Justification of order and problems

The close association of *Caliciaceae* with *Mycocaliciaceae* and *Sphinctrinaceae* were supported by shared morphological characteristics in the ascoma and spore ornamentation despite several genera having passive spore dispersal and the absence of mazaedium development (Wedin & Tibell 1997). However, Tibell's (1984) hypothesis on the monophyly of the core of *Caliciales* was not supported by molecular studies (Gargas et al. 1995, Wedin & Tibell 1997). Wedin & Tibell (1997) found that *Caliciaceae* nested with *Lecanorales* and stated that *Caliciales* should be synonymized under *Lecanorales*. The presence of secondary substances and prototunicate ascus also supported the placement of these two families within *Lecanorales* (Wedin et al. 2000a).

Wedin et al. (2002) and Tibell (2003) suggested that *Caliciaceae* and *Physciaceae* could be congeneric. However, broad taxon sampling with multigenes is important to clarify the phylogenetic relationship between these two families. Morphologically similar species have shown independent phylogenetic evolution (e.g., *Physcia aipolia*) and chemical production (e.g., *Acroscyphus sphaerophoroides*) (Niu et al. 2008, Elix et al. 2009). Thus, broad sampling is also needed for species delineation (Elix et al. 2009). In addition, chemical characteristics also need to be considered in the taxonomy of calicioid fungi (Elix et al. 2009). Gaya et al. (2012) proposed two subfamilies *Buellioideae* and *Calicioideae* under *Calciaceae*. These two families share true excipulum, Beltraminia-type ascospores and similar ascospore ontogeny and ornamentation (Helms et al. 2003, Gaya et al. 2012). However, this hypothesis was not accepted due to lack of phenotypic differences and extensive taxon sampling is needed to establish the subfamily.

Significance

Ecological and economic roles

Several taxa of *Caliciaceae* such as *Amandinea*, *Bacidia*, *Dirinaria* and *Pyxine* have been reported on monuments in India, thus considered as biodeterioration agents (Behera et al. 2020). They cause undesirable changes by their vital activities on culturally valuable structures (Behera et al. 2020). Some species have been used in the fossil calibration of fungi (Prieto & Wedin 2013). Rikkinen et al. (2018) reported three fossils confidently assigned to *Calicium* on Baltic and Bitterfeld amber dating back 24–47 MYA. Some halotolerant species such as *Dirinaria picta*, *Physcia atrostriata*, and *Pyxine retirugella* produce photoprotective pigments and atranorin to ensure efficient

photosynthesis. Some phycobionts also produce polyols to enhance the desiccation tolerance of their mycobiont partners (Delmail et al. 2013).

Some species have specificity for substrate as well as ecology (Middelborg & Mattsson 1987). Molins et al. (2020) found that same species associated with different photobionts, such as *Trebouxia cretacea*, *T. asymmetrica* and *Trebouxia* sp. *`arnoldoi´*. This kind of association mainly influenced by bioclimatic factors, geography, and habitats. Consequently, Moya et al. (2021) found photobionts also influenced by geography as well as habitats. Several species also have been reported from harsh environments such as mangrove ecosystem which indicates their tolerance to solar radiation, desiccation, salinity, and human interruption (Nayaka et al. 2012, Delmail et al. 2013). Calicioid fungi are sensitive for external environment activities such as air pollution and fire and are often included in red lists due to habitat degradations (Puntillo & Puntillo 2009). They have also been reported as bioindicators (Tibell 1992, Kruys & Jonsson 1997, Aguirre-Hudson et al. 2007, Puntillo & Puntillo 2009, Behera et al. 2020). Some species are used as 'key species' or 'indicator species' in forests and other habitats with high conservation values due to specific ecological requirements (Tibell & Knutsson 2016).



Figure 132– Asci and ascospores morphology of *Caliciales* a *Acolium yunnanense*. b *Pyxine berteriana*, c–e, i *Caliciales* sp. f, g *Sculptolumina* sp. h. j *Acroscyphus* sp. k–m, q *Caliciales* sp. n *Pyxine berteriana*. o *Sculptolumina* sp. p *Acolium yunnanense*. Scale bars: a, j–l, o, q = 20 µm, d–h = 30 µm, m, n = 10 µm.

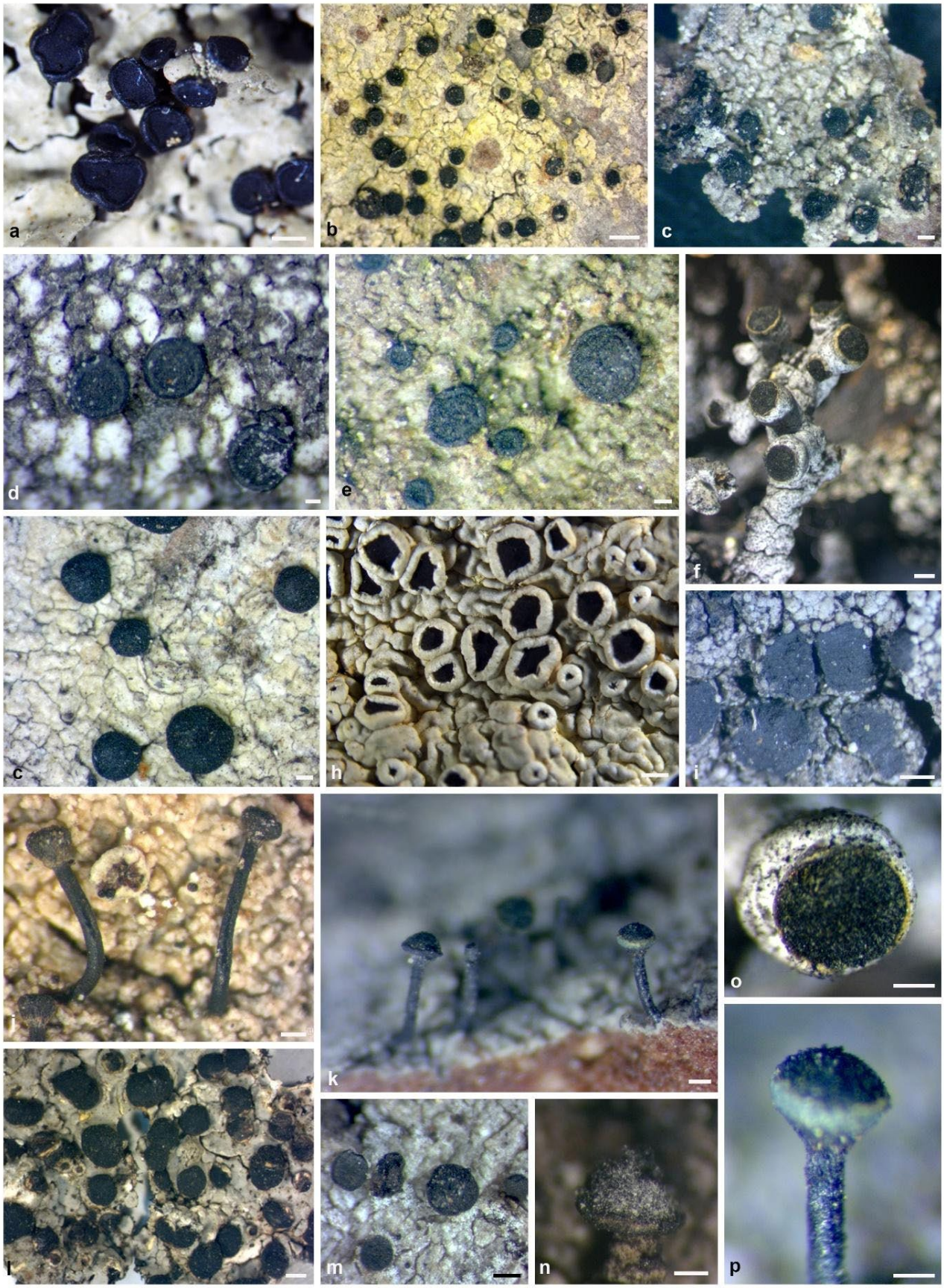


Figure 130 – Thallus morphology of *Caliciales.* a, l *Pyxine* sp. b *Buellia* sp. c, d, g, m *Caliciales* sp. e *Sculptolumina* sp. h *Dirinaria* sp. j, k, p *Calicium* sp. n *Acolium yunnanense*. f, o *Acroscyphus* sp. Scale bars: a, b, f, h, i, l = 500 µm, c, g, j, k, n, o = 200 µm, d, e, m, p = 100 µm.



Figure 131 – Ascomata morphology of *Caliciales* a, l *Pyxine* sp. b *Buellia* sp. c, h *Acolium yunnanense*. d1, d2 *Acroscyphus* sp. e *Dirinaria* sp. f, g, i–k *Caliciales* sp. Scale bars: a, d1, l = 500 µm, b, d2, g, h, i, k = 100 µm, c, e, f, j = 200 µm.

Chemical diversity

Calicioid species are associated with a wide range of chemical production (Tibell 1996a). Several species in genera such as *Amendinea*, *Cyphelium*, *Calicium* and *Bacidia* produce secondary metabolites such as anthraquinones, atranorin, chodectonic acid, confluentic acid depsidones, dichlorolichenoxanthone, divaricatic acid, graciliformin, lichenoxanthane, N orstictic acid, norlichenoxanthon acid, norstictic acid, pulvinates, stictic acid, triterpene, triterpenoids, xanthones and β-orcinol depsides (Aguirre-Hudson et al. 2007, Elix et al. 2009, Behera et al. 2020). The importance of some chemical substances needs further investigations for beneficial applications (Studzinska-Sroka et al. 2017). However, these chemical substances are not exclusive for neither *Caliciaceae* nor *Physciaceae*. This indicates a close sister-group relationship between these families, but the quantity of chemicals can be varied. Tetronic acid derivatives are common in *Caliciaceae* and rare in *Physciaceae* whereas atranorin and b-orcinol depsidones are common in *Physciaceae* but rare in *Caliciaceae* (Wedin et al. 2002).

Other relevant data and future recommendations

Despite their ecological roles and production of secondary metabolites, calicioid species are often threated by anthropogenic activities such as application of fertilizers, herbicides or pesticides in the vegetative field, inappropriate collection, climate change and elevated sulphur or nitrogen levels in the atmosphere (Thor 1998, Marmor & Randlane 2007, Sujetovienė 2010). Air pollution causes serious threats for red listed species (Thor 1998, Aptroot & Seaward 1999). The changes in the pH of bark influenced by air pollution affect the species composition of some epiphytic lichens such as *Calicium viride*, *Physcia adscendens*, *P. dubia* and *P. tenella* (Marmor & Randlane 2007, Sujetovienė 2010, Spier et al. 2010).

Some species have been overlooked in the field and many calicioid fungi are yet to be described (Prieto et al. 2020). The type species *Calicium viride* had confusion with *Calicium corynellum* which has been treated as a red listed species in Britain. Yahr (2015) treated *C. corynellum* under *C. viride* based on molecular evidence and suggested to re-evaluate conservation status. Prieto et al. (2020) studied both species from several fresh and herbarium collections from whole known distribution and found that they are two distinct species based on morphology, phylogeny, and chemical diversity. Thus, detailed investigation on calicioid species is required for future conservation as well as better taxonomic resolution (Prieto et al. 2020). The generic and species delineation of several taxa remains uncertain (Scheidegger et al. 2001). Several genera such as *Ciposia*, *Endohyalina*, *Hypoflavia*, *Orcularia*, *Sphinctrinopsis* and *Tylophoropsis* lack molecular data and need further studies for generic classification (Gaya et al. 2012, Lücking et al. 2017).

***Graphidales* Bessey, University of Nebraska Studies 7: 298 (1907)**

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Ostropomycetidae*

Introduction

The taxa within *Graphidales* are distinguished by their lichenized nature, featuring apothecioid to frequently lirellate ascomata, and thick-walled asci containing a ring-shaped structure protruding into the lumen (Lücking 2019). The order *Graphidales* consists of six families, with Xavier-Leite et al. (2023) recently introducing 17 new and reinstated genera to this taxonomic group.

History

Graphidales was previously placed in the lower class *Ascosporeae* and the taxa were characterized by elongated apothecium opened by a narrow slit often black-margined (Bessey 1914). Gilenstam (1969) proposed the inclusion of lichenized genera *Graphis*, *Diploschistes*, and *Thelotrema* in *Graphidales* when transferring *Conotrema* to *Ostropaceae*. *Ostropales* was originally introduced to accommodate *Ostropaceae* (Nannfeldt 1932). *Conotrema* was previously placed in *Diploschistaceae* and was closely associated with *Graphis*, *Diploschistes*, and *Thelotrema* in having the same development of the apothecium, structure of the excipulum, ascus type, and the production of conidia. Henssen & Jahns (1973) divided *Ostropales* into two suborders, 1) *Ostropineae* (*Stictidaceae* including *Conotrema* and *Thelotremataceae*) and 2) *Graphidineae* (*Graphidaceae*) which was further accepted by Eriksson & Hawksworth (1993b) and Hawksworth et al. (1995). However, Poelt (1973) questioned the relationship between the order *Ostropales* with *Graphidales*. Sherwood (1977b) accepted two orders, *Graphidales* with 'graphidean' ascospores and *Ostropales* with normal sequence of ascospore septation. Lumbsch et al. (1997) found that irregular ascospore septation is also found in *Diploschistes* (*Graphidales*). Thus, declined to separate the orders based on ascospore septation. Eriksson & Hawksworth (1998) accepted eight families in *Ostropales* including *Asterothyriaceae*, *Gomphillaceae*, *Graphidaceae*, *Odontotremataceae*, *Phaneromycetaceae*, *Solorinellaceae*, *Stictidaceae*, and *Thelotremataceae*. Winka et al. (1998a) suggested including *Graphidales* under *Ostropales* based on the phylogenetic analysis conducted for SSU sequence data using the representative genera of *Conotrema*, *Cyanodermella* (*Stictidaceae*),

Diploschistes (*Thelotremataceae*) and *Graphis* (*Graphidaceae*) and these families formed a monophyletic clade with strong bootstrap support (82%). However, the author also mentioned that separating the orders *Graphidales* and *Ostropales* would require extensive taxon sampling.

The familiar classification of the order changed over time (Staiger et al. 2006, Plata & Lumbsch 2011, Lücking et al. 2013). Lücking et al. (2017) accepted *Coenogoniaceae*, *Gomphillaceae*, *Graphidaceae (Fissurinoideae*, *Graphidoideae*, *Redonographoideae)*, *Gyalectaceae*, *Phlyctidaceae*, *Porinaceae*, *Protothelenellaceae*, *Sagiolechiaceae*, *Stictidaceae*, *Thelenellaceae* and *Thrombiaceae* under *Ostropales*. Further, *Thelotremataceae* was treated under *Graphidaceae* which was previously proposed by Mangold et al. (2008) based on molecular phylogeny. Kraichak et al. (2018b) resurrected *Graphidales* based on a temporal band approach and accepted *Diploschistaceae*, *Fissurinaceae*, *Gomphillaceae*, *Graphidaceae* and *Thelotremataceae* under this order and didn't include the subfamily *Redonographoideae* in the analyses. Further *Coenogoniaceae*, *Gyalectaceae*, *Phlyctidaceae*, *Sagiolechiaceae*, and *Porinaceae* (= *Trichotheliaceae*) were placed in *Gyalectales*, *Protothelenellaceae* and *Thrombiaceae* (= *Protothelenellaceae*) were placed in *Baeomycetales*, *Thelenellaceae* was placed in *Thelenellales* and *Stictidaceae* was placed in *Ostropales* (Kraichak et al. 2018b). This classification was also accepted in the outline of Wijayawardene et al. (2022a). However, Lücking (2019) did not completely accept the classification of Kraichak et al. (2018b) and accepted only the ordinal classification (*Graphidales*, *Gyalectales*, *Ostropales sensu stricto*, *Thelenellales*) and followed the previous studies for familial, subfamilial and tribe classification that were proposed. Thus, *Gomphillaceae* and *Graphidaceae* (*Fissurinoideae*, *Graphidoideae*, *Redonographoideae*) are accepted under *Graphidales* further the tribes *Acanthothecieae*, *Diploschisteae*, *Leptotremateae* and *Wirthiotremateae* were accepted under the subfamily *Graphidoideae* (Lücking et al. 2017, Lücking 2019). The monophyletic nature of *Graphidales* was also confirmed in the phylogenetic analyses conducted by Guterres et al. (2020).

General description

Thallus crustose. with or without pruinose. *Photobiont* trentepohlioid. Sexual morph: *Ascomata* apothecioid, perithecioid, lirellate, and pseudostromatic ascomata, immersed to sessile, solitary or aggregated. *Disk* dark to pigmented. *Excipulum* carbonized or not carbonized *Hamathecium* comprised anastomosing, gelatinous, simple or branched paraphyses. *Periphysoids* present or not. *Asci* clavate to cylindrical, inamyloid to amyloid. *Ascospores* transversely septate to muriform, oblong to ellipsoid, hyaline to brown, euseptate to distoseptate, inamyloid to amyloid, thin-to-thick walled, lumina lens-shaped to rounded or rectangular. Asexual morph: *Conidiomata* pycnidial, conidia or hyphophores, usually stipitate but sometimes disc-shaped or campylidioid (Fig. 133).

Families included in *Graphidales*

Diploschistaceae Zahlbr.
Fissurinaceae (Rivas Plata, Lücking & Lumbsch) B.P. Hodk.
Gomphillaceae Walt. Watson
Graphidaceae Dumort.
Redonographaceae (Lücking, Tehler & Lumbsch) Lumbsch
Thelotremataceae Stizenb.

Evolution

The evolution of *Graphidaceae* has been extensively studied (Staiger et al. 2006, Plata & Lumbsch 2011, Lücking et al. 2013). Plata & Lumbsch (2011) investigated the parallel evolution and phenotypic divergence of *Graphidaceae* by conducting ancestral character reconstruction for broad phenotypic traits across five clades: *Fissurina*, *Ocellularia*, *Graphis*, *Topeliopsis*, and *Thelotrema*. Their study revealed the independent evolution of lirellate ascomata in all these clades, as well as the independent development of columella structures in the *Fissurina* and *Ocellularia* clades. These independent evolutionary events may be driven by ecological constraints, but the mechanisms and constraints underlying this parallel evolution require further investigation.

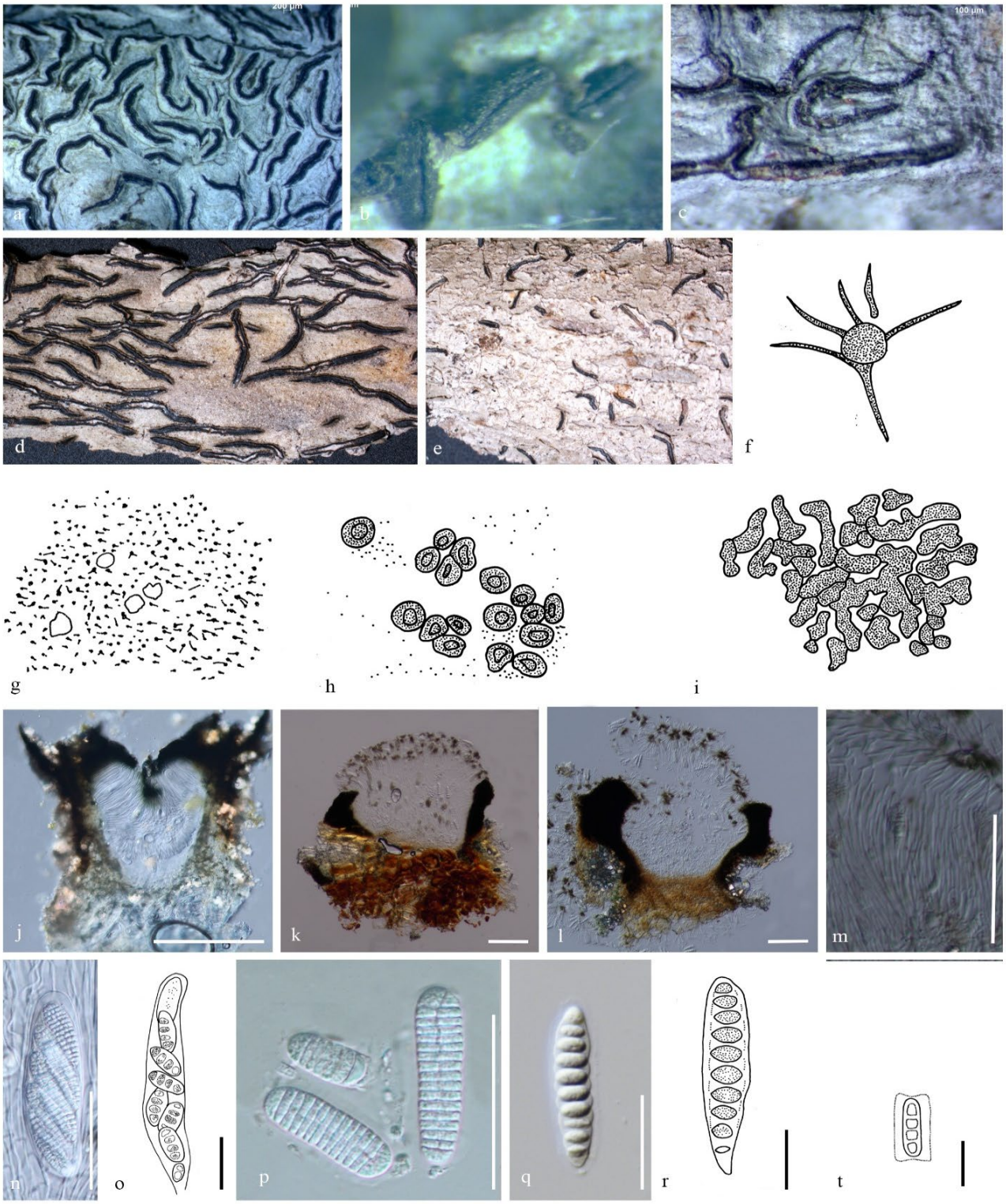


Figure 133 – Morphology of *Graphidales.* a–i Thallus morphology of *Graphidales* (a–e *Graphidales* sp., f *Spinomyces aggregatus,* g *Microxyphiomyces similis,* h *Glyphis scyphulifera*, i *Glyphis cicatricose*). j–l Vertical sections through ascomata (*Graphidales* sp.). m Paraphyses (*Graphidales* sp.). n, o Ascus (n *Graphidales* sp., o *Fissurina verrucosa*). p–t Ascospores (p, q *Graphidales* sp., r *Glyphis cicatricose*, s *Gymnographopsis corticicola*). (drawn from Archer 2001, Makhija & Adawadkar 2007, Mangold et al. 2008, Miranda-González et al. 2020, Guzmán-Guillermo et al. 2021, Xavier-Leite et al. 2023). Scale bars: j–m = 100 µm, n = 30 µm, o–r = 20 µm, s = 10 µm.

Justification of order and problems

The classification of *Graphidales*, including its ordinal, familial, and generic concepts, has undergone significant changes over time. However, several recent advancements in classification

have not been considered in several studies. *Graphidaceae* stands out as one of the largest lichenized families, yet the reported species within it are believed to be underestimated (Lücking et al. 2014). Several characters, such as carbonization patterns and ascospores septation have been used to delimit the generic concept. However, subsequent studies have revealed the non-monophyletic nature of these characters, indicating their parallel evolution within *Graphidaceae* (Staiger et al. 2006).

Significance

Ecological and economic roles

The taxa are predominantly lichenized and are commonly found in tropical and subtropical regions on a wide range of substrates. The taxa of *Gyalideopsis* comprised obligately lichenicolous species (Etayo & Diederich 2001). *Corticifraga* and *Taitaia* grow on species of *Peltigerales* which associate with cyanobiont *Crocodia* cf. *clathrata* and are reported as mycoparasites (Pino-Bodas et al. 2017, Diederich et al. 2018, Suija et al. 2018). *Cladosterigma* (*Gomphilaceae*) is reported as an obligate hyperparasite living on a phyllachoraceous species that infects the internal leaf tissue of a *Eugenia* species (Guterres et al. 2020). *Furcaspora* and *Rubikia* (subfamily *Rubikioideae*) and *Papilionovela* (subfamily *Graphidoideae*) in *Graphidaceae* are commonly reported as non-lichenized fungi (da Silva Cáceres et al. 2020). *Furcaspora eucalypti* was associated with brown leaf spots of *Mycosphaerella cryptica* in the conidiomatal asexual morph (Crous et al. 2007c). All members of *Rubikia* were reported as saprobes on leaves exhibiting coelomycetous asexual morphs (Crous et al. 2016a). Diederich et al. (2019) stated that 66 lichenicolous species are known to grow on *Graphidales* hosts worldwide. *Chroodiscus* (*Graphidaceae*) occurs on living leaves of vascular plants (Lücking & Grube 2002).

Chemical diversity

Stictic acid, constictic acid, norstictic acid, lichexanthone, and salazinic acid have been reported in members of *Graphidales* (Aptroot et al. 2023, van den Boom et al. 2023). *Graphidaceae* is the most species-rich family in terms of producing medullary and/or apothecial pigments among all known groups of lichenized *Ascomycota*.

Other relevant data and future recommendations

Several species became vulnerable due to anthropogenic activities. Thus, the protection of natural forests is important for their distribution (Miranda-González et al. 2020).

Gyalectales **Henssen ex D. Hawksw. & O.E. Erikss., Systema Ascomycetum 5(1): 179 (1986)**

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Ostropomycetidae*

Introduction

Gyalectales presently comprises 18 genera that are included in five families, *Coenogoniaceae*, *Gyalectaceae*, *Phlyctidaceae*, *Sagiolechiaceae* and *Trichotheliaceae* (Wijayawardene et al. 2022a).

History

Gyalectales was introduced by Henssen & Jahns (1974). However, Hawksworth & Eriksson (1986) formally established the order for a single family with nine genera. Later, Eriksson & Hawksworth (1998) accepted this order with one family (*Gyalectaceae*) and nine genera (*Belonia*, *Bryophagus*, *Coenogonium*, *Cryptolechia*, *Dimerella*, *Gyalecta*, *Pachyphiale*, *Ramonia*, and *Semigyalecta*) with *Belonia* and *Bryophagus* as doubtful members of the family. *Gyalectales* and *Ostropales* were listed within the 'Unitunicate Ascohymenials' based on ascus anatomy and ultrastructure in the lichenized classification of fungi (Tehler 1996). However, Henssen & Jahns (1974) considered that they were distantly related, yet both orders shared similar morphology in ascospores, ascoma ontogeny, and anatomy. Phylogenetic analyses conducted based on SSU and LSU gene regions supported the close relationship between *Ostropales* and *Gyalectales*

(Bhattacharya et al. 2000, Lutzoni et al. 2001). In the phylogenetic analyses conducted by Kauff & Lutzoni (2002), the orders recovered in the closely associated clades and further suggested subsuming *Gyalectales* under *Ostropales* as *Ostropales* was the oldest order. Eriksson (2006) recognized two families in the order *Gyalectales*. However, this was not accepted in the later studies and *Gyalectaceae* was treated as a family of *Ostropales* (Lücking et al. 2017, Wijayawardene et al. 2018). *Gyalectales* was resurrected by Kraichak et al. (2018b) for the families *Gyalectaceae*, *Sagiolechiaceae*, *Coenogoniaceae*, *Phlyctidaceae* and *Trichotheliaceae* based on the temporal band approach. The order was recognized within the Subclass *Ostropomycetidae*. The first description of *Gyalectaceae* dates back to 1862 and was established in the 'Tribus *Lecideaceae*' as a family of crustose lichens with a conspicuous excipulum proprium and urceolate fruiting bodies. *Sagiolechiaceae* is the recently established family within *Gyalectales* (Baloch et al. 2010). Kraichak et al. (2018b) treated *Porinaceae* as a synonym of *Trichotheliaceae* citing ICN Art. 18.3. and 32.1.(c), and this classification was further accepted by Wijayawardene et al. (2022a).

General description

The taxa were mainly characterized by their unique hemiangiocarpous ontogeny, in connection with a pseudoparenchymatic excipulum proprium and the presence of lateral paraphyses (Kauff & Büdel 2005).

Sexual morph: *Ascomata* apothecioid, perithecioid or lirelliform, with or without a proper exciple. *Paraphyses* unbranched or simple or partly branched. *Asci* unitunicate, cylindrical-clavate. *Ascospores* fusiform to ellipsoid aseptate or transversely septate to muriform. Asexual morph: *Conidiomata* pycnidia, sorediate (Figs. 134, 135).

Families included *Gyalectales*

Coenogoniaceae (Fr.) Stizenb.
Gyalectaceae (A. Massal.) Stizenb.
Phlyctidaceae Poelt & Vězda ex J.C. David & D. Hawksw.
Sagiolechiaceae Baloch, Lücking, Lumbsch & Wedin
Trichotheliaceae Bitter & F. Schill. (=*Porinaceae* Walt. Watson; = *Porinaceae* Rchb.)

Evolution

The diverse morphologies of ascomata, including apothecioid, perithecioid, and lirelliform forms, along with other morphological features among taxa, require further investigation to fully understand the evolutionary relationships within the *Gyalectaceae* family (Ertz et al. 2021).

Justification of order and problems

The genus *Thelopsis* has shown a close phylogenetic relationship with the family *Gyalectaceae*. However, it was not merged under *Gyalecta* due to significant morphological differences, despite some shared characteristics among the members. Recently, several new genera, including *Francisrosea*, *Neopetractis*, and *Saxiloba* (Lücking et al. 2020, Ertz et al. 2021), were introduced to this order, while several genera were found to be polyphyletic. Thus, the re-examination of these members, incorporating broad taxon sampling along with fresh collections, is needed for a better taxonomic understanding of the order.

Significance

Ecological and economic roles

The taxa are reported as lichenized fungi worldwide in corticolous and saxicolous habitats. One *Sagiolechia* species has been reported as a lichenicolous fungus on saxicolous lichen (Ertz & Tønsberg 2021).

Chemical diversity

Lichen acids such as stictic, constictic, norstictic, connorstictic, salazinic, psoromic, neopsoromic, and protocetraric acids are present in the *Phlyctis* (Galloway & Guzmán 1988).

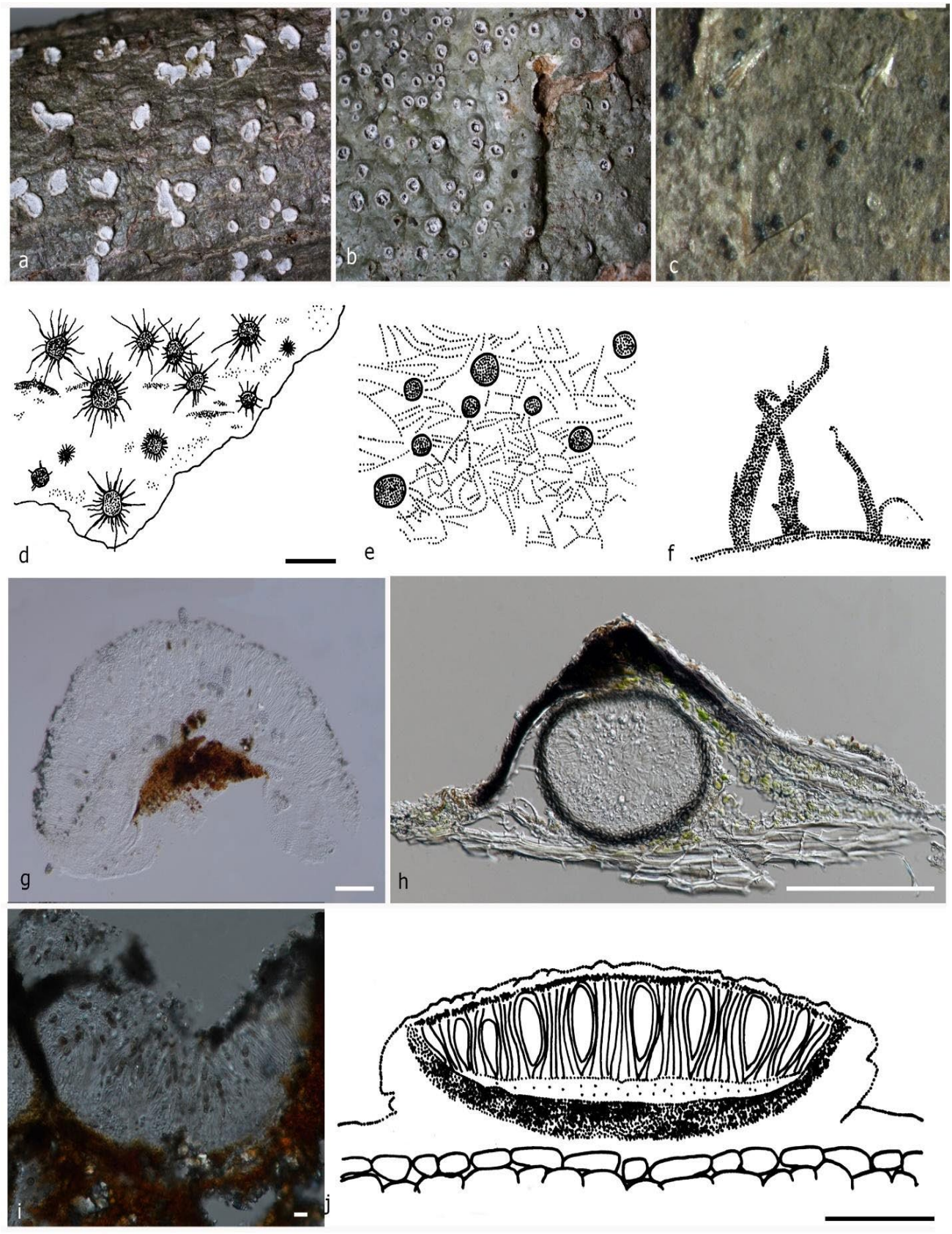


Figure 134 – Morphology of ascomata of *Gyalectales*. a–f Ascomata on substrate (a, b *Gyalecta* species, c *Porina aenea*, d *Trichothelium longisetum*, e *Coenogonium disjunctum*, f *Coenogonium* aff. *Barbatum*). g–j Vertical section through ascomata (g *Gyalecta* sp., h *Porina aenea*, i *Gyalecta* sp., j *Phlyctis tolgensis*) (drawn from McCarthy & Palice 2003, Rivas Plata et al. 2006, McCarthy & Elix 2017a). Scale bars: d = 1000 µm, e = 3 mm, f = 0.7 mm, g, h = 100 µm, i = 20 µm, j = 200 µm.

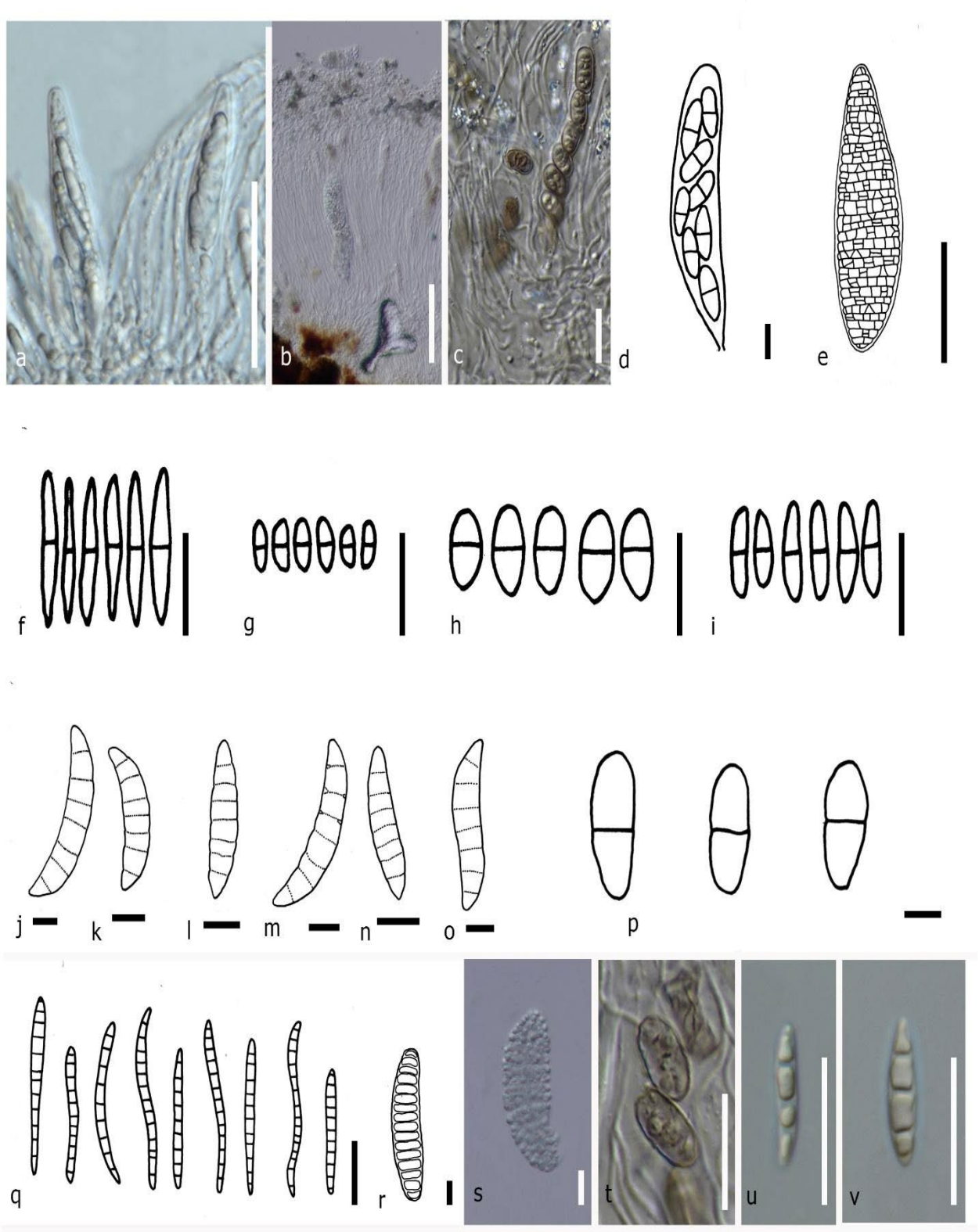


Figure 135 – Morphology of asci and ascospores of *Gyalectales*. a–d Asci and Paraphyses (a *Porina aenea,* b, c *Gyalectales* sp., d *Sagiolechia monoseptata*). e–v Ascospores (e *Phlyctis tolgensis*, f *Coenogonium aciculatum*, g *Coenogonium byssothallinum*, h *Coenogonium luteum*, i *Coenogonium siquirrense*, j–o *Phlyctis atomella*, p *Sagiolechia monoseptata*, q *Trichothelium longisetum*, r *Phlyctis boliviensis*, s, t *Gyalecta* sp., u,v *Porina aenea*) (redrawn from McCarthy & Palice 2003, McCarthy & Elix 2017a, Muscavitch et al. 2017, Ertz & Tønsberg 2021, Ansil et al. 2023). Scale bars: a = 30 µm, b =100 µm, c, q–t =20 µm, e = 50, d, f–i, j–o, u, v = 10 µm, p = 5 µm.

Other relevant data and future recommendations

After the resurrection of the order by Kraichak et al. (2018b), a detailed investigation of the familial relationship has not been done yet. Broad taxon sampling, including newly introduced genera/species with family-level investigation, can provide a better resolution of the taxonomy of the order.

***Lecanorales* Nannf., Nova Acta Regiae Societatis Scientiarum Upsaliensis Ser. 4 8(no. 2): 68 (1932)**

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Lecanoromycetidae*

Introduction

Lecanorales is the largest lichenized order (Lücking et al. 2017) which comprises more than 6,231 species and 234 genera (Lücking et al. 2017). The taxa are mainly characterized by varied thallus, predominantly apothecial ascomata, usually unbranched paraphyses, mostly thick-walled unitunicate asci (often amyloid), and varied ascospores (Kirk et al. 2008a). The order includes some familiar lichens such as *Alectoria* (witch's hair), *Cladonia* (reindeer and cup lichens), *Parmelia* and related genera (shield lichens), *Ramalina* (strap lichens), *Sphaerophorus* (coral lichens) and *Usnea* (beard lichens) (Ekman et al. 2008).

History

Lecanorales was introduced by Nannfeldt (1932). The subordinal classification of *Lecanorales* was proposed by Henssen & Jahns (1973) based mainly on ascoma ontogeny, and Poelt (1974b) proposed based on ascus characteristics. Rambold & Triebel (1992) revised the subordinal delimitation and provided a forward Lecanoralean classification. Unitunicate structure and amyloid reaction of the ascus were considered as important characters of this order. However, the restriction of the amyloid reaction to the hymenial gelatin or its complete absence was reported in many lecanorean taxa and some genera also possess bitunicate asci (Honegger 1978). Hafellner (1988) circumscribed this order mainly based on the ascus apical structure and consequently, several taxa were excluded from *Lecanorales*. Eriksson & Hawksworth (1991b) accepted 39 families within *Lecanorales*. Diverse thallus organization and secondary chemistry, many structural peculiarities, and numerous species, and several, often parallel, evolutionary lines made problems in the circumscription of *Lecanorales* (Henssen & Jahns 1973, Poelt 1974b, Hafellner 1988).

Later, Hafellner (1994) provided a detailed classification of the order based on morphological and anatomical characters with a focus on ascus characters and proposed suborders including *Acarosporineae*, *Agyriineae*, *Cladoniineae*, *Lecanorineae* and *Umbilicariineae*. With the advent of molecular phylogeny, the ordinal circumscription further narrowed and several taxa were recovered outside of *Lecanorales* such *Acarosporales*, *Caliciales* (with the *Physciaceae*), *Candelariellales*, *Lecideales*, *Peltigerales*, *Pertusariales*, *Teloschistales*, and *Umbilicariales* (e.g., Miadlikowska & Lutzoni 2004, Reeb et al. 2004, Wedin et al. 2005b, Miadlikowska et al. 2006, Schmull et al. 2011, Gaya et al. 2012,). The order presently accommodates 18 families and among them, *Cladoniaceae*, *Lecanoraceae*, *Parmeliaceae*, and *Ramalinaceae* are considered species-rich families (Lumbsch & Huhndorf 2010).

General description

Lecanorales are considered as typical lichenized discomycetes which accommodate large foliose and fruticose-type thallus (Henssen et al. 1981). Unitunicate asci with amyloid reaction was used to characterize this order. However, later electron microscopy studies proved the restriction or complete absence of the amyloid reaction and the presence of bitunicate asci in several genera (Honegger 1978). The ascus morphology is diverse among the taxa such as Bacidia-type, Lecanora-

type, Micarea-type and Psora-type (Ekman et al. 2008). Several genera, such as *Lepraria* lack sexual structures.

Sexual morph: Thallus foliose and fruticose, crustose. *Prothallus* present or absent. *Ascomata* apothecial, stalked to sessile, mostly disc-shaped, concave to plane, proper margin present or absent. *Mazaedium* present or absent. *Pruinose* present or absent. *Hypothecium* hyaline to pigmented. *Excipulum* well or poorly developed, mostly strongly melanized. *Hymenium* inspersed with oil droplets or not, hyaline to brown, comprising sparingly branched or unbranched paraphyses and asci. *Paraphyses* sometimes swollen at the tips. *Epihymenium* present or absent. *Asci* Bacidia-type, Lecanora-type, Micarea-type and Psora-type. *Ascospores* ellipsoid to oblong, with or without distinct wall thickenings, 1-septate to muriform, sometimes slightly constricted at the septum, hyaline to dark brown, mostly ornamented. Asexual morph: Coelomycetous pycnidia, form macro or microconidia. Isidia, phyllidia, soredia or goniocysts present in some genera (Figs. 136, 137, 138).

Families included in *Lecanorales*

Biatorellaceae M. Choisy ex Hafellner & Casares-Porcel
Bruceomycetaceae Rikkinen & A.R. Schmidt
Catillariaceae Hafellner
Cladoniaceae Zenker (= *Squamarinaceae* Hafellner; = *Stereocaulaceae* Chevall.)
Gypsoplacaceae Timdal
Haematommataceae Hafellner
Lecanoraceae Körb. (= *Carbonicolaceae* Bendiksby & Timdal)
Malmideaceae Kalb, Rivas Plata & Lumbsch
Megalariaceae Hafellner
Pachyascaceae Poelt ex P.M. Kirk, P.F. Cannon & J.C. David
Parmeliaceae Zenker
Pilocarpaceae Zahlbr.
Psilolechiaceae S. Stenroos, Miądl. & Lutzoni
Ramalinaceae C. Agardh
Ramboldiaceae S. Stenroos, Miądl. & Lutzoni
Scoliciosporaceae Hafellner
Sphaerophoraceae Fr.
Tephromelataceae Hafellner

Lecanorales genera *incertae sedis*
Catinaria Vain.
Compsocladium I.M. Lamb
Coronoplectrum Brusse
Corticiruptor Wedin & Hafellner
Lichenosticta Zopf
Myochroidea Printzen, T. Sprib. & Tønsberg
Neopsoromopsis Gyeln.
Nimisiostella Calat., Barreno & O.E. Erikss.
Psoromella Gyeln.
Puttea S. Stenroos & Huhtinen
Ramalea Nyl.
Tasmidella Kantvilas, Hafellner & Elix
Umbilithecium Etayo
Umushamyces Etayo

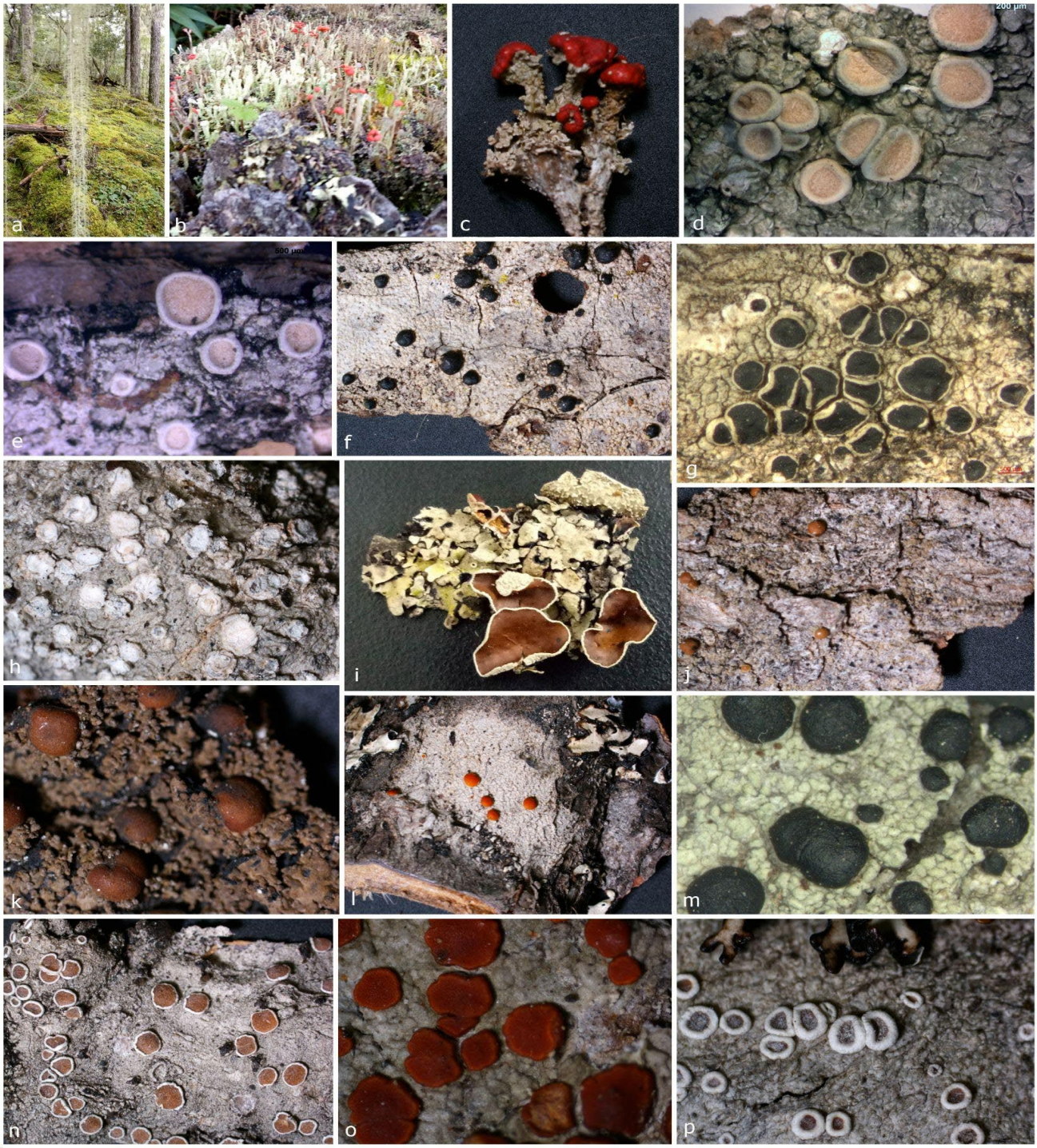


Figure 136 – Thallus morphology of *Lecanorales*. a, d, k *Lecanorales* sp. b, c *Cladoniaceae* sp. e, h *Ochrolechiaceae* sp. f, m, g *Tephromelataceae* sp. i *Parmeliaceae* sp. k *Pannariaceae* sp. l, o–n *Lecanoraceae* sp.



Figure 137 – Vertical sections through ascomata of *Lecanorales.* (a, b *Cladoniaceae* sp., c, e, l, m *Lecanoraceae* sp., d *Parmeliaceae* sp., f–h, n *Ochrolechiaceae* sp., i–k *Tephromelataceae* sp.). Scale bars: a, c–e, l, m = 100 µm, b = 20 µm, f, j, k = 1000 µm, h, i = 200 µm, g, n = 500 µm.



Figure 138 – Asci, ascospores and paraphyses morphology of *Lecanorales*. a–d Paraphyses (a *Parmeliaceae* sp., b *Lecanoroceae* sp., c *Ochrolechiaceae* sp., d *Tephromelataceae* sp). e–n Asci and paraphyses (e, f, j *Lecanoroceae* sp., g, i, l *Tephromelataceae* sp., k *Pannariaceae* sp., m, n *Ochrolechiaceae* sp). Ascus (o *Tephromelataceae* sp.). p–z Ascospores (p, z *Lecanoroceae* sp., q, r, y *Tephromelataceae* sp., s, v, w *Ochrolechiaceae* sp., t *Ramalinaceae* sp., u *Cladoniaceae* sp., x *Parmeliaceae* sp.). Scale bars: a, x = 25 µm, b, e–h, j, p, t–v, z = 20 µm, c, k = 30 µm, d, g, i, l, n, q–s, w, y = 50 µm, m = 100 µm, o = 10 µm.

Evolution

Lecanorales shows more variation in the ascus structures, which has also considered in the classification over the years. Ekman et al. (2008) studied the ascus evolution in *Lecanorales* with the aid of phylogeny and found that Lecanora-type ascus may have been ancestral in the *Lecanorales*.

Justification of order and problems

Several largest families and their genera of *Lecanorales* do not form monophyletic groups. Thus, their monophyletic nature has been debated for a long time (Gueidan et al. 2015). Several groups are heterogenous and the phylogenetic placement of several taxa/groups is unsettled. In the study of Kekuda et al. (2018), *Heterodermia* (*Physciaceae*) is considered under *Lecanorales* which

is now accepted under *Caliciales*. Numerous studies were conducted focusing only on familial classification. However, the complete reinvestigation of the order can provide some better taxonomic resolution among familial and generic concepts of the order.

Significance

Ecological and economic roles

The members are mainly reported as lichenized and lichenicolous fungi and several taxa also host many lichenicolous fungi (Zhao et al. 2016, Diederich et al. 2018) and are distributed worldwide. *Puttea margaritella* has been reported as necrophyte on bryophytes (Lestari et al. 2023).

Chemical diversity

Depsidone fumarprotocetraric acid and dibenzofuran usnic acid are reported in *Cladonia foliacea* (Hillmann & Grummann 1957, Huneck & Yoshimura 1996, Smith et al. 2009, Wirth et al. 2013). *Cladonia* is a species-rich genus and many *Cladonia* species are chemically diverse and different specimens of the same species synthesize different secondary metabolites (Ahti 2000) which have antibiotic, antiherbivory, light screening and antioxidant properties (Ahti & Stenroos 2013). Beta-orcinol depside atranorin was reported in *Lecanora farinacea* which appear as white, crustose and the color of apothecia results from the occurrence of crystals of calcium oxalate (Calcott et al. 2018). Antioxidant, antimicrobial, and anticancer activities are also reported in several *Cladonia* species (Kosanić et al. 2014).

Lecideales Vain., (1934)

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Lecanoromycetidae*

Introduction

Lecideales comprised two families *Lecideaceae* and *Lopadiaceae*. *Lecideaceae* comprises a heterogenous group with crustose taxa, lecideine or biatorine apothecia, simple hyaline ascospores and a Lecidea- or Porpidia-type ascus structure and is also considered as one of the species-rich families (Fryday & Hertel 2014, Fryday et al. 2024).

History

Schmull et al. (2011) resurrected *Lecideales* based on the six gene phylogenetic analyses by incorporating saxicolous taxa from *Lecidea sensu stricto* and members of *Porpidia* and accommodated a single family *Lecideaceae*. The order formed a sister clade phylogenetic relationship to *Peltigerales* (Miadlikowska et al. 2014). *Lecideaceae* was originally erected as '*Lecideae*' by Chevallier (1826) to accommodate lecideoid genera which comprised a heterogeneous assemblage of taxa with crustose or squamose thalli and apothecia lacking a thalline margin. The family initially included all crustose lecideoid genera (Chevallier 1826).

Watson (1929) defined this family as having crustaceous, occasionally squamulose thallus, sometimes evanescent, heteromerous, not rhizinose below, green algal cells, circular, discoid or patellate apothecia without a thalline margin, 8-spored asci with simple and hyaline ascospores and accepted *Biatora*, *Lecidea*, *Mycblastus*, *Orphniospora*, *Phyllopsora* and *Psora*. *Lecidea* was originally described by Acharius (1803) and was considered as a heterogenous assemblage and one of the largest lichenized genera (Zahlbruckner 1925, 1932). *Lecideaceae* was placed in the suborder *Lecideineae* in *Lecanorales* (Tehler & Wedin 2008). Hafellner (1984) reinvestigated *Lecideaceae* and *Lecanoraceae* and segregated several families from the taxa of *Lecideaceae* based on ascus characters, including *Porpidiaceae*.

Porpidiaceae was erected with *Porpidia* as the generic type and the members differ from *Lecideaceae* in having an ascus with an amyloid tube structure (Porpidia-type), halonate ascospores, and branched and anastomosing paraphyses. *Lecideaceae* is characterized by lecideine apothecia, simple hyaline ascospores, and a Lecidea or Porpidia-type ascus structure. Both *Lecideaceae* and

Porpidiaceae recovered as paraphyletic relative to each other and the species were intermixed in the studies of Buschbom & Mueller (2004) and Miadlikowska et al. (2006). The sequence data used for *Lopadium disciforme* was recovered in a sister position to *Caliciales* with low statistical support and placed in *Lecanoromycetidae incertae sedis* (Miadlikowska et al. 2014). Lücking et al. (2017) treated *Porpidiaceae* under *Lecideaceae* and accepted both *Lecideaceae* and *Lopadiaceae* under *Lecideales* and the classification was further accepted by Wijayawardene et al. (2022a). *Lopadium* was previously placed in *Lecideaceae* and placed in a new family *Lopadiaceae* by Hafellner (1984). The family was introduced to accommodate a single genus *Lopadium* with *L. pezizoideum* as the type species (Hafellner 1984).

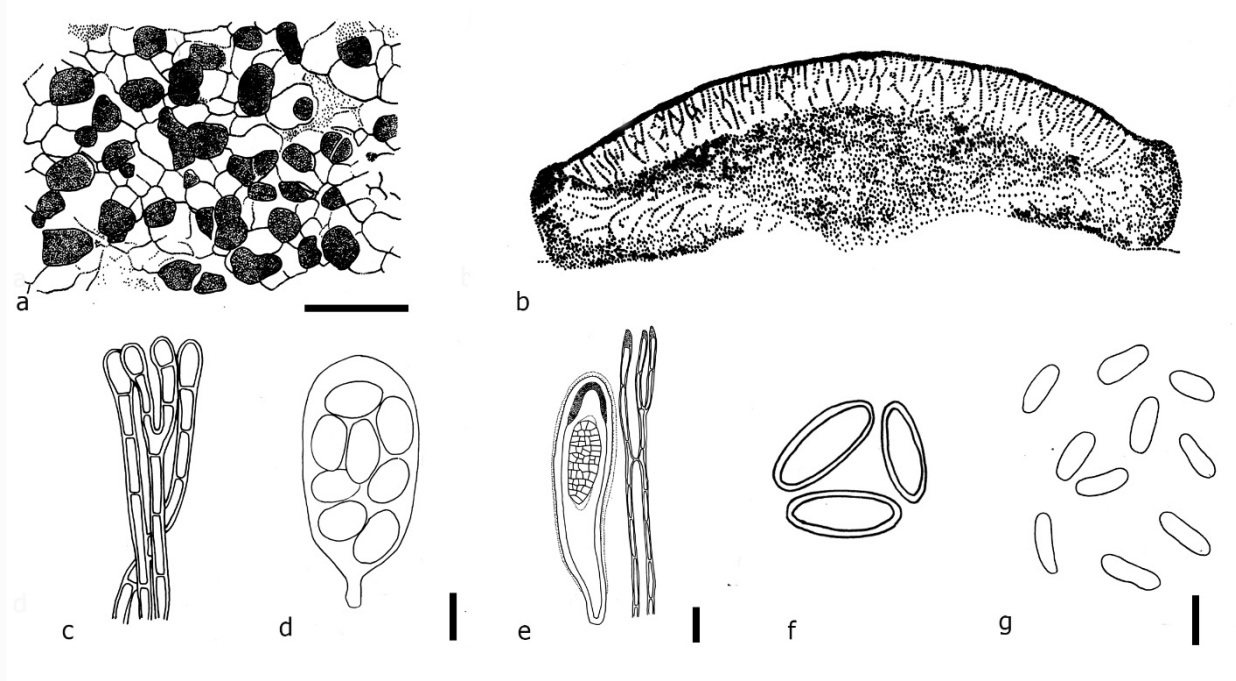


Figure 139 – Sexual morphology of *Lecideales*. a Thallus and apothecia (*Lecidea glacierensis*). b Section through apothecia (*Lecidea fuscoatrata*). c Upper part of the paraphyses (*Lecidea fuscoatrata*). d, e Ascus (d *Lecidea glacierensis*, e *Lopadium pezizoideum*). f Ascospores (f *Lecidea fuscoatrata*, g *Lecidea andersoni*) (drawn from Inoue 1982, Zhao et al. 2017, Mamut et al. 2022, redrawn from Hafellner 1984). Scale bars: a = 3 mm, d, g = 10 μm, b × 60, c, f × 1000.

General description

Genera of *Lecideaceae* have lecideine apothecia except *Bellemerea* and *Koerberiella*, which have lecanorine apothecia (Xie et al. 2022). Filiform or bacilliform conidia are reported in the asexual morph (Fryday & Hertel 2014). However, thalloconidia are reported in *Immersaria fuliginosa* (Fryday & Hertel 2014).

Sexual morph: *Thallus* crustose or rarely subsquamulose, squamulose, sometimes areolate, sometimes immersed, rarely absent (inlichenicolous species). *Photobiont* chlorococcoid, sometimes secondary photobiont present. *Ascomata* apothecia, immersed to sessile, thalline margin usually absent, true exciple absent, weakly to very strongly developed and usually black, the disc domed to concave, usually dark. *Hymenium* usually blueing in iodine; hypothecium colorless, brown, pale or dark brown. *Interascal tissue* of sparsely to richly branched and anastomosed paraphyses, often swollen at the apices, often pigmented or with an epithecial layer. *Asci* cylindrical to clavate, Lecidea-type or Porpidia-type, thick-walled, with an I+ apical cap, often with a more strongly staining tube-like structure and an outer I+ gelatinized layer. *Ascospores* cylindrical to ellipsoidal, hyaline, aseptate, thin-walled, amyloid or inamyloid, with or without a gelatinous sheath. Asexual morph: *Conidiomata* immersed, dark-walled, sometimes with a broad ostiole. *Conidiogenous cells*

cylindrical to flask-shaped, apparently proliferating both percurrently and sympodially. *Conidia* cylindrical to bacilliform or filiform, hyaline, aseptate. Soredia or isidia sometimes present (Fig. 139).

Families included in *Lecideales*

Lecideaceae Chevall.
Lopadiaceae Hafellner

Evolution

The evolution of families in *Lecideales* is largely unexplored, which needs further studies.

Justification of order and problems

The taxonomy of *Lecidea* is extremely complex because of the enormous morphological variation within and between species (Schmull et al. 2011). The phylogenetic position of many taxa of *Lecidea* is unknown or poorly studied (Ruprecht et al. 2010). Intraspecific variability based on morphological or chemical differences among species of *Lecidea* often showed subtle differences for species level variation with the aid of molecular data. Thus, morphological and chemical analyses often result in the underestimation of the number of species. Hence, there are many chances for discovering new species in poorly studied areas, also hidden under known species names (Hawksworth & Rossman 1997, Sipman & Aptroot 2001, Arnold & Lutzoni 2007, Ruprecht et al. 2010). The delimitation of the order is also needing revision with more loci to improve phylogenetic confidence (Miadlikowska et al. 2014). Spribille et al. (2020) provided the sequence data for the type *Lopadium pezizoideum* but did not use it in the phylogenetic construction and the family is currently accepted under *Lecideales*. Thus, the phylogenetic placement of *Lopadiaceae* also needs further investigation.

Significance

Ecological and economic roles

Lecideaceae taxa are mainly studied in the Northern Hemisphere and are less studied in the Southern Hemisphere. They are abundant and rich in species in Antarctica and a few species occur in more extreme environmental conditions of Antarctica and are mainly reported on rock and pebbles (Hertel 1987, 2007). Many of the endemic species in Antarctica have been reinterpreted as variations due to extreme climatic conditions such as *Lecidea cancriformis* (Castello 2003, Hertel 2007, Ruprecht et al. 2010).

Chemical diversity

The chemical diversity of *Lecideaceae* is not well-explored (Culberson & Culberson 1970). Dibenzofurans, gyrophoric acid, orsellinic acid unit are reported in the family (Culberson & Culberson 1970, Xie et al. 2022). Seo et al. (2011) reported three PTP1B (protein tyrosine phosphatase 1B) inhibitory metabolites; hopane-6α.22-diol, brialmontin 1, and atraric acid along with two aromatic metabolites; atranorin and methyl haematommate from *Lecidella carpathica*. PTP1B therapeutic target for diabetes contributes to the negative regulation of the insulin signaling pathway. *Lecidea oreophila* produces 2′-O-methylmicrophyllinic acid, confluentic acid and 2′- O-methylperlatolic acid (Knudsen & Kocourková 2014).

***Leprocaulales* Lendemer & B.P. Hodk., Mycologia 105(4): 1007 (2013)**

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Lecanoromycetidae*

Introduction

Leprocaulales presently comprises three genera, *viz*. *Halecania*, *Leprocaulon* and *Speerschneidera*. The taxa are reported as lichenized and lichenicolous fungi in corticolous and saxicolous habitats (Cannon et al. 2022).

History

Leprocaulales was introduced by Lendemer & Hodkinson (2013) to accommodate a single family *Leprocaulaceae* based on reinvestigating *Leprocaulon* with evidence from morphological and phylogenetic analyses. Currently, the order accommodates a single family *Leprocaulaceae,* with three genera *viz*. *Halecania*, *Leprocaulon* and *Speerschneidera* (Wijayawardene et al. 2022a). The order formed a sister clade relationship to *Caliciales* in the phylogenetic analyses (Lendemer & Hodkinson 2013). *Leprocaulon* was previously included in *Stereocaulon* and resembles the thallus of *Lepraria* but is distinguished from the latter by the absence of corticate phyllocladia, cephalodia, pycnidia, and chemistry. *Halecania* also shares similar morphology to *Catillaria* in the structure of asci, paraphyses and conidiomata but differs in having apothecia with a thalline margin and ascospores with three distinct perispores (Cannon et al. 2022).

General description

The taxa are primarily sterile and the sexual morph has lecanorine apothecia, Halecania-type asci, that produce hyaline ascospores (Lendemer & Hodkinson 2013). The thallus is crustose, effuse and rimose-cracked, granular to warted, or with a diffuse and powdery leprose primary thallus from which small and delicate branched pseudopodetia may develop with chlorococcoid as photobiont.

Sexual morph: *Ascomata* apothecia, sessile. *Thalline margin* with a broad algal zone and a broad to indistinct cortex. *Exciple* thin laterally, usually expanding above with a surface layer of apically brown-capped cells. *Hymenium* I+ blue. *Hypothecium* hyaline. *Hamathecium* comprised unbranched or occasionally forked, septate paraphyses, with swollen, mostly dark brown, capitate apices. *Asci* 8-spored, clavate to subcylindrical, Catillaria-type. *Ascospores* hyaline, 1-septate, perispore swelling markedly in K (not apparent in over-mature spores). Asexual morph: *Conidiomata* pycnidia, immersed; wall colorless except around the ostiole. *Conidiogenous cells* arranged in branched chains. *Conidia* aseptate, bacilliform, hyaline (Fig. 140).

Families included in *Leprocaulales*

Leprocaulaceae Lendemer & B.P. Hodk.

Justification of order and problems

The order includes a single family with three genera and nearly 35 species. However, the largest genus in the family, *Halecania*, lacks molecular data for many of its species, which need further investigation.

Significance

Ecological and economic roles

In Britain and Ireland, both *Halecania* and *Leprocaulon* have been documented (Cannon et al. 2022). However, *Speerschneidera* is less frequently encountered due to its coloration, which closely resembles limestone when dry. Despite its inconspicuousness, it can be abundant in calcareous rock habitats, particularly on shaded, steep, north-facing exposures (Hafellner & Egan 1981). *Halecania* exhibits a lichenicolous lifestyle, often found on saxicolous and corticolous substrates, but can also occur independently as lichens (Cannon et al. 2022, Westberg et al. 2023).

Chemical diversity

Pannarin, argopsin and usnic acid are found in asexually producing *Leprocaulon* species (Lendemer & Hodkinson 2013).

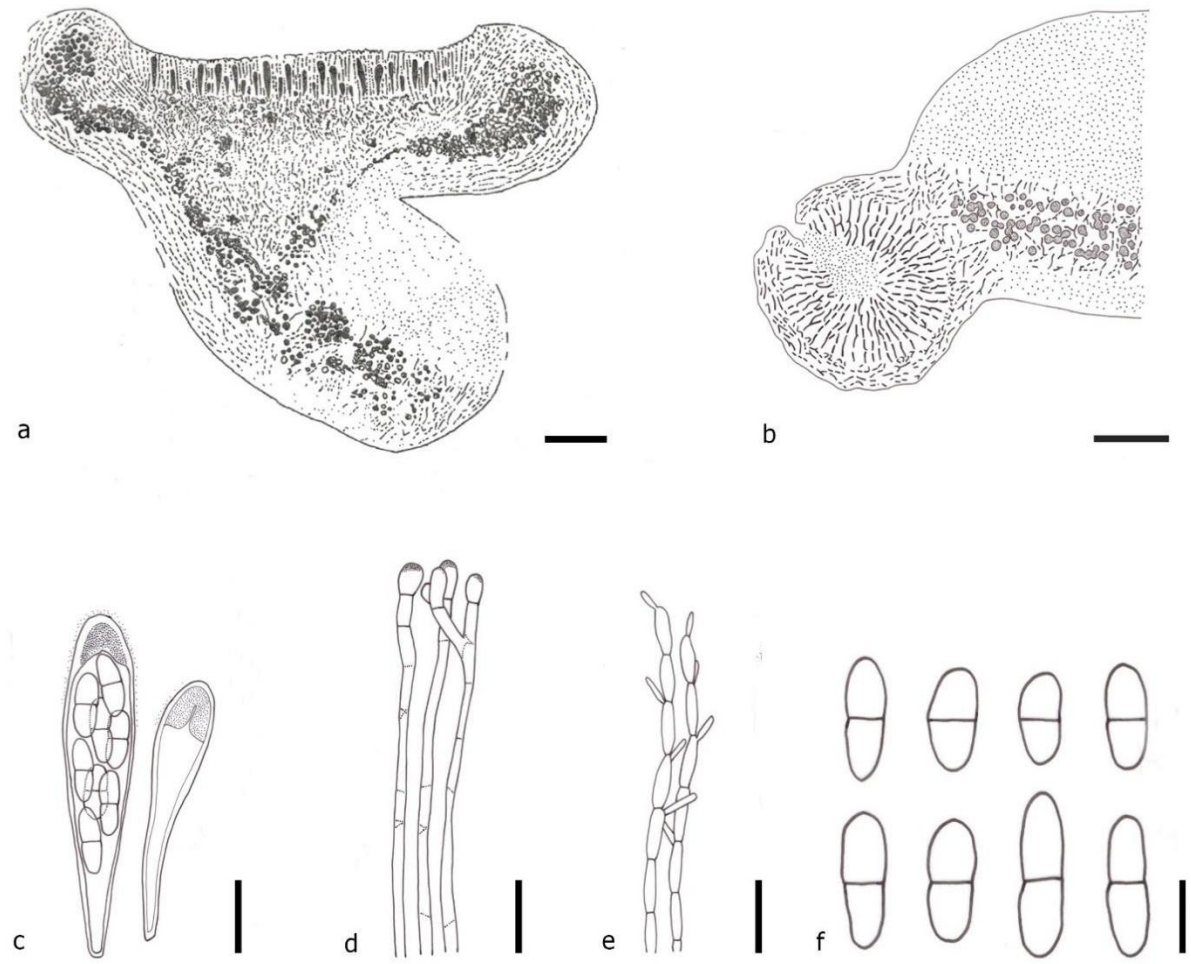


Figure 140 – Morphology of *Leprocaulales* (*Speenchneidera euploca*). a Apothecium. b Pycnidium. c Asci. d Paraphyses. e Conidiophores with conidia. f Conidia (redrawn from Hafellner & Egan 1981). Scale bars: a, b = 100 μm, c–f = 10 μm.

Micropeltidales **X.Y. Zeng, H.X. Wu & K.D. Hyde, Fungal Diversity 97: 402 (2019)**

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Incertae sedis*

Introduction

Micropeltidales comprises eight genera assigned to one family that was introduced by Zeng et al. (2019). *Micropeltidaceae*, known for their 'flyspeck' fungi characterized by shiny, black, round to oval, sclerotium-like bodies without an apparent mycelial mat, has been classified within the *Microthyriales* (*Dothideomycetes*) due to morphological similarities with *Asterinaceae*, *Microthyriaceae*, and *Phaeothecoidiellaceae* (Yang et al. 2010, Li et al. 2011, Wu et al. 2011). However, species within *Micropeltidaceae* are not distinctly separable from related families based on morphology alone (Wu et al. 2011). The phylogenetic placement of *Micropeltidaceae* within the *Lecanoromycetes* is supported by DNA sequence data that was supported from two species available in GenBank (Hongsanan & Hyde 2017). The taxonomic boundaries of *Micropeltidaceae* species have been unclear for over half a century, with no significant taxonomic revisions since the study of Batista (1959). Resolving the taxonomy of *Micropeltidaceae* and other related 'grey' families is crucial for a better understanding of their evolution and taxonomic classification. Zeng et al. (2019) placed *Micropeltidales* in *Lecanoromycetes* based on morpho-molecular and divergence time estimate analyses.

History

Montagne (1842) introduced the genus *Micropeltis*. Saccardo (1883c) included taxa that are characterised by superficial, black, dimidiate, flattened, membranous or carbonaceous perithecia in the new family *Microthyriaceae*. Höhnel (1910) suggested that those fungi with non-radiating upper walls should be excluded from *Microthyriaceae*. Theissen (1913) agreed with Höhnel (1910) and introduced a new order *Hemisphaeriales*, along with a new family *Hemisphaeriaceae* to accommodate taxa that are characterized by ascomata with meandering upper walls. Arnaud (1918) proposed to place *Microthyriaceae* and *Hemisphaeriaceae* under the new order *Microthyriales.* Clements & Shear (1931) synonymised *Hemisphaeriaceae* under *Micropeltidaceae*, with 29 genera and 186 species. However, the family name *Micropeltidaceae* was not formally accepted until the monograph published by Batista (1959), which included 45 genera. Kirk et al. (2008a) included 27 genera and Lumbsch & Huhndorf (2010) included 24 genera in *Micropeltidaceae*. Wu et al. (2011) transferred *Byssopeltis*, *Caudella* and *Scolecopeltidium* from *Microthyriaceae* to *Micropeltidaceae* based on the structure of the upper wall. Hyde et al. (2013) revised the taxonomy of *Micropeltidaceae* and accepted 12 genera. Hongsanan et al. (2014) transferred *Anariste* to *Micropeltidaceae* from *Asterinaceae*. The outlines provided by Wijayawardene et al. (2018) included 14 genera in *Micropeltidaceae*. Wu et al. (2011), who provided the first sequence data (LSU and SSU sequences of *Micropeltis zingiberaceicola*), started the modern study of *Micropeltidaceae*. Abarca et al. (2011) investigated the phylogenetic relationships of the asexual genera, *Heliocephala* and *Holubovaniella*, and concluded that *Stomiopeltis betulae* is the closest relative sexual genus. Hongsanan & Hyde (2017) excluded *Chaetothyrina* from *Micropeltidaceae*, and placed it in *Phaeothecoidiellaceae* based on molecular data and disease symptoms. These phylogenetic studies were based on the putative fact that *Micropeltidaceae* is a member of *Dothideomycetes*. Hongsanan & Hyde (2017) concluded that *Micropeltidaceae* should be transferred from *Dothideomycetes* to *Lecanoromycetes* based on the phylogeny. The placement of *Micropeltidales* in *Lecanoromycetes* is supported by morphological characterization along with phylogeny and divergence time estimates (Zeng et al. 2019).

General description

Sexual morph: *Epiphytic* on living leaves, epiphyllous or hypophyllous, visible as black, solitary dots on host surface. *Hyphae* superficial, hyaline, difficult to detect. *Ascomata* superficial, solitary, mostly gregarious, black bule-green, flattened, circular, dimidiate, with a central ostiole. *Upper wall* greenish or bluish in water, membranous, comprising overlapping, net-like or puzzle-like, compact or sparse, lacking a basal plate. *Hamathecium* comprising asci inclined from the base towards the ostiole. *Paraphyses* present or absent. *Asci* 8-spored, bitunicate, cylindrical to clavate, hyaline. *Ascospores* overlapping, 2-seriate, cylindrical to subclavate, aseptate or uni- to multi-septate, constricted at septa when mature, hyaline, head cell larger than others, middle cell globose, tail cell longer than others (Fig. 141). Asexual morph: Undetermined.

Families included in *Micropeltidales*

Micropeltidaceae Clem. & Shear

Evolution

The divergence time of the *Micropeltidaceae* crown group is about 130 (165–104) MYA, which also supports its rank as an order (diverging from 220–100 MYA). The evolutionary histories between *Micropeltidaceae* species and host plants are interpreted by co-phylogenetic analyses calibrated by their divergence times. The result indicates that the diversification of *Angiospermae* (130–80 MYA) fosters the formation of genera of *Micropeltidaceae* mainly via cospeciating events, and this co-divergent period would be an important reference when establishing generic boundaries of epifoliar fungi (Zeng et al. 2019).

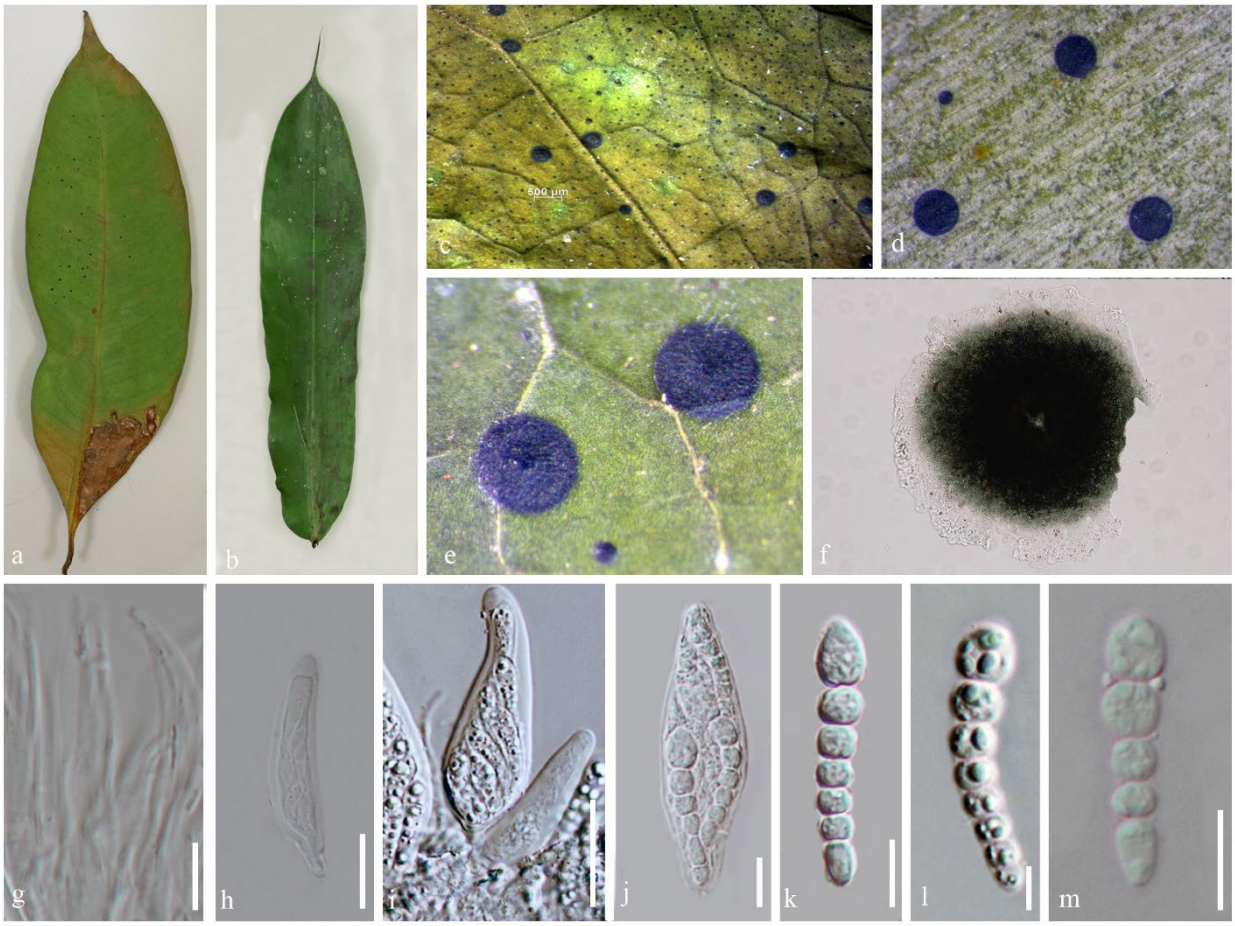


Figure 141 – Sexual morphology of *Micropeltidales.* a, b The host leaf (a *Dictyothyriella garciniae*, b *Micropeltis amomi*). c–e Ascomata on leaf surface (c *Micropeltis* sp., d *M. amomi*, e *M. asiatica*). f Squash mount of ascoma (*Scolecopeltidium menglaense*). g Paraphyses (*Micropeltis asiatica*). h–j Asci (h *Micropeltis* sp., i *S. menglaense*, j *M. asiatica*). k–m (k *M. asiatica*, l *S. menglaense*, m *Micropeltis* sp.). Scale bars: g, h, j, k, m = 10 µm, i = 20 µm, l = 5 µm.

Justification of order and problems

Previous descriptions for *Micropeltidaceae* included 24 genera with bluish-green upper walls with a meandering arrangement of cells in the ascomata (Lumbsch & Huhndorf 2010, Hyde et al. 2013). However, many of those genera (*Bonaria*, *Caudella*, *Clypeolina*, *Cyclopeltis*, *Chaetothyrina*, *Dictyopeltis*, *Hansfordiopsis*, *Mendoziopeltis*, *Mitopeltis*, *Muricopeltis*, *Stigmatodothis*. *Stigmatophragmia*, *Stomiopeltis*, *Stomiotheca*, *Thyriodictyella* and *Polypedia*) have brown and similar structures of the upper walls as in *Micropeltidaceae*. The morphological features of *Micropeltidaceae* are very similar to *Asterinaceae*, *Microthyriaceae* and *Phaeothecoidiellaceae*. (Wu et al. 2011, Hongsanan et al. 2014). However, phylogenies data are mostly absent for many species. Greater attention should be given to these fungal species, with an emphasis on obtaining additional molecular data to clarify their phylogenetic relationships and establish a more natural taxonomic framework.

Significance

Ecological and economic roles

Members of *Micropeltidaceae* are highly diverse in tropical regions and can be found during cold seasons when asci and ascospores are mature (Batista 1959). They are mostly epiphyllous and distributed over a wide range and records indicate that they are not host-specific (Acosta 1995, Batista 1959, Reynolds & Gilbert 2005, 2006). Similar to other sooty blotch and flyspeck fungi, species of *Micropeltidaceae* cause no damage to the underlying hosts. They neither produce haustoria to obtain nutrients from the living organisms, nor utilize the constituent elements from the dead bodies (Batista

1959, Marasinghe et al. 2022b, 2023). Species of *Micropeltidaceae* are entirely superficial and commensal with their host plants. They use mineral and organic substances resulting from transpiration residues and epidermal secretions (e.g., potassium, calcium salts and phosphatides) to satisfy their growth, even in very small quantities, and the exchange of gases between host plants and the environment also benefits these fungi (Batista 1959).

Chemical diversity

The chemical diversity of *Micropeltidales* has not yet been explored.

Other relevant data and future recommendations

The *Micropeltidales* group are generally difficult to culture, as they either rarely sporulate, or grow extremely slowly and thus can be easily contaminated by saprobes, and this has resulted in a poor understanding of the group. Numerous attempts have been made to explore ways to cultivate *Micropeltidaceae* species under artificial laboratory environments, but without success (Batista 1959, Zeng et al. 2019).

***Odontotrematales* Lücking Critical Reviews in Plant Sciences 38 (3): 233 (2019)**

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Ostropomycetidae*

Introduction

Odontotrematales was established by Lücking (2019) to accommodate a single family *Odontotremataceae*. The order comprised 11 genera with *Odontotrema* as the type. *Odontotremataceae* was introduced by Hawksworth & Sherwood (1982). The taxa are mostly characterized by small and dark apothecia with ascohymenial, hemiangiocarpic development, dark exciple, cylindric, unitunicate asci with a thickened apex and hyaline ascospores. The apothecia form perithecioid ascomata when immature and become deeply urceolate disks at maturity (Sherwood-Pike 1987).

The family was considered as paraphyletic and closely related to *Stictidaceae* but differs in several morphological features, including carbonized, non-crystalline ascoma margin and non-filiform ascospores (Sherwood-Pike 1987, Diederich et al. 2002). Wedin et al. (2005a) provided the first phylogenetic position for this family within *Ostropales* by including two undefined *Odontotrema* species (*Odontotrema* 1 and 2). The family formed a sister clade relationship to *Stictidaceae* in that study. However, the family and the type genus were recovered as polyphyletic with broad taxon sampling conducted by Baloch et al. (2010). *Odontotremataceae sensu stricto* formed a sister clade to *Stictidaceae*. The next clade nested within *Stictidaceae* included two undescribed *Odontotrema* species (also included in Wedin et al. 2005a); *O. cassiopes* and *O. diffindens*, and *Bryodiscus arctoalpinus* (Baloch et al. 2010). Consequently, Baloch et al. (2013) accepted the name *Sphaeropezia* for the latter clade.

History

Hawksworth & Sherwood (1982) accepted seven genera, including *Bryodiscus*, *Lethariicola*, *Odontotrema*, *Odontura*, *Skyttea*, *Spilomela* and *Stromatothecia* within *Odontotremataceae*. Sherwood (1981) also reported these groups in her studies, which formed a natural group. Hawksworth & Sherwood (1982) stated the relationship between *Odontotremataceae* and *Triblidiaceae* as the latter was also placed in *Ostropales*. *Triblidiaceae* differs from *Odontotremataceae* in that the covering stroma splits stellately or by a slit to expose the hymenium, the presence of distinct epithecium, and ascospores with either transversely septate or lenticular cells or muriform and show turning reddish-purple reaction to iodine. However, *Triblidiaceae* is presently affiliated within *Rhytismatales* (*Leotiomycetes*) (Karakehian et al. 2019). Hawksworth & Sherwood (1982) stated the possibility of placing the lichenized genera *Bryophagus* and *Ramonia* and were later placed in *Stictidaceae* (Aptroot et al. 2014) and *Gyalectaceae* (Ertz et al. 2021), respectively.

Sherwood-Pike (1987) published a monograph for *Odontotremataceae*, in which the circumscription of the family again changed by excluding *Spilomela* and by the inclusion of two genera *Coccomycetella* and *Pleospilis*. Later several new genera were introduced such as *Potriphila*, *Rogellia* and *Xerotrema* (Döbbeler 1996, 1999) while several genera were transferred to other families; *Bryodiscus* (a synonym of *Sphaeropezia* in *Stictidaceae*), *Geltingia* (a genus of *Helicogoniaceae* in *Phacidiales*), *Lethariicola* (a synonym of *Sphaeropezia* in *Stictidaceae*), *Paschelkiella* (a synonym of *Cryptodiscus* in *Stictidaceae*), *Pleospilis* (a synonym of *Spirographa* in *Ostropomycetidae*), *Rhymbocarpus* and *Skyttea* (two genera of *Cordieritidaceae* in *Helotiales*) and *Sphaeropezia* (a genus of *Stictidaceae*) (Holien & Triebel 1996, Diederich et al. 2002, 2018, Baloch et al. 2013, Zhurbenko & Yakovchenko 2014, Suija et al. 2015b, Wijayawardene et al. 2018). Yang et al. (2019a) recently introduced a new genus *Parakarstenia* from China. Furthermore, Yang et al. (2019a) transferred *Karstenia* to *Odontotremataceae* based on phylogenetic analyses and morphological characters such as non-crystalline apothecial margin, pronounced periphysoids and vermiform, cylindrical to clavate ascospores. These features supported the placement of the genus within *Odontotremataceae* (Sherwood 1977b, Wilberforce 1999).

Calatayud et al. (2001) established a lichenicolous genus *Paralethariicola* within *Odontotremataceae* which shows similar morphology to lichenicolous genus *Odontotrema*. However, the genus has unique features such as inner excipular margin with hairs, ascus wall apically with a distinct KI+, blue ring, distinctly flattened ascus apex, 2–3(–4) µm diam paraphyses, curved, falcate or slightly helicoid, with more or less pointed ends, and 3-septate ascospores (Calatayud et al. 2001, Diederich et al. 2002). The genus was treated under *Odontotremataceae* (Lumbsch & Huhndorf 2007, Wijayawardene et al. 2018) but recently the genus was treated as *incertae sedis* (Yang et al. 2019a, Wijayawardene et al. 2022a). *Claviradulomyces* was established to accommodate *Claviradulomyces dabeicola* in *Odontotremataceae* (*Ostropales*) due to its unusual ecology with the combination of unique morphological characters. The species was isolated on lenticels of the bark of *Erythroxylum mannii* and formed round gall-like blisters (up to 2 mm diam), with excessive cracking and flaking symptoms. The apothecia are minute with long-cylindric and sigmoid ascospores, rough-walled periphysoids, and pycnidial anamorph (Evans et al. 2010). Barreto et al. (2012) introduced a second species to this genus, which was also isolated from lenticels of *Xylopia sericea* and fits the morphology of *Odontotremataceae*. However, the genus was placed in *incertae sedis* within *Ostropales* based on the phylogenetic analyses conducted for LSU and SSU sequence data. Duarte et al. (2021) introduced five new *Claviradulomyces* from Brazil in different plant species, and they shared similar morphological features in the asexual morph. Subsequently, a new family *Claviradulomyceae* was introduced to accommodate this genus based on phylogenetic analyses conducted for LSU and RPB2 sequences. The family formed a sister clade to *Phlyctidaceae* and was basal to the families *Coenogoniaceae*, *Gyalectaceae*, *Phlyctidaceae*, *Sagiolechiaceae* and *Trichotheliaceae* that are placed in the order *Gyalectales* (Duarte et al. 2021). Presently, eleven genera, namely *Coccomycetella*, *Karstenia*, *Odontotrema*, *Odontura*, *Paralethariicola*, *Parakarstenia*, *Potriphila*, *Rogellia*, *Stromatothecia*, *Tryblis* and *Xerotrema* are accepted in *Odontotremataceae,* while a single genus is placed in *Claviradulomyceae* (Hyde et al. 2024b).

General description

The morphology is mainly used for the classification of odontotremataceous genera. The asexual morph is distinguished by the size and shape of the conidiophores and conidiogenous cells, the size of conidia and color of pycnidium, as well as the shape and length of the neck alone or in combination and these characteristics were mainly used in the identification of *Claviradulomyces* species (Barreto et al. 2012, Duarte et al. 2021).

Sexual morph: *Ascomata* apothecia, hemiangiocarpic, immersed-erumpent to sessile, scattered to gregarious, obrotund to irregular shape, determinate, marginate, single or immersed in a stroma, excipulum hyphal, usually dark colored and in some genera carbonaceous. *Paraphyses* simple or branched at the base, septate. *Asci* cylindrical, the lateral walls thin and the apex thickened, I-, with or without an apical pore, inoperculate, 8 or multi-spored. *Ascospores* ovoid, sigmoid, filiform,

hyaline, simple, transversely septate or muriform. Asexual morph: Pycnidial. *Pycnidia* spherical to subspherical ostiolate, rostrate, producing filiform to narrow acerose conidia, commonly aseptate and often bearing a subtle heel next to the base (Fig. 142).

Families included in *Odontotrematales*

Claviradulomyceae L.L.Duarte, D.M.Macedo & R.W.Barreto
Odontotremataceae D. Hawksw. & Sherwood

Justification of order and problems

When *Claviradulomyceae* was established, the treatment of Lücking's (2019) classification and the order *Odontotrematales* were not considered in the study of Duarte et al. (2021). The recent outline of Wijayawardene et al. (2022a) treated *Claviradulomyces* in *Odontotremataceae*. Here we treat this family under *Odontotrematales*. Yang et al. (2019a) transferred the genus *Karstenia* to *Odontotremataceae* based on the evidence from molecular and morphological data. However, this classification has not been accepted in later studies and was accepted in *Stictidaceae* (Thiyagaraja et al. 2021b, Wei et al. 2021a, Wijayawardene et al. 2022a). Here we followed Yang et al. (2019a) classification and placed this genus within *Odontotremataceae*.

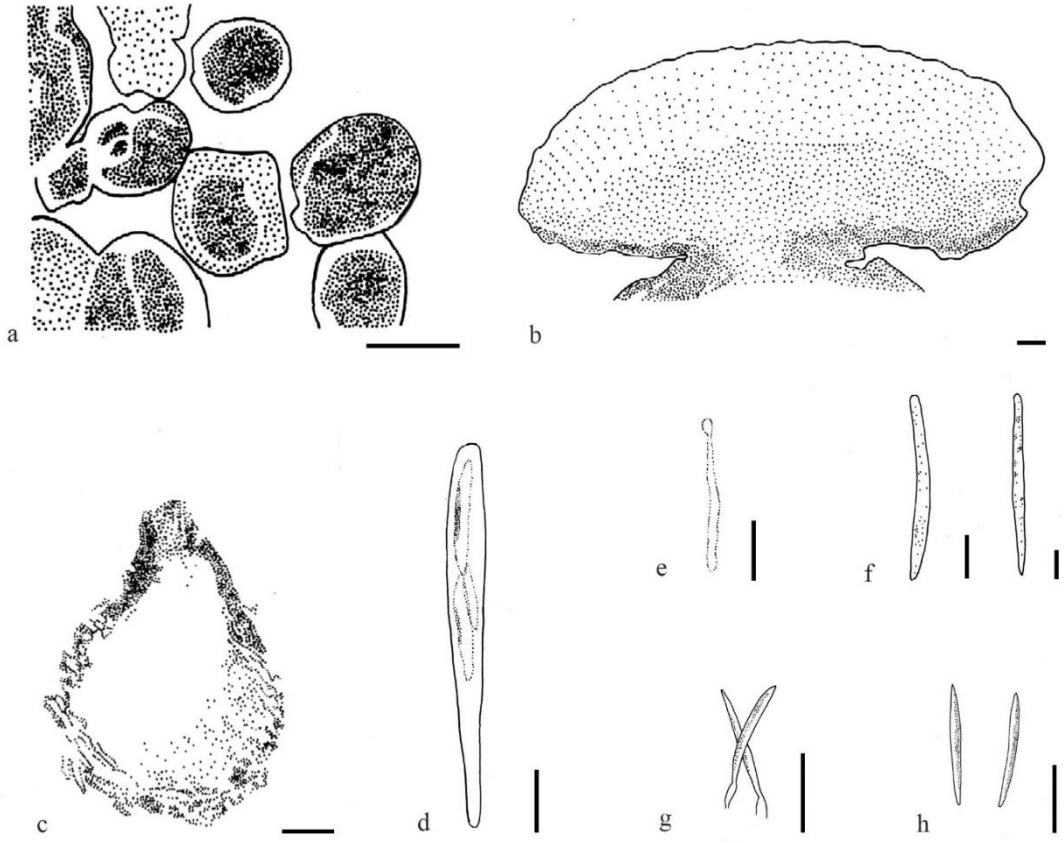


Figure 142 – Morphology of *Odontotrematales*. a Ascomata on the host substrate (*Parakarstenia phyllostachydis*). b Cross section of Apothecium (*P. phyllostachydis*). c Vertical section of pycnidium (*Claviradulomyces dabeicola*). d Ascus of *P. phyllostachydis*. e Paraphyses of *P. phyllostachydis*. f Ascospores of *P. phyllostachydis*. g Conidiogenous cells of *C. dabeicola.* h Spermatial microconidia of *C. dabeicola* (drawn from Yang et al. 2019a, Duarte et al. 2021). Scale bars: a = 2 mm, b = 50 µm, c–e, g, h = 20 µm, f = 10 µm.

Significance

Ecological and economic roles

The species have been reported as saprobes on wood and dead herbaceous material, and parasites or commensals on lichens or mosses (Hawksworth & Sherwood 1982). Several genera or species are reported as parasites on living stems and lenticels (Evans et al. 2010, Barreto et al. 2012, Yang et al. 2019a, Duarte et al. 2021). The members of *Claviradulomyces* show an unusual lifestyle, sporulating on hosts with abnormal, hypertrophied and spongy lenticels in different host species (Duarte et al. 2021). The members of *Claviradulomyces* show an unusual lifestyle, sporulating on hosts with abnormal, hypertrophied and spongy lenticels in different host species (Duarte et al. 2021). Barreto et al. (2012) hypothesized that these fungi can be endophytic colonizers of tropical woody plants, with the ability to sporulate on the lenticular tissues of living plants. However, *Claviradulomyces* are largely overlooked due to their appearance and ecology. The fungi grow very slowly in culture and most species do not produce ascospores or conidia *in vitro* (Duarte et al. 2021).

The pathogenic nature of *Claviradulomyces dabeicola* and *C. schini* has been assumed to cause die-back and defoliation in the host tree. However, their parasitic association and host association need further studies. *Claviradulomyces schini* occurs on *Schinus terebinthifolia* (Brazilian pepper tree), which is a major pantropical weed. *Claviradulomyces schini* can be used as a classical biological control agent (Duarte et al. 2021). *Parakarstenia* was reported as parasitic on living to nearly dead stems of bamboo from China.

Other relevant data and future recommendations

Odontotremataceae is a poorly studied group. Many species were introduced mainly based on morphology. Therefore, the phylogenetic position of several species and genera remains uncertain due to a lack of molecular data. Several genera, such as *Coccomycetella*, *Odontura*, *Paschelkiella*, *Potriphila*, *Rogellia*, *Tryblis*, *Stromatothecia* and *Xerotrema* accommodate only one to three species.

Ostropales **Nannf., Nova Acta Regiae Societatis Scientiarum Upsaliensis Ser. 4 8(no. 2): 68 (1932)**

= *Gyalectales* Henssen ex D. Hawksw. & O.E. Erikss.
= *Trichotheliales* Hafellner & Kalb
Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Ostropomycetidae*

Introduction

Ostropales is the largest non-lichenized order within the primarily lichenized class *Lecanoromycetes*. It was originally introduced to accommodate a single family *Ostropaceae* (Nannfeldt 1932) based on ascus and ascospores morphology. Baloch et al. (2013) synonymized *Ostropaceae* under *Stictidaceae*.

Ostropales presently comprises three families *viz*. *Phaneromycetaceae*, *Spirographaceae* and *Stictidaceae* (Wijayawardene et al. 2022a). *Phaneromycetaceae* accommodates a single non-lichenized discomycetous genus *Phaneromyces* (Gamundí & Spinedi 1985). *Stictidaceae* entirely comprised non-lichenized taxa until Gilenstam (1969) added the lichenized genus *Conotrema*. The genus was transferred from *Diploschistaceae* to *Ostropaceae* based on similar morphological features, such as the shape of the apothecia and the ascus structure. Gilenstam (1969) also assumed that non-lichenized *Stictis* and lichenized *Conotrema* can be congeneric due to shared morphological characters (except for their lifestyle) and suggested that several lichenized genera such as *Graphis*, *Diploschistes* and *Thelotrema* should be included in *Ostropales sensu stricto*. However, Sherwood (1977b) noted the presence of a crystalline layer of calcium oxalate or other substances between the periphysoids and the ascocarp wall in *Stictis* which was apparently absent in *Conotrema*. The third family, *Spirographaceae* comprises a single genus *Spirographa*. Its taxa are reported as lichenicolous

and fungicolous fungi in their sexual and asexual states (Flakus et al. 2019). An additional five genera are tentatively assigned within the order (Wijayawardene et al. 2022a).

The phylogenetic placement, concept and delimitation of *Ostropales* have changed over time due to huge diversity in phenotypic characters (Baloch et al. 2010). Different phylogenetic signals emitted by various molecular data sets and different taxon samplings revealed different phylogenetic placements of *Ostropales* (Kauff & Lutzoni 2002, Wedin et al. 2005a, Miadlikowska et al. 2006, Lumbsch et al. 2007a). Lumbsch et al. (2007a) investigated the phylogenetic position of *Ostropales* based on mitochondrial, nuclear and protein coding regions which supported the placement within *Lecanoromycetes*.

History

The history of *Stictidaceae* started with the introduction of the genus *Stictis*. Henssen & Jahns (1973) accepted two suborders, namely *Ostropineae* (*Stictidaceae* and *Thelotremataceae*) and *Graphidineae* (*Graphidaceae*). Both suborders shared similar ascomatal development and ascus structure (Gilenstam 1969, Henssen & Jahns 1974). Poelt (1973) proposed to combine the orders *Ostropales* and *Graphidales*. Sherwood (1977b) treated two orders, namely *Graphidales* for those with 'graphidean' ascospores (macrocephalic ascospores) and *Ostropales* for those with a normal sequence of ascospore septation with microcephalic ascospores. The 'graphidean' spores can be recognized in the immature state by having longer segments in polar cells than median cells cut off the trans septa. The septation proceeds from the primary septum towards each end. The septa of microcephalic spores form more or less equal size segments. Sherwood (1977b) also mentioned the presence of hysterothecial ascomatal shape in *Graphidaceae* and the distance relationship to *Stictidaceae*. However, ascomatal shape was often used in the family level classification within the *Graphidales*. Eriksson & Hawksworth (1995) and Hawksworth (1995) proposed keeping *Graphidales* in the *Ostropales*. However, Lumbsch et al. (1997) disagreed with the separation of these orders since both types of ascospores that had been reported in *Diploschistes* belong to the *Thelotremataceae* which was placed in *Graphidales*.

The phylogenetic analyses conducted by Winka et al. (1998a) showed the close relationships of *Stictidaceae* and *Graphidaceae*. Eriksson & Hawksworth (1998) accepted eight families in *Ostropales,* including *Asterothyriaceae*, *Gomphiliaceae*, *Graphidaceae*, *Odontotremataceae*, *Phaneromycetaceae*, *Solorinellaceae*, *Stictidaceae* (including *Petractis*), and *Thelotremataceae*. Consequently, several orders and families such as *Gyalectales* (Kauff & Lutzoni 2002), *Trichotheliales* (Grube et al. 2004), *Gomphillaceae* (Lücking et al. 2004), and *Phlyctidaceae* (Wedin et al. 2005b) were transferred to this order. Lumbsch & Huhndorf (2007) accepted 11 families, namely *Coenogoniaceae*, *Gomphillaceae*, *Graphidaceae*, *Gyalectaceae*, *Myeloconidaceae*, *Odontotremataceae*, *Phaneromycetaceae*, *Phlyctidaceae*, *Porinaceae*, *Stictidaceae* and *Thelotremataceae*. Mangold et al. (2008) synonymized *Thelotremataceae* under *Graphidaceae* based on the phylogenetic analyses. Subsequently, Lumbsch & Huhndorf (2010) accepted ten families, namely *Coenogoniaceae*, *Gomphillaceae*, *Graphidaceae*, *Gyalectaceae*, *Myeloconidaceae*, *Odontotremataceae*, *Phaneromycetaceae*, *Phlyctidaceae*, *Porinaceae* and *Stictidaceae*. The same year, Baloch et al. (2010) established a new family *Sagiolechiaceae*, for *Sagiolechia* and *Rhexophiale*.

Nelsen et al. (2014a) synonymized *Myeloconidaceae* under *Porinaceae* based on morphological and molecular evidence. Consequently, Resl et al. (2015) treated *Protothelenellaceae* and *Thrombiaceae* under *Ostropales* with the aid of phylogeny. Lücking et al. (2017) excluded *Odontotremataceae* and *Phaneromycetaceae* in *Ostropale*s, but Wijayawardene et al. (2018) accepted 13 families in *Ostropale*s, namely, *Coenogoniaceae*, *Gomphillaceae*, *Graphidaceae*, *Gyalectaceae*, *Odontotremataceae*, *Phaneromycetaceae*, *Phlyctidaceae*, *Porinaceae*, *Protothelenellaceae*, *Sagiolechiaceae*, *Stictidaceae*, *Thelenellaceae* and *Thrombiaceae*. *Ostropales* (including *Stictidaceae* and *Odontotremataceae*) formed a monophyletic clade with *Graphidales* and *Gyalectales* and together formed a sister clade to *Thelenellales* in the temporal band approach method (Kraichak et al. 2018b). Lücking (2019) accepted *Ostropales*, *Graphidales*, *Gyalectales*, *Ostropales*

sensu stricto and *Thelenellales* and established a new order *Odontotremat*ales for *Odontotremataceae*. Subsequently, Flakus et al. (2019) established a new family *Spirographaceae* to accommodate the lichenicolous and fungicolous genus *Spirographa*. The family formed a sister clade to the lichenized families *Fissurinaceae*, *Gomphillaceae* and *Graphidaceae* without considering Lücking's (2019) classification. The lichenicolous genus *Cornutispora* was previously placed in *Odontotremataceae* (Hawksworth & Sherwood 1982) and synonymized under *Spirographa* based on the recent phylogenetic analyses (Flakus et al. 2019). Previously, Diederich & Etayo (2000) suggested that the genus *Spirographa* should be placed in *Helotiales* close to *Skyttea* due to the inadequate presence of cleistohymenial ascomata with positive iodine reaction.

Wijayawardene et al. (2022a) accepted three families namely *Phaneromycetaceae*, *Spirographaceae* and *Stictidaceae*. *Phaneromyces* was introduced for a single species *Phaneromyces macrosporus* and the genus was treated in *Stictidaceae* (Saccardo 1889b). Sherwood (1977b) placed it in *Lecanorales* and suggested the possible placement within *Patellariaceae*. Gamundí & Spinedi (1985) reexamined the genus and found that *Phaneromyces macrosporus* and *P. platensis* are congeneric and were distantly related to *Patellariaceae*, on the basis of absence of blackish, carbonaceous apothecia with a black epithecium and dark excipulum of "*textura angularis*" or "*textura globulosa*" but the possession of bitunicate asci. Subsequently, a new family *Phaneromycetaceae* was established to accommodate the genus *Phaneromyces*. The phylogenetic placement of the family remains uncertain due to the absence of molecular data, but has been placed in *Ostropales* due to shared morphological features. *Phaneromyces* is characterized by crystalline excipulum, bitunicate asci (J-) and hyaline phragmospores (Gamundí & Spinedi 1985). Presently three families are accepted under *Ostropales* and five genera are listed under *Ostropales* genera *incertae sedis* that are listed below.

General description

The majority of the genera in *Stictidaceae* have a sexual morph, which mainly forms apothecioid ascomata, with the exceptions of *Geisleria* and *Ostropomyces* which form perithecioid ascomata. The asci are cylindrical to clavate with 1–2-spored to poly-spored, fusiform, oblong, ellipsoidal to short clavate, aseptate, multi-septate and muriform (*Ingvariella* and *Topelia)* ascospores (Sherwood 1977b, 1978). The polyspored ascospores are reported in *Carestiella*, *Schizoxylon*, *Stictis* and *Xyloschistes*. In contrast, *Ingvariella* comprises 1–2-spored asci (Sherwood 1977b, Spribille 2008). Asexual morphs in *Stictidaceae* are characterized by pycnidial conidiomata. A few exceptions are *Biostictis*, which forms hyphomycetous sporulation structures and *Dendroseptoria* which forms sporodochial fruiting bodies (Sherwood 1978, Koukol et al. 2017). The conidiogenesis can be blastic-phialidic, blastic-sympodial, blastic-retrogressive and thallic-arthric, which forms aseptate, one-celled to multiseptate, ellipsoidal to long cylindrical and occasionally tetraradiate conidia (Sherwood 1978, Johnston 1985, Crous et al. 2018a). The taxa are mostly small and delicate. Lichen forming species form crustose or rarely filamentous thalli (Baloch et al. 2010). *Spirographaceae* also form both sexual and asexual morphs. The sexual morph is characterized by apothecioid or perithecioid or cleistohymenial ascomata that are immersed or sessile on the host thalli or hymenia, single or aggregated on a stroma, with honey-brown, dark-brown or black pigments, a persistent exciplex, I– and K/I– hymenium, simple to branched paraphyses, unitunicate asci with 16–32-spored, 1-septate, hyaline, narrowly ellipsoidal to fusiform, curved or sigmoid ascospores. The asexual morph of *Spirographa* is represented by *Cornutispora* (Punithalingam 2003) and was characterized by immersed, pycnidial conidiomata, hyaline to yellowish-brown or dark brown, disintegrating irregularly at the top to release conidia, hyaline, septate, branched conidiophores, holoblastic, synchronous or sympodial conidiogenous cells, and hyaline, Y-shaped, with a main axis and two diverging arms, or triangular, or tetra- to polyhedral conidia (Flakus et al. 2019). Several morphological differences are also observed in the optionally lichenized species. The saprotrophic species differ from respective lichenized species in the formation of larger fruit bodies that are often sessile on the substrate, heavily pigmented ascoma wall and often well-developed and distinct lower wall structures and well developed paraphysoids (Wedin et al. 2006). In *Stictidaceae*, genera have

been reported in either sexual states or asexual states whereas several other genera have been reported in both sexual and asexual states such as *Acarosporina*, *Biostictis*, *Cyanodermella*, *Fitzroyomyces*, *Ostropomyces*, *Schizoxylon* and *Stictis* (Crous et al. 2014b, 2017a, Ekanayaka et al. 2019b, Phukhamsakda et al. 2020, Thiyagaraja et al. 2021b, Wei et al. 2021a).

Sexual morph: *Ascomata* apothecioid, perithecioid, cleistohymenial, immersed or sessile. Paraphyses simple to branched. *Asci* cylindrical to clavate, unitunicate to bitunicate asci, 1–8-spored, poly-spored. *Ascospores* elongated clavate, long-cylindrical to filiform, short clavate, fusiform, oblong, ellipsoidal, obovoid, curved or sigmoid ascospores, simple to multiseptate, muriform. Asexual morph: hyphomycetous, sporodochial, pycnidial conidiomata, hyaline to dark brown, hyaline, septate, branched conidiophores, holoblastic, synchronous, sympodial conidiogenous cells (Figs. 143, 144, 145).

Families included in *Ostropales*

Phaneromycetaceae Gamundí & Spinedi
Spirographaceae Flakus, Etayo & Miadlikowska
Stictidaceae Fr.

Ostropales genera *incertae sedis*
Aabaarnia Diederich
Biazrovia Zhurb. & Etayo
Elongaticonidia W.J. Li & Camporesi & K.D. Hyde
Normanogalla Diederich
Paralethariicola Calat., Etayo & Diederich

Evolution

Lutzoni et al. (2001) suggested the occurrence of delichenization in *Ostropales* which was later supported in the molecular study conducted by Thiyagaraja et al. (2021b). The saprotrophic taxa evolved from secondary de-lichenization, which was observed several times independently throughout the family. Several genera and species show high plasticity in their lifestyles. The taxa of *Cryptodiscus* show three different lifestyles; saprotrophic (*Cryptodiscus pini* and *C. pallidus*), lichenized (*C. gloeocapsa*) and lichenicolous (*C. epicladonia* and *C. cladoniicola*). Both lichenized and saprotrophic lifestyles are observed in the species of *Schizoxylon albescens*, *Stictis confusum*, *S. mollis* and *S. populorum* (Wedin et al. 2004, 2006). The traditional classification of *Ostropales* was mainly based on phenotypic characteristics such as ascoma margin, the presence of wall layers and pigmentation and the formation of crystals. However, later studies revealed high plasticity in their morphology at the generic and species level (Wedin et al. 2004, Baloch et al. 2010).

Justification of order and problems

The taxon sampling of *Stictidaceae* is poorly studied in the phylogenetic analyses that have been conducted for *Ostropales* (Lutzoni et al. 2001, Kauff & Lutzoni 2002, Wedin et al. 2005b, Miadlikowska et al. 2006). When Lücking (2019) made significant taxonomic changes in the *Ostropales*, his classification was not considered by Flakus et al. (2019) who established the new family *Spirographaceae*. In Flakus's treatment, the family formed the sister clade to the extended lichenized families which were previously accommodated in *Ostropales*. Wijayawardene et al. (2020) included *Spirographaceae* in *Ostropales*, but it was excluded from later phylogenetic analyses for *Stictidaceae* group (Thiyagaraja et al. 2021b, Wei et al. 2021a).

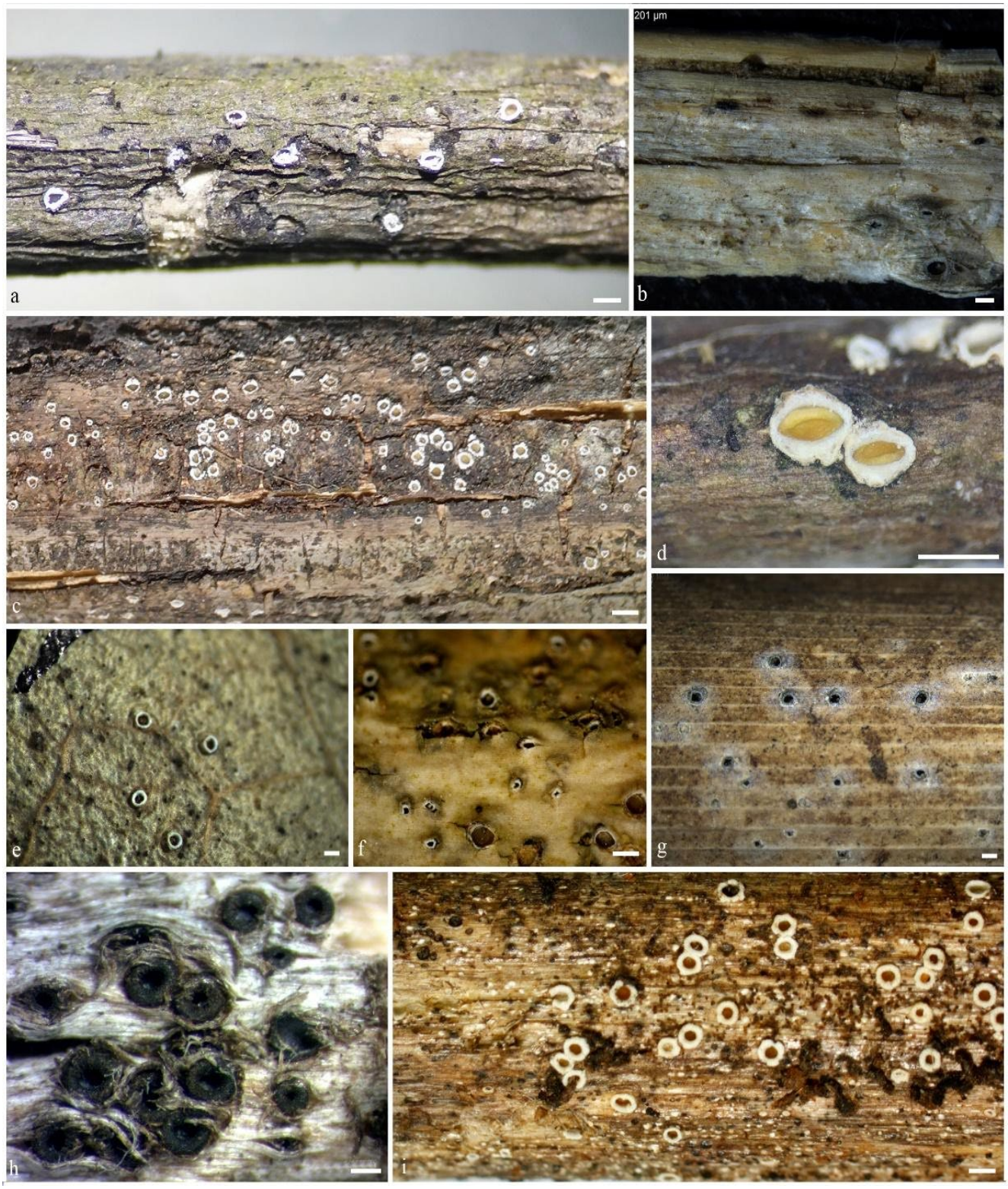


Figure 143 – Thallus morphology of *Ostropales*. a *Fitzroyomyces* sp. b, i *Fitzroyomyces cyperacearum*. c *Fitzroyomyces yunnanensis*. d *Phacidiella kunmingensis*. e *Stictis fici*. f *Fitzroyomyces xishuangbannaensis*. g *Ostropomyces pruinosellus*. h *Sphaeropezia shangrilaensis*. Scale bars: a, g, d = 500 µm, b, e, h, i = 200 µm, c, f = 1000 µm.

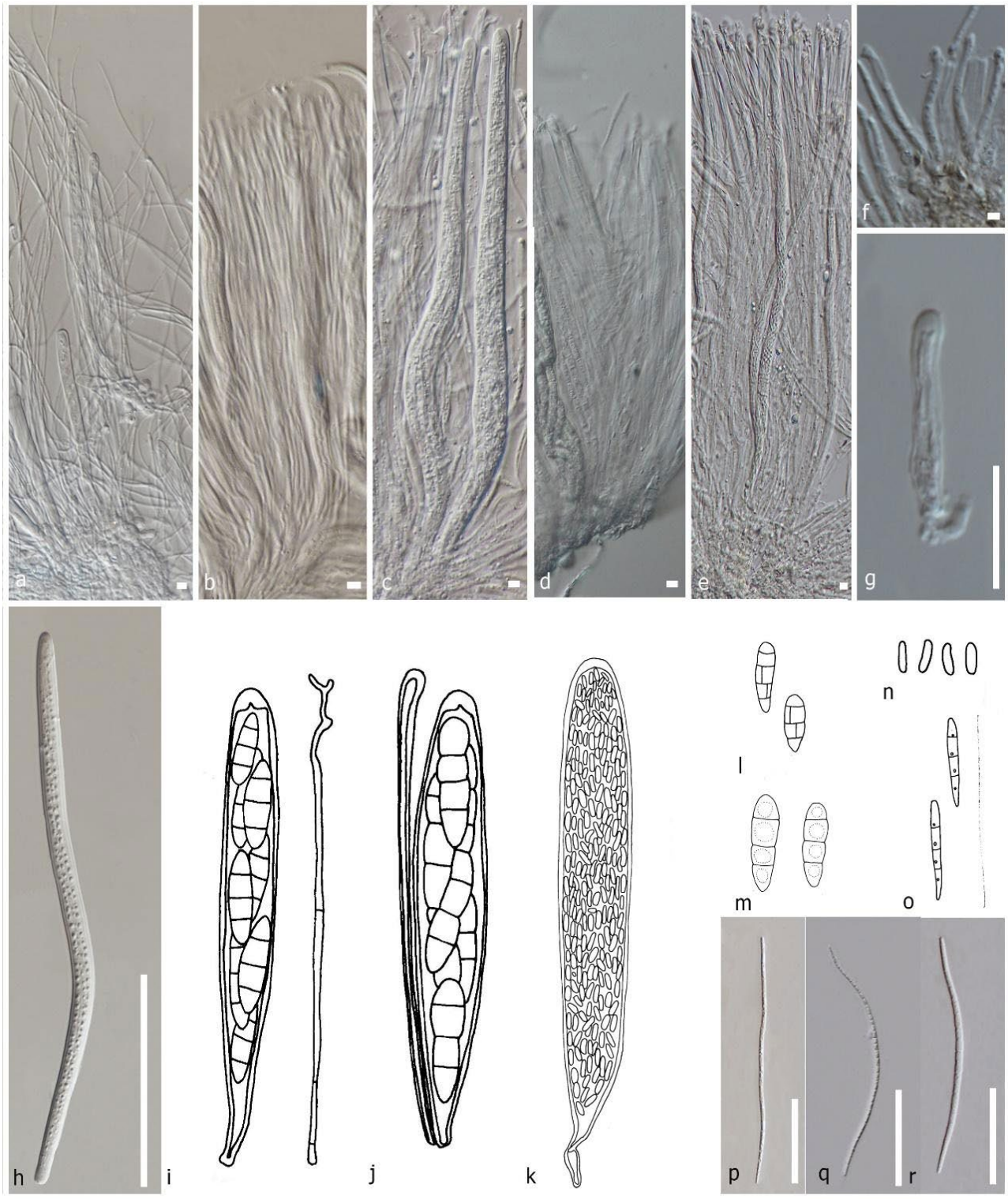


Figure 144 – Sexual morph of *Ostropales*. a–e Paraphyses of *Stictidaceae* species. g–k Asci (g *Sphaeropezia shangrilaensis*, h *Ostropomyces pruinosellus*, i *Stictis quadrinucleata*, j *Cryptodiscus pallidus*, k *Schizoxylon nigrellum*). l–r Ascospores (l *Delpontia pulchella*, m *Cryptodiscus pallidus*, n *Schizoxylon nigrellum*, o *Stictis minor*, p *Fitzroyomyces xishuangbannaensis*, q *F. Cyperacearum*, r *F. yunnanensis*) (redrawn from Sherwood 1977b). Scale bars: a–f = 5 µm, g = 10 µm, h, p–q = 50 µm.

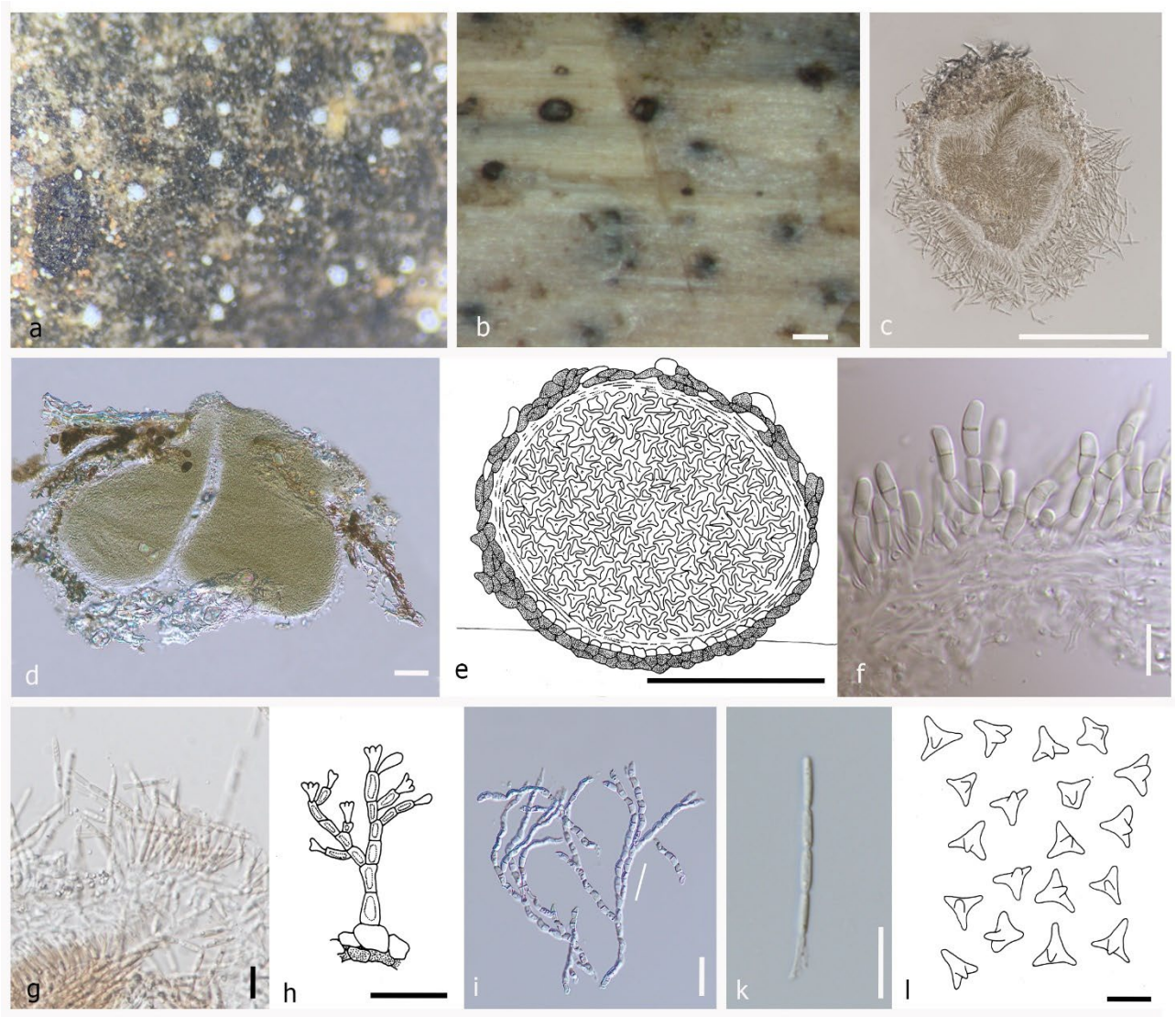


Figure 145 – Asexual morph of *Ostropales*. a, b Conidiomata on host substrate (a *Neohormodochis septispora*. b *Ostropomyces thailandicus*). c–e Vertical section through Conidiomata (e *Asteroglobulus giselae*). f–h Conidiophore with conidiogenous cells and young conidia (f *Neohormodochis septispora*, g *Ostropomyces thailandicus*, h *Asteroglobulus giselae*). i–k Conidia (I *N. septispora*, j *O. thailandicus*, k *A. giselae*) (redrawn from Valadbeigi & Von Brackel 2011). Scale bars: b = 500 µm, c = 200 µm, d–i = 10 µm.

The ostropalean members (especially lichenized species) often form thin, inconspicuous, ephemeral thalli with minute apothecia. Therefore, they are often overlooked in the field (Bielczyk & Kiszka 2001, Baloch et al. 2010). Molecular data are lacking for many genera such as *Biostictis*, *Conotremopsis*, *Delpontia*, *Dendroseptoria*, *Karstenia*, *Lillicoa*, *Nanostictis*, *Phaneromyces*, *Propoliopsis*, *Stictophacidium* and *Topelia* (Gamundí & Spinedi 1985, Wei et al. 2021a), while several genera are largely polyphyletic (e.g., *Stictis*). Most of the parasitic genera lack molecular data, which prevents definitive conclusions regarding lifestyle changes in the family. The sexual and asexual links have been made for *Schizoxylon pseudocyanosporum* based on morphological features (Johnston 1985). Thiyagaraja et al. (2021b) and Wei et al. (2021a) also found sexual and asexual species of *Ostropomyces* from the same substrate. However, sexual and asexual connections were not supported by all genetic markers of interspecific genetic diversity. Molecular data are important for linking sexual and asexual morphs.

Li et al. (2020) recently introduced a new asexual genus *Elongaticonidia* in *Ostropales* and placed in *incertae sedis*. The genus formed a sister clade to *Mulderomyces* in LSU phylogenetic

analysis and differs in the form of conidia and conidiogenous cells from *Mulderomyces*. However, both genera formed a close clade with lichenized groups that were treated before Lücking's (2019) study. Li et al. (2020) accepted *Phacidiella* under *Ostropales incertae sedis*. However, the genus was accepted under *Helotiales incertae sedis* by Wijayawardene et al. (2020, 2022a). Other *incertae sedis* genera include *Aabaarnia*, *Biazrovia* and *Normanogalla*. These comprise lichenicolous fungi without molecular data (Zhurbenko & Etayo 2013, Diederich 2014). The lichenicolous genus *Parallethariicola* was originally introduced within *Odontotremataceae* (Calatayud et al. 2001). Yang et al. (2019a) treated this genus in *Ostropales incertae sedis*. This treatment was also accepted in Wijayawardene et al. (2022a). Due to a lack of molecular data, we suggest retaining this genus in *Odontotremataceae* following the original paper in which the genus was introduced.

Significance

Ecological and economic roles

The order mainly comprises non-lichenized saprobes, but also includes endophytes, lichenized and lichenicolous species. Several species show optional lichenization (Wedin et al. 2004, Baloch et al. 2013). Wedin et al. (2004) initially reported optional lichenization. They found that several *Stictis* species were lichenized when growing on bark, but saprotrophic when growing on wood. The species were confounded in the molecular phylogeny, potentially due to their environmental plasticity (Wedin et al. 2004).

Spirographa is a cosmopolitan genus. However, the majority of the species are poorly known. *Spirographa* members are host-specific and harbor a variety of lichens and non-lichenized fungi (Flakus et al. 2019). *Spirographa galligena* is known to form galls on the host thallus (Flakus et al. 2019). Several genera, such as *Acarosporina*, *Biostictis*, and *Rogergea* are reported from living plants (Sherwood 1977b). *Sphaeropezia leucocheila* has been reported as a parasite on liverwort and mosses (Johnston et al. 2019a). The species of several genera such as *Stictis*, *Schizoxylon* and *Robergea* formed persistent vegetative mycelium on agar, which suggested that they may survive under unfavourable conditions (Sherwood 1977b). *Glomerobolus gelineus* was recorded as a halotolerant fungus from salt marshes in North Carolina (Kohlmeyer & Volkmann-Kohlmeyer 1996).

Chemical diversity

Calcium oxalate is commonly found in the excipular margin in *Stictidaceae* and *Phaneromycetaceae* species. It is a by-product of metabolism and reflects the need for an immersed fungus to dispose of its waste products (Sherwood 1977b).

***Peltigerales* Walt. Watson, New Phytologist 28: 9 (1929)**

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Lecanoromycetidae*

Introduction

Lichens that were primarily associated with cyanobacteria as primary symbionts were mainly classified into three distantly related taxonomic groups, including *Arctomiaceae* (*Baeomycetales*), *Lichinales*, and *Peltigerales* (Lumbsch et al. 2005a, Wedin et al. 2005b). Among them, *Peltigerales* are an important group due to their symbiotic associations with multiple partners. In these lichens, a single mycobiont associates with both green algae and cyanobacteria, forming a unified thallus (Magain 2014).

History

Peltigerales was introduced to accommodate *Peltigeraceae*, *Stictaceae* and *Pannariaceae* in the sub-class *Ascolichens* in the class *Lichens* based on having unstalked apothecia with algal cells generally belonging to *Cyanophyceae*. *Peltigera* is one of the earliest described lichenized genera (Willdenow 1787). However, the genus is poorly understood compared to other macrolichens. These cyanolichens are characterized by foliose, lobate thalli and cyanobacterial photobiont arranged in a

more or less distinct layer beneath the cortex and others produce conspicuously gelatinous thalli without a specialized photobiont layer ('homoiomerous thalli'), and usually without a differentiated cortex. The gelatinous habit formed by *Nostoc* photobiont has a sheet around the filamentous thread-like colonies and swells and becomes extremely gelatinous when wet. The taxa are traditionally been classified in *Collemataceae* also known as 'jelly lichens' and a few species are also reported in *Pannariaceae* (Jørgensen 1994).

Peltigerales are often treated in the sub-ordinal level, *Peltigerineae*, within *Lecanorales*. The classification for the order has undergone several changes. Henssen & Jahns (1973) accepted *Peltigerineae*, *Peltigeraceae*, *Lobariaceae* and *Placynthiaceae*. Poelt (1974a) additionally included *Nephromataceae* and Hafellner (1988) included *Solorinaceae* and the classification continued with several upward and downward counts of the families of the order (Rambold & Triebel 1992, Tehler 1996, Kirk et al. 2001, Eriksson et al. 2003b, Wiklund & Wedin 2003). Miadlikowska & Lutzoni (2004) accepted two suborders, *Collematineae* (*Collemataceae*, *Placynthiaceae*, and *Pannariaceae*) and *Peltigerineae* (*Lobariaceae*, *Nephromataceae*, and *Peltigeraceae*) based on LSU and SSU sequence data and *Peltigerales* recovered within *Lecanoromycetidae* and formed a close phylogenetic relationship to *Baeomycetales*, *Ostropales* and *Pertusariales* (*Ostropomycetidae*). A similar topology also resulted in the phylogenetic study conducted by Wedin & Wiklund (2004) but lower statistical support was found for *Collematineae*. Wedin et al. (2007) established a new family *Massalongiaceae* to accommodate *Massalongia,* which was previously placed in *Pannariaceae* and *Peltigeraceae* (Zahlbruckner 1926, Henssen 1963a, b). Hibbett et al. (2007) also accepted *Peltigerales* as a separate order following the study of Miadlikowska & Lutzoni (2004). In contrast, Tehler & Wedin (2008) accepted suborder *Peltigerineae* under *Lecanorales* and treated *Coccocarpiaceae*, *Collemataceae*, *Lobariaceae*, *Massalongiaceae*, *Nephromataceae*, *Pannariaceae*, *Peltigeraceae* and *Placynthiaceae*. Later, Wedin et al. (2011) and Spribille & Muggia (2013) established new families, *Vahliellaceae* and *Koerberiaceae,* within *Peltigerales,* respectively. Kraichak et al. (2018b) synonymized *Lobariaceae* and *Nephromataceae* under *Peltigeraceae* based on the temporal band approach and this classification was further accepted. Hyde et al. (2024b) accepted eight families *Coccocarpiaceae*, *Collemataceae*, *Koerberiaceae, Massalongiaceae*, *Pannariaceae*, *Peltigeraceae*, *Placynthiaceae* and *Vahliellaceae* within *Peltigerales* with two genera are being placed under *incertea sedis*.

General description

The taxa of this order are characterized by foliose, subfruticose, or granular-squamulose thalli with rhizines or tomentum on the lower side of the thalli, predominantly multiseptate, hyaline or brown ascospores with some lecanoralean features such as reactive a-layer and thick c-layer and mostly unbranched and free paraphyses. Both hemiangiocarpic and gymnocarpic ascomatal development are observed among species (Spribille & Muggia 2013). In the multiple associations with photobiont, the green photobiont is present in a well-delimited algal layer within the thallus whereas the cyanobacterium is compacted into specific internal or external structures named cephalodia (Henssen 1976). However, in some cases, phycobiont and cyanobiont can associated with morphologically different thalli structures but are associated with the same mycobiont (Armaleo & Clerc 1991), and the independent thalli are adapted to different environmental conditions, which stimulated their development (Green et al. 2002). Several *Collemataceae* species associate with cyanobionts, representing an independent transition from a generalist state (sexually reproducing mycobiont) to a strict specialist state (asexually reproducing mycobiont), resulting from the vertical photobiont transmission via specialized vegetative propagules (Otálora et al. 2010). The mycobiont in several species of *Nephroma*, *Parmeliella* and *Peltigera* are highly selective towards their cyanobiont partners and even selective to specific strain or species of *Nostoc* in the genera *Sticta* and *Pseudocyphellaria* (Stenroos et al. 2006). In *Peltigera*, the level of cyanobacterial specialization showed a certain level of the variable where the mycobiont associates with either one or two of the cyanobacterial lineages (O'Brien et al. 2013).

Sexual morph: *Thallus* nearly crustose, dendroid-fruticose, microfruticose, foliose, placodioid to ribbon-like squamulose. *Hypothallus* and lower surface poorly developed to lacking, well developed or absent. Photobiont; Cyanobiont *Scytonemataceae*, *Nostoc*, *Hyphomorpha*, *Chlorobiont Coccomyxa*, *Dictyochloropsis*, *Myrmecia*. *Ascomata* laminal, on lobe tips, rarely lobe undersurfaces. *Asci* apical apparatus Pannaria-type, Micarea-type, Vahliella-type, Coccocarpia-type. *Ascospores* simple, 1-septate, multiseptate to muriform. Asexual morph: *Conidia* bacilliform, ellipsoid to pyriform, or truncate oblong to bacilliform, with or without end thickenings (Figs. 146, 147).

Families included in *Peltigerales*

Coccocarpiaceae Henssen ex Henssen
Collemataceae Zenker
Koerberiaceae T. Sprib. & Muggia
Massalongiaceae Wedin, P.M. Jørg. & E. Wiklund.
Pannariaceae Tuck.
Peltigeraceae Dumort. (= *Lobariaceae* Chevall.; = *Nephromataceae* Wetm. ex J.C. David & D. Hawksw.)
Placynthiaceae Å.E. Dahl
Vahliellaceae Wedin

Peltigerales genera *Incertae sedis*
Aberratus W.L Strong
Erinacellus T. Sprib. Muggia & Tønsberg

Evolution

Peltigerales may be considered as advanced from *Collemales* or as derivatives from *Parmeliales* by Watson (1929). Hawksworth (1982) proposed that peltigeralean lichens can be an ancient lineage within the *Pezizomycotina* based on several observations such as semifissitunicate asci, hosting large number of obligatory lichenicolous fungi, wide species distribution, great diversity of secondary metabolites and cyanobacteria as the photobiont but later phylogenetic analyses didn't support this hypothesis (Eriksson & Strand 1995, Lutzoni et al. 2001, Kauff & Lutzoni 2002). Since the peltigeralean lichens are primarily associated with cyanobacteria are known to be of ancient origin and among the earliest potential photobionts available for any emerging fungi (Hawksworth 1988). The group might have originated in palaeophytic or proterophytic times. The number of morphological characters transformations in the exciple structure (ring-shaped to a disc-shaped), gelatinosity (non-gelatinous to a gelatinous thallus), and ascus apex (gains and losses of internal structures in the ascus apex) structure in the order was higher than the minimum possible (Wedin et al. 2009b).

Justification of order and problems

The order formed non-monophyletic groups, indicating that further investigation is needed for the evolutionary history through extensive phylogenetic taxon sampling. The families associated with gelatinous taxa *Collemataceae* and *Pannariaceae* also need to be re-circumscribed (Wedin et al. 2009b).

Significance

Ecological and economic roles

Peltigeralean lichens are distributed worldwide. *Lobariaceae* (=*Peltigeraceae*) is common in the Southern Hemisphere, whereas other families are more common and diverse in the Northern Hemisphere (Galloway 1988, Miadlikowska & Lutzoni 2004). The taxa grow on mosses, rocks, soil, or bark, and mostly in moist to humid wooded habitats (Miadlikowska & Lutzoni 2004). Cyanolichens, which harbor cyanobacterial photobionts, are sensitive to air pollution. They are also used for early-warning bio monitors across different latitudes and are among the highest priority

species for conservation efforts (Richardson & Cameron 2004). Several *Sticta* taxa are used to monitor the environmental health of forest ecosystems in New Zealand (Ranft et al. 2018).

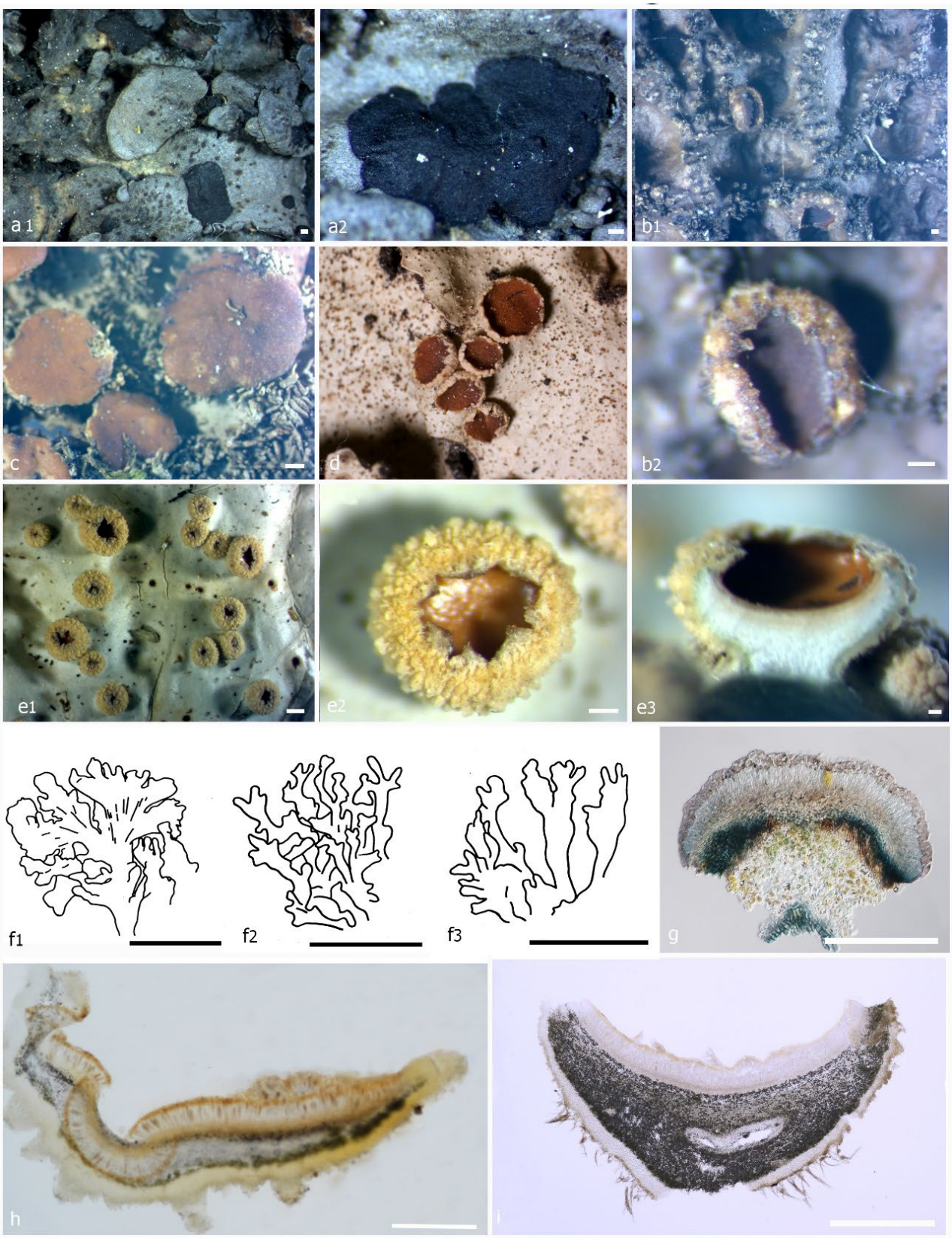


Figure 146 – Thallus and apothecial morphology of *Peltigerales*. a1, a2 *Coccocarpiaceae* sp., b1–e3, h, i *Peltigerales* species. f1–f3 *Koerberia* sp., g *Coccocarpiaceae* sp. (redrawn from Henssen 1963a). Scale bars: a1–b2, e2, g = 200 µm, c, e1, i = 500 µm, f1–f3, h = 1000 µm.

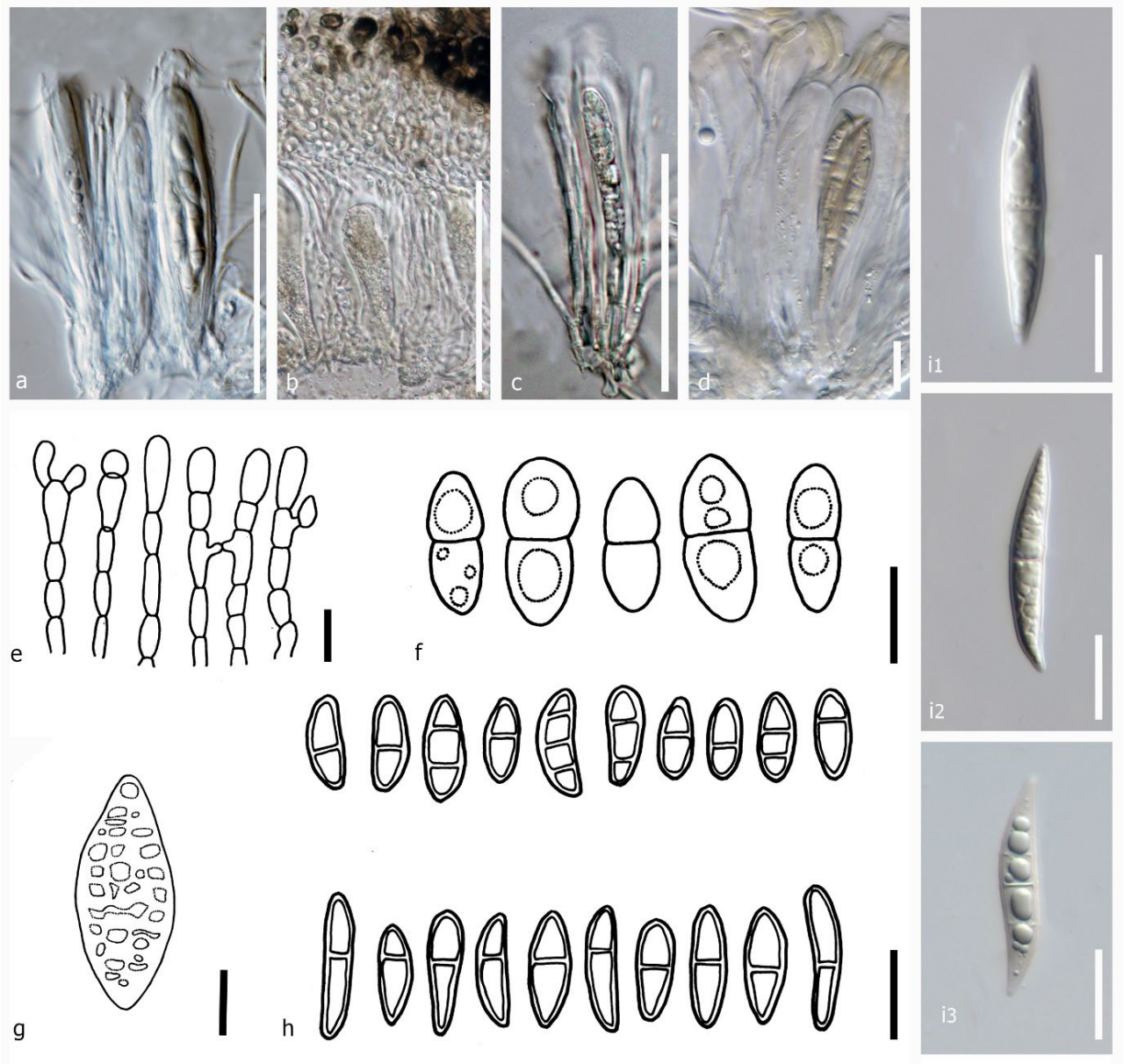


Figure 147 – Paraphyses, asci and ascospores morphology of *Peltigerales*. a–d Asci and Paraphyses. (a, c, d *Peltigerales* species, b *Coccocarpiaceae* sp.). e Paraphyses (*Placynthium australiense*). f–i3 Ascospores (f *Placynthium australiense*, g *Leptogium lichenoides*, h *Massalongia patagonica*, I *M. carnosa*). j1–j3 *Peltigerales* species (redrawn from Henssen 1963a, Otálora et al. 2013, Jørgensen et al. 2019). Scale bars: a = 30 µm, b, c = 50 µm, d, h, i, j1–j3 = 20 µm, e, f = 10 µm.

Chemical diversity

All three major pathways of secondary metabolism in lichens are found in *Peltigerales* including 1) the acetate-polymalonate pathway (producing orcinol depsides, j-orcinol depsides and depsidones and usnic acid), 2) shikimic acid pathway (producing terphenylquinones and pulvinic acid derivatives) and 3) mevalonic acid pathway (producing sterols and terpenoids). Triterpenoids are compounds with varying numbers of carbon atoms derived from C-5 (isoprenoid) units and are richly found in *Nephroma*, *Peltigera* and *Pseudocyphellaria* and are used as a useful taxonomic character for species-level identification (Galloway 1985, 1988, 1991). Tanas et al. (2010) studied the anti-inflammatory effects of the methanol extract of the lichen species *Peltigera rufescens*.

Other relevant data and future recommendations

Many taxa lack molecular data and have not been thoroughly analyzed in broad phylogenetic analyses. Even in comprehensive phylogenetic analyses, taxon sampling for cyanolichens remains relatively low (Spribille & Muggia 2013).

Pertusariales **M. Choisy ex D. Hawksw. & O.E. Erikss., Systema Ascomycetum 5(1): 181 (1986)**

= *Agyriales* Clem. & Shear

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Ostropomycetidae*

Introduction

Pertusariales was introduced by Hawksworth & Eriksson (1986) and the order presently comprises nine families including *Agyriaceae*, *Coccotremataceae*, *Icmadophilaceae*, *Megasporaceae, Microcaliciaceae*, *Ochrolechiaceae*, *Pertusariaceae*, *Varicellariaceae* and *Variolariaceae* (Hyde et al. 2024b). The taxa are characterized by hemiangiocarpous ascoma development, thick-walled, more or less amyloid asci, relatively large ascospores, a crustose to subfruticose growth form and green algae as primary photobiont (Schmitt et al. 2006).

History

Pertusariales was formally regarded as a suborder of *Lecanorales* (Hafellner et al. 1993). In the earlier classifications, Henssen & Jahns (1973) accepted only one family (*Pertusariaceae*) within the suborder *Pertusariineae* of *Lecanorales*. However, Eriksson & Hawksworth (1991b) distinguished two families in the order *Pertusariales*: *Coccotremataceae* and *Pertusariaceae*. However, several authors preferred to keep the order separately due to differences in ascus-type and ascoma development (Ott & Lumbsch 2001).

The non-monophyly of this order was also reported in the study of Lumbsch et al. (2004b). However, the order was recovered as a monophyletic clade with *Icmadophilaceae* in the phylogenetic analysis conducted by Reeb et al. (2004), and this clade was found in the newly established subclass *Ostropomycetidae* in their study. *Pertusariales* are now considered as a more closely related group to the *Lecanorales* than *Ostropales sensu lato* (Lücking et al. 2004, Lumbsch et al. 2004b, Reeb et al. 2004). Lumbsch et al. (2007b) suggested *Agyriales* to be a synonym of *Pertusariales* based on the phylogenetic analyses conducted using the type species *Agyrium rufum*, a non-lichenized, saprobic fungus that formed a sister clade to *Coccotremataceae* and *Pertusariaceae*. This was further confirmed in the phylogenetic analyses conducted by Schmitt et al. (2010) in which *Agyrium rufum* nested with *Pertusariaceae sensu stricto*. Thus, *Pertusariales* was synonymized under *Agyriales* based on the priority given to the older name *Agyriales* rather than *Pertusariales*. Consequently, Hodkinson & Lendemer (2011) rejected the synonymy of *Pertusariales* and argued to retain *Pertusariales* because the principle of priority is not mandatory for taxa above the family rank, and the name *Agyriales* was most recently misapplied to a monophyletic group, including the family *Trapeliaceae*, now recognized as a new order *Trapeliales*. *Coccotremataceae*, *Pertusariaceae*, and *Ochrolechiaceae* were traditionally retained under *Pertusariales* (Poelt 1973, Henssen & Jahns 1974, Henssen 1976, Eriksson & Hawksworth 1986c) and the placement of several genera and families has been a subject of debate for many years. For example, *Megasporaceae* was described by Lumbsch et al. (1994) to accommodate the single species *Megaspora verrucosa* and placed in *Pertusariales*. The genus has been erected by Hafellner & Wirth (in Wirth 1987) and was previously classified as a subgenus of *Aspicilia* (Clauzade & Roux 1985) and is now considered as a separate genus within *Megasporaceae*. Hyde et al. (2024b) accepted nine families under *Pertusariales* which are listed below.

General description

The presence of pruina has no systematic value and is found on the cortical surfaces of many *Pertusariae*. However, the pruina that occurs with apothecia has a value for subgeneric segregation level. Ornamentation of spore walls is rare among lichenised fungi but this character was reported in eight *Pertusariae* species from North America. Isidia and soredia are also used as species indicators that associate with *Pertusariae* species that have distinct chemical, ecological, or geographical attributes. Four kinds of isidia are reported including granular and papillate that associate with thalloid and columnar and coralloid isidia that occur lateral or terminal apothecia and may or may not act vegetatively.

Sexual morph: *Photobiont* green, trebouxoid. Thallus crustose to subfruticose growth, *Soridia*, *Isidia* frequently present. *Ascomata* ontogeny hemiangiocarpous, apothecia. *Excipulum* zeorine, cupulate. *Hymenium* amyloid, hemiamyloid or nonamyloid. *Paraphysoids* richly branched, forming an epithecium. *True paraphyses* lacking. *Asci* 1- to 8-spored, broadly cylindrical, thick-walled, more or less amyloid. *Ascospores* relatively large, hyaline, aseptate to transversely septate. Asexual morph: Conidiomata *Pycnidia. Conidia* straight, ± acicular or bacilliform, Isidia and soredia sometimes present (Fig. 148).

Families included in *Pertusariales*

Agyriaceae Corda (= *Miltideaceae* Hafellner)
Coccotremataceae Henssen ex J.C. David & D. Hawksw.
Icmadophilaceae Triebel
Megasporaceae Lumbsch
Microcaliciaceae Tibell
Ochrolechiaceae R.C. Harris ex Lumbsch & I. Schmitt
Pertusariaceae Körb. ex Körb.
Varicellariaceae B.P. Hodk. R.C. Harris & Lendemer ex Lumbsch & Leavitt
Variolariaceae Fée ex Zenker

Evolution

Lumbsch et al. (2006) studied the evolution of different characters such as apothecial type, ascus type, number of ascospore walls and chemical characters in the order and found that ascus-type and disciform apothecial type are plesiomorphic in *Pertusariaceae* and *Pertusariales,* respectively. The number of ascospore walls was found as homoplasious and the presence of chlorinated xanthones is restricted to *Pertusaria sensu stricto* (subgenera *Pertusaria* and *Pionospora*). However, their taxon sampling was done using 18 taxa with LSU sequence data.

Justification of order and problems

The morphology of *Pertusaria* exhibits considerable diversity, coupled with complex chemistry, and is found to be polyphyletic (Lumbsch et al. 2006). Within the *Pertusariaceae*, there is notable diversity in the types of ascomata, ranging from disciform, equivocal, poriform, to pseudodisciform.

Some species even display gyalectoid ascomata, leading to occasional confusion with species of *Gyalecta* in the field. However, they can be distinguished by their simple ascospores and different ascus types (Lumbsch et al. 2006). Despite these morphological variations, phylogenetic analyses have supported the inclusion of several groups within *Pertusariales*, including *Coccotremataceae* (Lumbsch et al. 2002, Gueidan et al. 2015). Nevertheless, the taxonomy of several taxa within the order remains unsettled.

Significance

Ecological and economic roles

Members of the order *Pertusariales* are found in all regions, from the tropics to the arctic and occur on a wide range of hosts and substrates (Gueidan et al. 2015).

Chemical diversity

Pertusariaceae shows a great diversity of secondary compounds (Ott & Lumbsch 2001, Schmitt & Lumbsch 2004), including aliphatic acids, depsides, depsidones, depsones, and xanthones and the chemical compounds are also used in the identification of taxa, even at the supraspecific level, at the beginning of lichenological studies. These chemical components are important in the identification of taxa that are known in the sterile material (Schmitt & Lumbsch 2004).

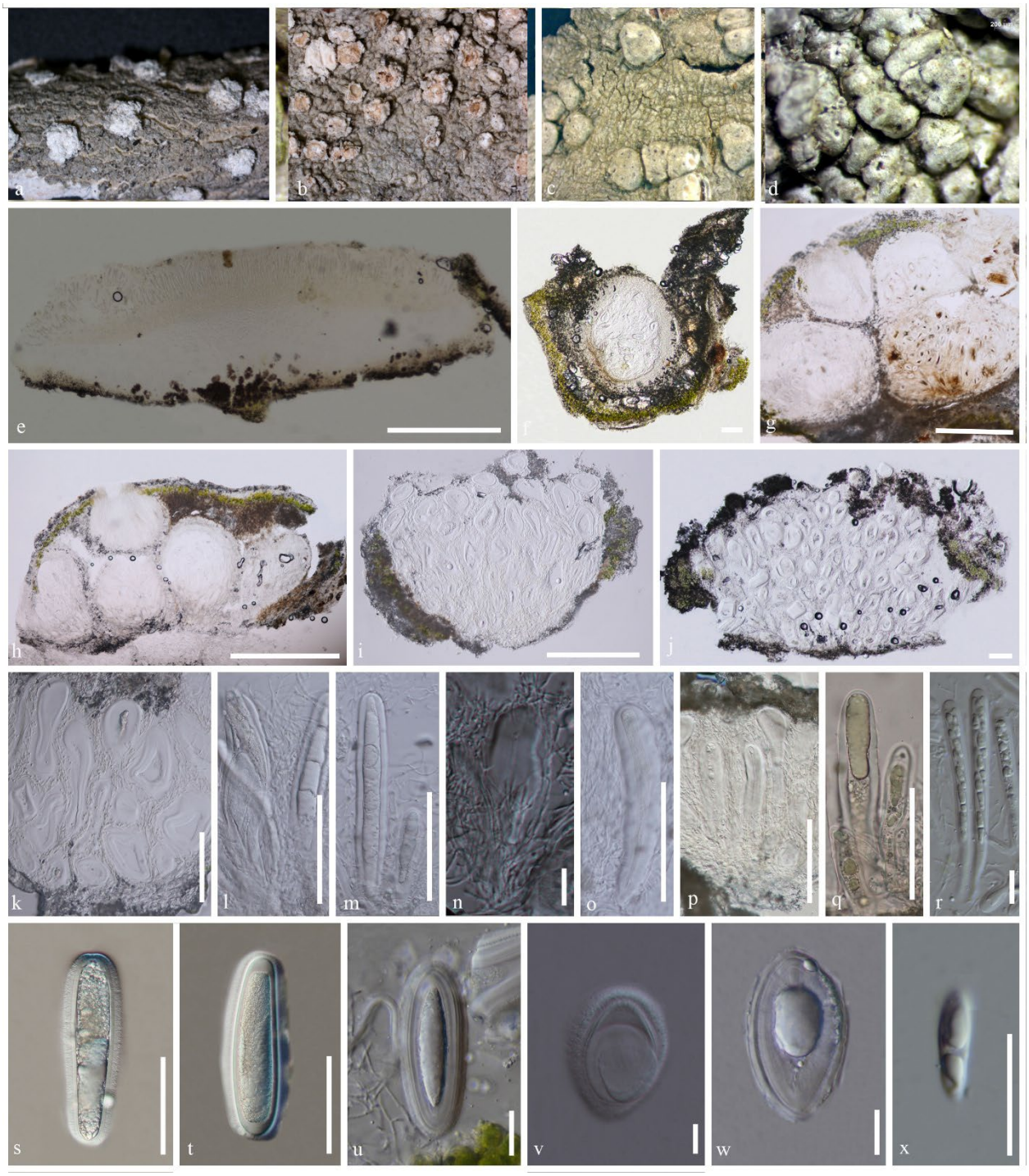


Figure 148 – Morphology of *Pertusariales*. a–d Thallus morphology (*Pertusariales* sp.). e–j Vertical section through ascomata of (f–j *Pertusariaceae* species, e *Icmadophilaceae* sp.). k–r Asci and Paraphyses (k–q *Pertusariaceae* sp., r *Icmadophilaceae* sp.). s–x Ascospores (s–w *Pertusariaceae* species, x *Icmadophilaceae* sp.). Scale bars: h, e = 500 µm, g = 300 µm, i = 200 µm, f, j–m, p, q, o =100 µm, n, r, u–x = 20 µm.

Rhizocarpales **Miądl. et al., Mycologia 98(6): 1097 (2007) [2006]**

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Lecanoromycetidae*

Introduction

Rhizocarpales comprised *Rhizocarpaceae* (*Catolechia*, *Epilichen*, *Poeltinula* and *Rhizocarpon*) and *Sporastatiaceae* (*Sporastatia* and *Toensbergia*) in *Lecanoromycetidae* (Miadlikowska et al. 2006, 2014, Lücking et al. 2017). *Rhizocarpon* is one of the earliest described genera and is one of the most speciose genera (Möller 2021). Thomson (1967) classified *Rhizocarpon* based on the presence of yellow substance rhizocarpic acid in subgenus *Rhizocarpon* and taxa lacking this substance in subgenus *Phaeothallus*. However, secondary substances in the thallus, and coloration, septation and size of the ascospores are considered as the most distinguishable characters to delimit the species.

History

Rhizocarpales was introduced by Miadlikowska et al. (2006) to accommodate *Rhizocarpaceae* and *Sporastatia*. Reeb et al. (2004) initially found that *Sporastatia* formed a close phylogenetic association with *Rhizocarpon*. Bendiksby & Timdal (2013) established *Sporastatiaceae* to accommodate the generic type *Sporastatia* and the newly established monotypic genus *Toensbergia*. *Sporastatia* was placed in *Catillariaceae* based on having Catillaria-type ascus, but it differs in its polyspory (Lumbsch & Huhndorf 2010) while *Toensbergia leucococca* was placed in *Hypocenomyce* and later in *Pycnora* and finally transferred to *Toensbergia* based on morphological, ecological and phylogenetic evidence. The ordinal placement was unknown when they established the family *Sporastatiaceae,* which recovered in the basal clade of *Lecanoromycetidae* in the multigene phylogenetic analysis (Bendiksby & Timdal 2013).

The close phylogenetic association between *Rhizocarpaceae* and *Sporastatiaceae* was also found in the study of Miadlikowska et al. (2014), which recovered in the basal clade in *Lecanoromycetidae*. However, the order had low statistical support. Lücking et al. (2017) combined *Rhizocarpaceae* and *Sporastatiaceae* under *Rhizocarpales*. Consequently, *Sporastatiaceae* formed a distinct clade and sister to *Rhizocarpales* in the temporal approach of Kraichak et al. (2017). Thus, a new order *Sporastatiales* was established to accommodate *Sporastatiaceae*. Lücking (2019) rejected the classification proposed by Kraichak et al. (2017) as *Rhizocarpaceae-Sporastatiaceae* split (208 MYA) is only slightly outside the ordinal band (176–194 MYA) proposed by Kraichak et al. (2017) and retained *Rhizocarpaceae* and *Sporastatiaceae* under *Rhizocarpales*. Wijayawardene et al. (2022a) accepted *Rhizocarpaceae* and *Sporastatiaceae* in each order *Rhizocarpales* and *Sporastatiales,* respectively.

General description

The taxa are strictly crustose and distinctly areolate. However, *Rhizocarpaceae* often form large, hyaline to brown, transversely septate to distinctly muriform ascospores whereas *Sporastatia* develops multiple, hyaline ascospores (Bendiksby & Timdal 2013, Möller 2021). Spore pigmentation, spore septation, amyloid reaction of the thalline medulla, presence of substances in the stictic acid complex and presence of rhizocarpic acid are considered as important characters to delimit the genera of *Rhizocarpaceae* (Ihlen & Ekman 2002). Chlorococcoid photobiont mostly found in the order. However, in several species, the photobiont was reported as an unidentified unicellular alga while *R. hensseniae* show cephalodia which shows the tri-membered association of photobiont (Möller 2021). Some *Rhizocarpon* species are mainly sterile and spread with isidia or soredia.

Sexual morph: Thallus crustose, black prothallus often present; photobiont chlorococcoid. *Ascomata* apothecial, immersed to sessile, lecideine or emarginate. *Hamathecium* unbranched (*Sporastatiaceae*) or branched and anastomosing (*Rhizocarpaceae*). *Paraphyses* amyloid. *Asci* semifissitunicate, clavate, with amyloid tholus lacking other structures (*Sporastatiaceae*) or weakly amyloid tholus with stronger amyloid cap (*Rhizocarpaceae*). *Ascospores* (1–)8 (*Rhizocarpaceae*) to

polyspory (ca. 100; *Sporastatiaceae*) per ascus, aseptate (*Sporastatiaceae*) or transversally septate to muriform (*Rhizocarpaceae*), ellipsoid, hyaline to dark brown, non-amyloid. Asexual morph: *Conidiomata* pycnidia. *Conidia* aseptate, bacillar to acicular or filiform, hyaline (Fig. 149).

Families included in *Rhizocarpales*

Rhizocarpaceae M. Choisy & Hafellner

Justification of order and problems

Rhizocarpon is among the cosmopolitan and speciose genera in this order. It comprised 225 accepted species. However, there are no comprehensive molecular studies available for genus or family-level relationships. Many species lack molecular data and the genus is also recovered as paraphyletic (Miadlikowska et al. 2014). Several species, such as *Rhizocarpon geminatum*, *R. eupetraeum*, *R. hochstetteri* and *R. umbilicatum* are species complexes. Many of the species need further studies to resolve their taxonomy (Möller 2021).

Significance

Ecological and economic roles

The lichenized taxa are mainly reported on rocks, exceptionally *Catolechia wahlenbergii* grows on soil and moss in shaded crevices in north-facing rock walls. They are distributed in the boreal and arctic-alpine, temperate, subtropical, and tropical regions and some genera are cosmopolitan. The lichenicolous members are reported in the genera *Epilichen* and *Rhizocarpon* on saxicolous lichens, rarely epiphytic on bark (Möller 2021). Some *Rhizocarpon* species, such as *R. intermediellum*, *R. norvegicum* and *R. parvum* may develop inside the areolae of a crustose host lichen and over time, they kill the host lichen, take over algae and become bright yellow and autonomous (Holtan-Hartwig & Timdal 1987). The type species *Rhizocarpon geographicum* was described by Linnaeus (1753) as *Lichen geographicus,* which is an abundant and globally distributed species and is used for dating rocks, moraines, piles, debris rafting, glacial debris, landslides and river terraces in the method called lichenometry (Bradwell 2009). *Rhizocarpon geographicum* causes biogeophysical and biogeochemical weathering serpentinized ultramafic rocks in an alpine environment (Favero-Longo et al. 2005).

Chemical diversity

Rhizocarpic acid is common in yellow species of *Rhizocarpon*. However, β-orcinol depsidone (norstictic acid, psoromic acid, stictic acid), orcinol para-depside (gyrophoric acid), β-orcinol para-depside (barbatic acid) and pulvinic acid derivative (rhizocarpic acid) were detected from lichen thalli of *Rhizocarpon* in Poland (Matwiejuk 2010). Depsides, depsidones, pulvinic acid derivatives are also reported in the members (Stocker-Worgotter & Elix 2009).

***Sarrameanales* B.P. Hodk. & Lendemer, Phytologia 93(3): 410 (2011)**

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Ostropomycetidae*

Introduction

Sarrameanales was established by Hodkinson & Lendemer (2011) for the single family *Sarrameanaceae*. The order comprised two genera, *Loxospora* and the generic type *Sarrameana*. Miadlikowska et al. (2006) used the name "*Loxosporales*?" for the clade which represented *Loxospora* species in the phylogenetic analysis but this name was not validly accepted in the later publication.

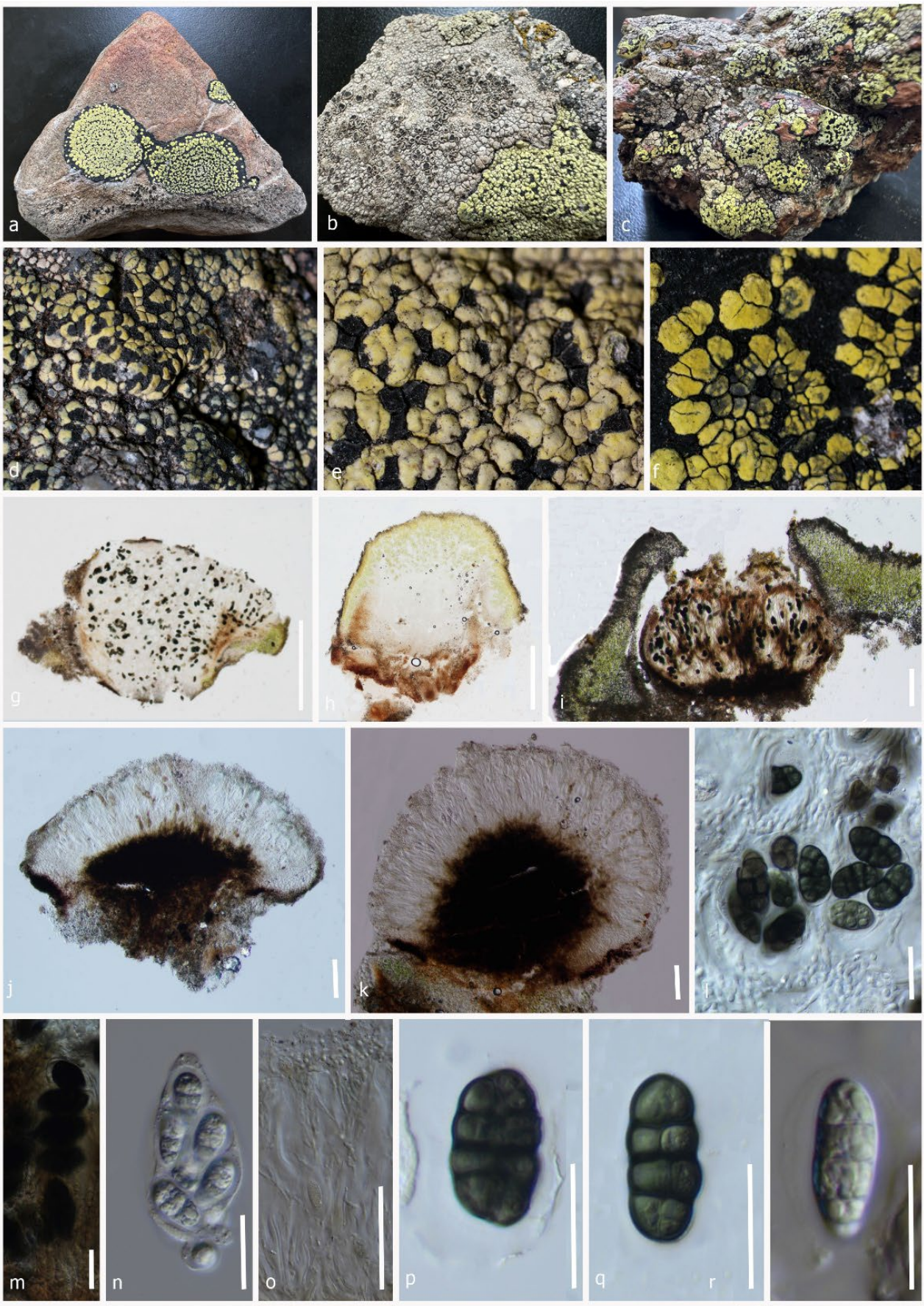


Figure 149 – Sexual morph of *Rhizocarpales.* a–f Thallus of *Rhizocarpales*. g–k Vertical section through ascomata. l–n Asci. o Paraphyses. p–r Ascospores. Scale bars: g, h = 500 µm, i–k =100 µm, l–r = 20 µm.

History

The type genus *Sarrameana* was established for the type *S. paradoxa* and was characterized by simple, cylindrical, spirally or irregularly curved, conspicuously thin-walled spores, each with attenuated ends which are extended into terminal, hair-like appendages. The genus showed a close association with *Lecidea* in habit but differs in the ontogeny of the apothecia (Vězda & James 1973). Later, *Sarrameana tasmanica* was added to this genus (Vězda & Kantvilas 1988). This lichenized genus presently comprises five species, including *Sarrameana albidoplumbea*, *S. cyamidia*, *S. paradoxa*, *S. septata* and *S. tasmanica*. The taxa are morphologically characterized by distinctive ascus and excipulum, mostly straight, simple paraphyses with thin-walled, spiralled, simple or spuriously septate ascospores (Kantvilas & Vězda 1996).

The second genus, *Loxospora* comprised 14 species (Index Fungorum 2023) with *Loxospora elatina* as the type. *Loxospora* was previously included in *Haematommataceae* in having pigmented apothecial discs and transversally septate ascospores. Staiger & Kalb (1995) established a new family *Loxosporaceae,* due to the differences in anatomical characteristics from *Haematomma*. Later, *Loxosporaceae* was synonymized under *Sarrameanaceae* (Kantvilas 2000). In the phylogenetic analysis conducted by Miadlikowska et al. (2006), the genus formed the most basal divergence within *Ostropomycetidae*. The taxa of *Loxospora* are characterized by hemiangiocarpic apothecial development. Young apothecia occur within the thallus in warts and slowly become emergent. Several species show asexual morphs, such as *Loxospora assateaguensis* and *L. confusa* (Lendemer 2013). Ptach-Styn et al. (2024) recently established a new genus *Chicitaea,* for several species that were previously placed in *Loxospora* based on anatomical and chemical characters.

General description

The members of the order are morphologically characterized by crustose thallus, unicellular green photobiont, eight spored asci, well-developed, dome-like, uniformly amyloid tholus lacking a masse axiale or any other discernible internal differentiation spiralled, simple or indistinctly septate, hyaline, non-halonate ascospores and simple or spiralled branched paraphyses (Kantvilas & Vězda 1996, Kantvilas 2000) (Fig. 150).

Sexual morph: *Thallus* crustose, corticolous, pale grey-green to olive-grey, thin or thick, surface smooth to verrucose, with or without a delimiting black prothallus. *Apothecia* lecanorine or lecanorine, sessile, concave. *Thalline margin* present, scabrid when young, later entire, dentate, persistent, often flexuose. *Disc* dark reddish-brown to black, epruinose. *Hymenium* colorless, inspersed with infrequent oil droplets. *Paraphyses* simple, unbranched, straight. *Hypothecium* colorless or pale yellow-brown. *Asci* claviform to obovate, I–, KI+ slightly blue-green, with or without an amyloid apical dome. *Ascospores* 6–8 per ascus, broadly ellipsoid to fusiform, straight, slightly bent, spiralled, thin-walled, simple or septate. Asexual morph: *Conidiomata* Pycnidia. *Conidia* simple, rod-like or bacilliform. Sorediate, isidate or without vegetative propagules.

Families included in *Sarrameanales*

Sarrameanaceae Hafellner

Justification of order and problems

The order presently accommodates three genera, including *Chicitaea*, *Loxospora* and *Sarrameana,* with a single family *Sarrameanaceae.* Kraichak et al. (2017) stated *Sarrameanales* as a separate order, which was also accepted in the latest outline (Hyde et al. 2024b). However, Lücking et al. (2017) accepted both *Sarrameanaceae* and *Schaereriaceae* under *Sarrameanales,* which was also stated in the later study by Lücking (2019). A comprehensive discussion regarding retaining both *Sarrameanaceae* and *Schaereriaceae* in separate orders is provided in the below entry.

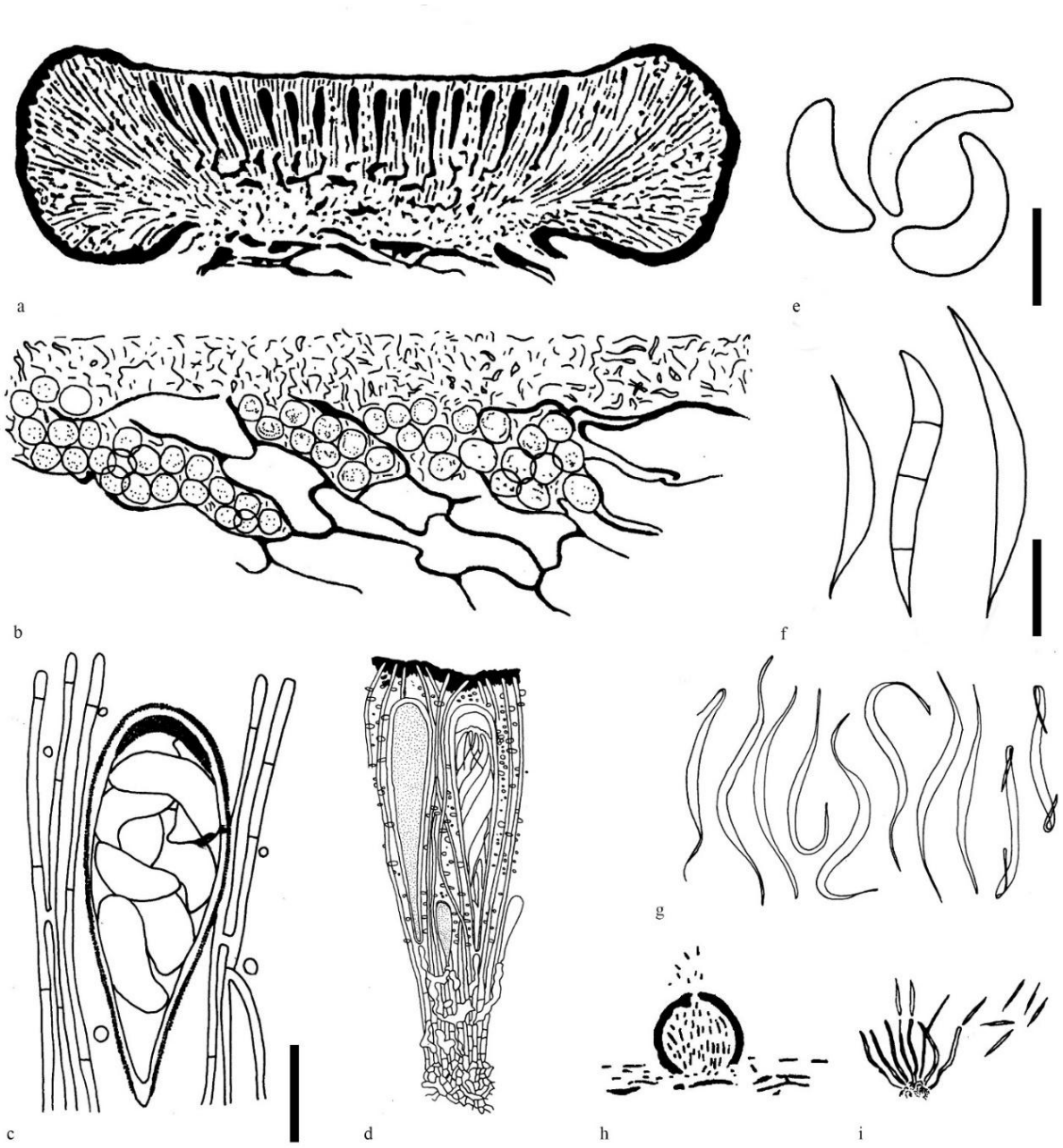


Figure 150 – Morphology of *Sarrameanales*. a Vertical section through the apothecia of *Sarrameana paradoxa*. b Thallus of *Sarrameana paradoxa*. c Ascus and paraphyses of *Sarrameana cyamidea* with amyloid parts stippled. d Ascus of *Sarrameana paradoxa*. e–g Ascospores (e *S. fasmanica*, f *S. albidoplumbea*, g *S. paradoxa*). h Pycnidia of *S. paradoxa*, i Sterignates and pycnospores of *S. paradoxa* (redrawn from Vězda & James 1973, Kantvilas & Vězda 1996). Scale bars: 15 μm.

Significance

Ecological and economic roles

Sarrameana species are mainly distributed in the cool temperate regions of the Southern Hemisphere (Kantvilas & Vězda 1996), whereas *Loxospora* species are primarily reported in cool temperate regions of the Northern Hemisphere (Kantvilas 2000).

Chemical diversity

Sterile lichens are difficult to identify due to a lack of ascomata. Thus, molecular analyses are important for their identification. A sterile lichen *L. cristinae* shared similar morphology in thallus color and the soralia usually become confluent but differ in the production of 2'-O-methylperlatolic

acid, while the latter produce variolaric and lichesterinic acids (sometimes also protolichesterinic acid) (Kukwa 2011). *Loxospora cristinae* resembles *Lecanora farinaria* and *L. substerilis* in sterile and sorediate thallus but these two species differ in the production of roccellic acid (sometimes accompanied by additional fatty acids) and atranorin (Tønsberg 1992, Kukwa & Kubiak 2007, Malíček et al. 2017).

***Schaereriales* Lumbsch & Leavitt, Index Fungorum 375: 1 (2018)**

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Ostropomycetidae*

Introduction

Schaereriales is an order consisting of lichenized species. It has a global distribution across all continents (Øvstedal & Lewis Smith 2009, GBIF.org 2023). Currently, it encompasses 11 to 12 accepted taxa at the species level, all assigned to a single genus known as *Schaereria* (Index Fungorum 2023, MycoBank 2023). Only a limited number of mycobionts have undergone thorough investigations concerning their associations with photobionts. For *Schaereria fuscocinerea*, it could be demonstrated that it is associated with *Trebouxia* sp. (*Trebouxiophyceae*). *Schaereria* species are predominantly found on siliceous rock surfaces. Two species (*S. corticola* and *S. dolodes*) are found on bark and one on soil or lichens (*S. parasemella*) (Rambold et al. 2001 onwards, Lumbsch 1997). However, it is worth noting that *Schaereria corticola* most likely is not a member of this order (further details provided below).

The species belonging to *Schaereriales* typically exhibit an episubstratal growth habit, meaning that they have a crustose to squamulose, rimose to areolate thallus. Their apothecia, which are hemi-angiocarpous, are either immersed or sessile and possess a cupulate excipulum. The asci in these species are subcylindrical to cylindrical and uniformly thin-walled, lacking any apical thickening or tholus. They produce one-celled, hyaline ascospores. The conidia in these species vary in shape, ranging from bacilliform to filamentous. Chemically, these species are characterized by the presence of orcinol para-didepsides and para-tridepsides (Rambold et al. 2001).

Currently, *Schaereriales* consist of a single family *Schaereriaceae* (Kraichak et al. 2018b). The family *Schaereriaceae* is monogeneric, solely including the type genus *Schaereria* (Körber 1855), based on *S. cinereorufa* as the type genus. The genus, accepted by Fries (1860), was resurrected by Poelt & Vězda (1977). The family *Schaereriaceae* was initially recognised by Choisy (1949), with its valid description later established by Hafellner (1984). For some time, there was uncertainty about the affiliation of the family, until Lumbsch in Hawksworth (1994) moved it into the relationship proximity of the *Agyriaceae*. Presently, *Schaereriaceae* remains a monotypic family (Index Fungorum 2025).

History

Schaereriales was established in the context of a revised classification of orders and families within the *Lecanoromycetes*, specifically *Lecanoromycetidae* and *Ostropomycetidae* subclasses. This classification was carried out by Kraichak et al. (2018b) using sequence data from five loci obtained from the NCBI Nucleotide Database. In their study, species of the genus *Loxospora* were selected as representatives of *Sarrameanaceae*. They formed a well-supported sister clade to *Schaereriales*. The family *Schaereriaceae* itself was found to be paraphyletic, suggesting that the corticolous representative of *Schaereria* (*S. corticola*) belongs to the *Sarrameanaceae* clade. Thus, the monotypic *Schaereriales*, within the *Ostropomycetidae*, emerged as the sister clade to *Sarrameanales*. Furthermore, both *Sarrameanales* and *Schaereriaceae* formed a sister clade to another group consisting of *Baeomycetales* and *Pertusariales*. The species of *Schaereriales* have not yet been presented in any comprehensive monograph. The characterisation of the different species is dispersed across a number of individual publications.

The terricolous species *Schaereria argentina* (Gyelnik 1934), *S. icterica* f. *Argentina* and *S. gresinonis* were previously described as or combined to *Schaereria* by Gyelnik (1937). They were treated by von Boom & Giralt (1996) as a species of *Psora* (*P. gresinonis*). Hertel & Schneider (Schneider 1979) realised that the taxon *Lecidea endocyanea*, originally described by Stirton (1877-1878), belongs to *Schaereria*. Clauzade & Roux (1985) assigned *Lecidea fuscocinerea* to the same genus despite the distinctive ascospore shape (ellipsoid), differing to that of the type species (globose). In 1986, a notable species named *S. fabispora* was described by Hertel & Zürn (1986). In 1989, *S. fuscocinerea* (treated as a synonym of *S. tenebrosa* and *S. endocyanea*) was documented from the Australian continent. *Schaereria xerophila xerophila* was described as a new species by H. Mayrhofer (Rambold 1989). Further details may be obtained from Lunke et al. (1996). In the subsequent years, several species were either described or reclassified, including *S. corticola* (Tønsberg 1992), *S. parasemella* from the Arctic (Lumbsch 1997), *S. bullata* from Tasmania (Kantvilas 1999), *S. porpidioides* from the Falkland Islands (Fryday & Common 2001), and *S. serenior* from Fennoscandia (Santesson et al. 2004). The species *Lecidea dolodes* (western North America) was combined to *Schaereria* in 2005 (Schmull & Spribille 2005). Finally, *S. albomarginata* and *S. brunnea* were described as new taxa from the Antarctic and from British Columbia respectively, based on morphological traits (Øvstedal & Lewis Smith 2009, Spribille et al. 2009). Phenotypic characters of the species can be retrieved from the LIAS light database (Rambold et al. 2001).

General description

Monokaryotic stage: All species of *Schaereriales* form a lichenised, mostly well-developed, crustose to squamulose thallus, being zonate with a cortical layer, sometimes covered by an epinecral layer, an algal layer with trebouxioid photobionts and a medullar layer. Lichenised dispersal structures (soredia) may occur (e.g., *S. corticola*, *S. fuscocinerea*). Hyaline conidia, probably functioning as spermatia (male gametes), are bacilliform to filiform and are terminally produced on Vobis type II conidiophores, being formed in pycnidia that are more or less immersed into the thallus. Correspondingly, trichogynes (representing extensions of female gamocytes, i.e. ascogones) raising up to the upper surface of the thallus, are formed from the ascomatal primordia. The thallus is mostly episubstratal and crustose to squamulose. The ascomata are apothecia that are sessile on the thallus or immersed into the areoles. They have a hemi-angiocarpous ontogeny (for further details see Lunke et al. 1996). The excipulum and hypothecium are more or less strongly pigmented, the hamathecium consists of simple true paraphyses being rather loosely coherent. The epihymenial zone is usually pigmented with green, blue-green, but also brownish and rarely violet colors and tones.

Dikaryotic stage: The ascogenous hyphae develop at the lower part of the primordium. Derived asci (i.e. the meiosporocysts) are cylindrical to subcylindrical. The ascus wall is of uniform thickness, meaning that the apical part of the internally inamyloid cell wall is not thickened, meaning that no so-called ‘tholus’ is formed. The aseptate, hyaline ascospores (i.e. the meiospores) are broadly ellipsoid, subglobose or globose. One species (*S. fabispora*) has been described by its bean-shaped ascospores. Information on the properties of the content of the living spores is not available. The ascospore walls are simple without a discernible perispore, except in *S. corticola* and *S. parasemella* (syn. *Hafellnera parasemella*), both of which should probably be assigned to the *Sarrameanales*, possibly under the name *Hafellnera.*

For identification based on morphology and ecology, traits considered as having diagnostic value are mainly the type of substrate, the development of the thallus, presence and composition of secondary metabolites, epihymenial pigments, ascospore shape and size (Fig. 151).

.**Families included in *Schaereriales***

Schaereriaceae Chevall.

Evolution

According to Kraichak et al. (2018b), the *Schaereriales* form a well-supported clade along with *Sarrameanales* within the *Ostropomycetidae*. Therefore, *Schaereriales* represent a monophyletic group, although the assignment of at least two species to this order is uncertain.

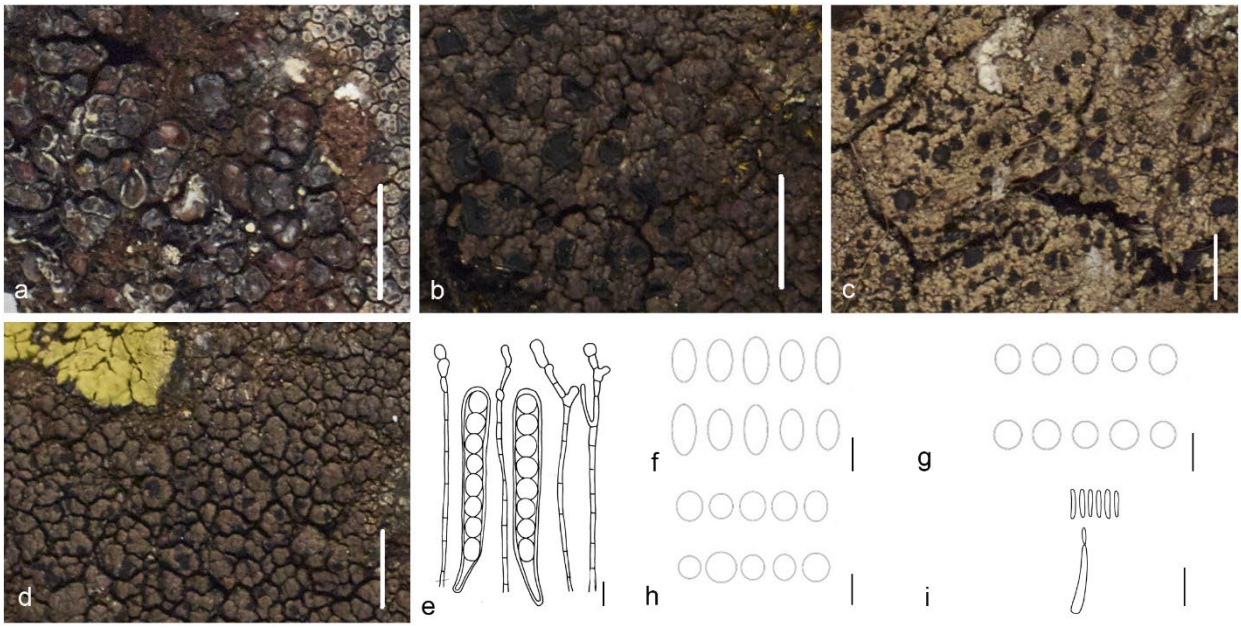


Figure 151 – Sexual and Asexual morphology of *Schaereriales*. a–d Morphology of thallus (a *Schaereria cinereorufa*, b *S. cinereorufa*, c *S. dolodes*, d *S. fuscocinerea*). e Asci, ascospores and paraphyses (*Schaereria bullata*). f–g Ascospores (f *Schaereria fuscocinerea*, g *S. dolodes*, h *S. cinereorufa*). i Conidiophore and conidia (*S. dolodes*) (redrawn from Kantvilas 1999, Schmull & Spribille 2005). Scale bars: a–e, i = 10 µm, f–h = 5 µm.

Justification of order and problems

Because *Schaereriales* and *Sarrameanales* have been recognized as having an ancient evolutionary history, the concept of 'temporal banding' (Kraichak et al. 2017) suggests that they should each be classified as separate orders. This assumption seems reasonable if one considers an essential difference between them, namely the apical wall structure of the ascus. The absence of a tholus in the *Schaereriales* compared to the *Sarrameanales*, is probably only a minor anatomical difference. The amyloidity of the ascus tip present in the *Sarrameanales* indicates that in this order a rostral wall structure elongates during the opening of the ascus tip and the process of ascospore discharge. This is not observed in most species of the *Schaereriales* with a both unthickened and inamyloid wall at the ascus tip. Consequently, spore release in the *Schaereriales* likely occurs by tearing the ascus wall, presumably releasing the spores in a less targeted manner.

This conjecture is also supported by their subglobose to globose shape in some species, in contrast to the mostly ellipsoid to fusiform and partly twisted ascospore shape in the *Sarrameanales*. In addition, the loosely adhered simple paraphyses indicate low lateral physical pressure within the hymenium or hamathecium during spore maturation, which usually necessitates the development of a tholus as an abutment to prevent premature ascospores release. Among the other known genera and families within the *Ostropomycetidae*, the combination of unthickened, nonamyloid ascus tips and globose spores is not observed, but among lichenized taxa mainly occur within groups with mazaedial hymenium (Rambold et al. 2001). In view of these factors, it seems justified to classify the *Schaereriales* as a separate order. However, it should be noted that within the clade of *Caliciales*, *Caliciaceae* without tholus and *Physciaceae* with tholus co-occur, suggesting that in this case the lack of a tholus in *Caliciaceae* is due to differences in their microhabitats favouring differing mazaedial development (for moisture absorption). Such a correlation does not exist in the

Schaereriales and their neighbouring clade, which means that the differences in ascus wall structure are probably due to other reasons.

Significance

Ecological and economic roles and associations

There is no major economic role of taxa in this order. However, they do contribute towards ecosystem services (Zedda & Rambold 2015). Crustose lichen thalli may serve as habitat and food source for small invertebrates, prokaryotic and eukaryotic microbial organisms. In the arctic, boreal and (sub-)Antarctic zones the saxicolous species of *Schaereriales* occur from montane to nival altitudes. They colonize siliceous rock surfaces, where they frequently co-occur with species of the genera *Lecidea*, *Miriquidica*, *Melanelia*, *Rhizocarpon*, *Umbilicaria*, *Usnea* and others. One terricolous or lichenicolous species of the Arctic (*S. parasemella*) is frequently associated with *Biatora vernalis* (Nimis et al. 2018).

Chemical diversity

The diversity of secondary metabolites produced by *Schaereriales* is relatively low, primarily comprising orcinol depsides (para-didepsides: lecanoric acid and para-tridepsides: gyrophoric acid, hiascic acid and 5-O-methylhiascic) and the ß-orcinol para-didepside atranorin. These are found in various combinations, e.g., gyrophoric acid with hiascic, lecanoric and orsellinic acid (in *Schaereria fuscocinerea*), atranorin with gyrophoric acid (in *S. dolodes*) (Schmull & Spribille 2005) and gyrophoric acid with lecanoric, orsellinic, hiascic and 5-*O*-methylhiascic acid plus unidentified substances (in *S. corticola*) (Tønsberg 1992, Lunke et al. 1996). The latter species is likely to be phylogenetically assigned to *Sarrameanales* (see above). In the case of *Schaereria porpidioides*, the presence of unidentified fatty acids has been observed (Fryday & Common 2001). Several species such as *S. albomarginata*, *S. bullata*, *S. fabispora* and *S. xerophila* either do not produce any known substances or have not been thoroughly studied in terms of secondary metabolite production.

Sporastatiales **Lumbsch & Leavitt, Huang, Nelsen, Leavitt & Lumbsch, Index Fungorum 375: 1 (2018)**

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Lecanoromycetidae*

Introduction

Sporastatiales is a small lichenized order in *Ascomycota* which comprises only a dozen species and several varieties from the two genera, *Sporastatia* and *Toensbergia,* from the single family *Sporastatiaceae*. Species of the type genus *Sporastatia* are arctic-alpine lichens occurring mostly on exposed hard siliceous or weakly calcareous rocks. Two species, *S. testudinea* and *S. polyspora*, are widely distributed throughout the Northern Hemisphere and are scattered in the Southern Hemisphere on subantarctic islands and in southern South America (Grube & Poelt 1993, Thomson 1997, Gilbert & Coppins 2009). The remaining species, *S. asiatica*, *S. subasiatica*, *S. karakorina* and *S. crassulata* are alpine endemics of Asia (Golubkova 1973, 1982, Poelt & Obermayer 1990, Yakovchenko & Davydov 2018). *Sporastatia testudinea* species complex is highly variable and requires additional studies to delimit taxa (Grube & Poelt 1993). *Sporastatia* was recently classified in a separate family *Sporastatiaceae* (Bendiksby & Timdal 2013). Based on molecular phylogenetic data, Bendiksby & Timdal (2013) placed into the family two phenotypically and ecologically different genera: *Sporastatia* and newly introduced genus *Toensbergia* with a single sterile species *T. leucococca*. Spribille et al. (2020) described a new species *Toensbergia blastidiata* and combined *Pertusaria geminipara* into *Toensbergia*. In molecular phylogenies *Sporastatiaceae* is sister to *Rhizocarpaceae* (Miadlikowska et al. 2014) and was subsequently raised to order *Sporastatiales* sister to *Rhizocarpales* (Kraichak et al. 2018b).

History

Sporastatia testudinea and *S. polyspora*, are widely distributed in polar and mountain regions. Therefore, it is not surprising that they were described at the early history of lichenology by Acharius (1808a) as *Lecidea cechumena* var. *testudinea*. Schaerer (1833) described as *Lecidea morio* var. *cinerea* and Nylander (1855), as *Gyrothecium polysporum*. These taxa and other relative species and varieties treated in the genera *Acarospora*, *Biatorella*, *Gyrothecium*, *Lecidea*, *Myriosperma*, *Myriospora*, and *Sarcogyne* in the past. The genus *Sporastatia* was introduced by Massalongo (1854). Fries (1861) assigned *Sporastatia* to the *Lecideaceae*, subfamily *Buelliei* together with *Sarcogyne*. Later, Fries (1874) considered *Sporastatia* and *Sarcogyne* as subgenera of *Biatorella*. Elenkin (1911b) treated *Sporastatia* as a subgenus of *Sarcogyne*, because both have lecideine apothecia. Zahlbruckner (1906, 1928) followed Fries, but considered *Sporastatia* and *Sarcogyne* as sections of *Biatorella*, and classified *Biatorella* to *Acarosporaceae*. Magnusson (1936) treated *Sporastatia* at the generic level within *Acarosporaceae*. The similarities of asci in *Sporastatia* to *Catillaria* rather than *Acarospora* were noted by Hertel & Rambold (1988). Rambold & Triebel (1992) moved the genus to *Catillariaceae* because of its catillaria-type ascus. Molecular phylogenetic studies demonstrated the sister relationship between the genera *Sporastatia* and *Rhizocarpon* (Buschbom & Mueller 2004, Lutzoni et al. 2004, Reeb et al. 2004, Miadlikowska et al. 2006, 2014); however, none of them included the genus *Toensbergia*. The type species of *Toensbergia*, *T. leucococca* was described as *Hypocenomyce leucococca* and also known as *Pycnora leucococca*. Molecular phylogenetic research (Bendiksby & Timdal 2013) showed *Hypocenomyce sensu* Timdal (1984) highly polyphyletic, and supported phylogenetic relation of *H. leucococca* with *Sporastatia*. Miadlikowska et al. (2014) proposed to transfer *Sporastatia* to the *Rhizocarpaceae* or following the data of Bendiksby & Timdal (2013), to place *Sporastatiaceae* (together with *Toensbergia*) to the *Rhizocarpales*. Subsequent molecular phylogenetic study included both sequences of *Sporastatia* and *Toensbergia* (Kraichak et al. 2018b) raised *Sporastatiaceae* to the order *Sporastatiales* (Kraichak et al. 2018a) related to *Rhizocarpales*. The phylogeny by Spribille et al. (2020) supported this placement and assigned other two species of *Toensbergia*, one is new for science – *T. blastidiata*, is similar to *T. leucococca* sterile; and another one – *T. geminipara*, is fertile and its ascomata traits are changing the circumscription of *Sporastatiaceae* significantly. The species was described as *Lecanora geminipara* (Fries 1871), and for a long time it was considered as *Ochrolechia geminipara*. Brodo (1984) emphasized considerable difference of these species from other representatives of *Ochrolechia* in thick-walled ascospores 2(3) per ascus, in the color of apothecial disc, as well as containing alectorialic acid, and moved it into *Pertusaria geminipara*. However, in molecular phylogenetic study by Spribille et al. (2020). *Pertusaria geminipara* clustered within *Toensbergia* outside of *Pertusaria*, a relationship that had not been suspected based on morphological data.

General description

Representatives of two families of *Sporastatiales* have varied appearance and anatomical traits, but share similar ascus type, i.e. with uniformly amyloid apical dome (catillaria-type and pertusaria-type). All species have chlorococcoid photobionts and lack cephalodia. *Sporastatiales* taxa form crustose to subsquamulose growth forms. Thalli of *Sporastatia* are areolate with areoles rounded or angular in center of thallus, but elongated and radiating at the margin; prothallus is well-developed, black and usually forming a rim around each areole, as well as around the whole thallus (Gilbert & Coppins 2009, Yakovchenko & Davydov 2018). Species of *Toensbergia* have rounded, convex, usually constricted below areoles or granules (subsquamiform) with apex bursting into soredia or blastidia; prothallus distinct or indistinct, thin, bluish-grey or dark grey, visible between areoles and along thallus margin (Cheewangkoon et al. 2009, Coppins 2009, Spribille et al. 2020). Chlorococoid green algae, *Myrmecia*, *Trebouxia* and probably others are commonly found as photobionts (Nash et al. 2004, Sanders & Masumoto 2021).

Two genera have contrast types of ascomata. Lecideine apothecia of *Sporastatia* (Fig. 152) are black, not pruinose with narrow, thin, brown outer edges, colorless within, or brown throughout the true exciple. Apothecia of *S. crassulata* can demonstrate pseudolecanorine appearance (Fig. 152)

with the prominent fertile squamules ascending margins surrounding the disc. Asci of Catillaria-type contain 100–200 simple, globose to ellipsoid, colorless spores without a distinct perispore (Poelt & Obermayer 1990, Gilbert & Coppins 2009). *Toensbergia geminipara* is the only species within the genus which sometimes fertile and possess lecanorine apothecia (Fig. 152) with Pertusaria-type asci contain 2(3) large ellipsoid spores with 2-zoned walls, similar to those known in *Pertusaria* (Brodo 1984). Pycnidia of *Sporastatiales* are immersed and contain bacilliform, simple, colorless conidia.

Sporastatia and *Toensbergia* have different strategies of reproduction. All species of *Sporastatia* reproduce by ascospores, but in addition thalloconidia (Hasenhüttl & Poelt 1978) are recorded and characteristic for one species, *S. karakorina* (Poelt & Obermayer 1990). Thalloconidia are mostly characteristic for *Umbilicaria* (Hasenhüttl & Poelt 1978, Hestmark 1990, but are also found in various lichen families (Poelt & Obermayer 1990). Opposite, all species of *Toensbergia* reproduce mostly vegetative, by soredia or blastidia (Chambers et al. 2009, Coppins 2009, Spribille et al. 2020)

Sexual morph: *Thallus* crustose to squamulose, areolate, with radiate marginal areoles, of granulose. *Prothallus* usually distinct bluish-grey or black. *Photobiont*: chlorococcoid. *Ascomata* apothecial, lecideine immersed or lecanorine, epruinose to slightly pruinose, angular to roundish, flat to slightly convex; disc often rough or wrinkled, proper margin present or absent. *Hypothecium* hyaline to pale brown. *Excipulum* narrow, thin, brown, or brown externally and hyaline within. *Hymenium* hyaline, amyloid. *Paraphyses*: simple to branched, free, septate, sometimes swollen at the tips. *Epihymenium* brown, greenish-brown or brownish with purple tint; with Atra-red Cinereorufa-green or unknown pigment. *Asci* clavate, unitunicate, thick walled with amyloid tholus without visible internal structures (Catillaria-type, Pertusaria-type), polysporous with 100–200 spores or disporous with 2(3) spores. *Ascospores* ellipsoid to globose, simple, hyaline, with thin wall, or thick 2-zoned wall. Asexual morph: *Pycnidia*, *blastidia*, *soredia*, *thalloconidia* (Fig. 152).

Families included in *Sporastatiales*

Sporastatiaceae Bendiksby & Timdal

Evolution

According to Kraichak et al. (2018b) *Sporastatiales* (i.e. *Toensbergia* and *Sporastatia*) is sister to the *Rhizocarpales* and together form a group sister to the rest of the subclass *Lecanoromycetidae*. *Sporastatiales+Rhizocarpales* lineage has a relatively old phylogenetic age and branched off in molecular clock analysis (Prieto & Wedin 2013) ca. 156-162 MYA at the beginning of the major diversification of *Lecanoromycetes*. The evolution within the order is obscure; the *Sporastatia* lineage includes saxicolous arctic-alpine lichens, whereas *Toensbergia* is combined terricolous arctic-alpine as well as corticolous forest species.

Justification of order and problems

The circumscription of *Toensbergia* and its sister relation to *Sporastatia* is strongly supported by molecular phylogeny and predominance of alectorialic acid (Bendiksby & Timdal 2013, Spribille et al. 2020), but makes *Sporastatiaceae* and *Sporastatiales* heterogeneous regarding ascomata and ascospores traits. *Sporastatia* and *Toensbergia* clades have different branch lengths and as was mentioned by Spribille et al. (2020) “the DNA sampling of *Sporastatiaceae* has not been extensive and we await more sequenced loci before further speculating on the phylogenetic relationships within this group”. Nevertheless, following the actual data (Bendiksby & Timdal 2013, Kraichak et al. 2018b, Spribille et al. 2020) we accept *Toensbergia* as a genus within *Sporastatiales*.

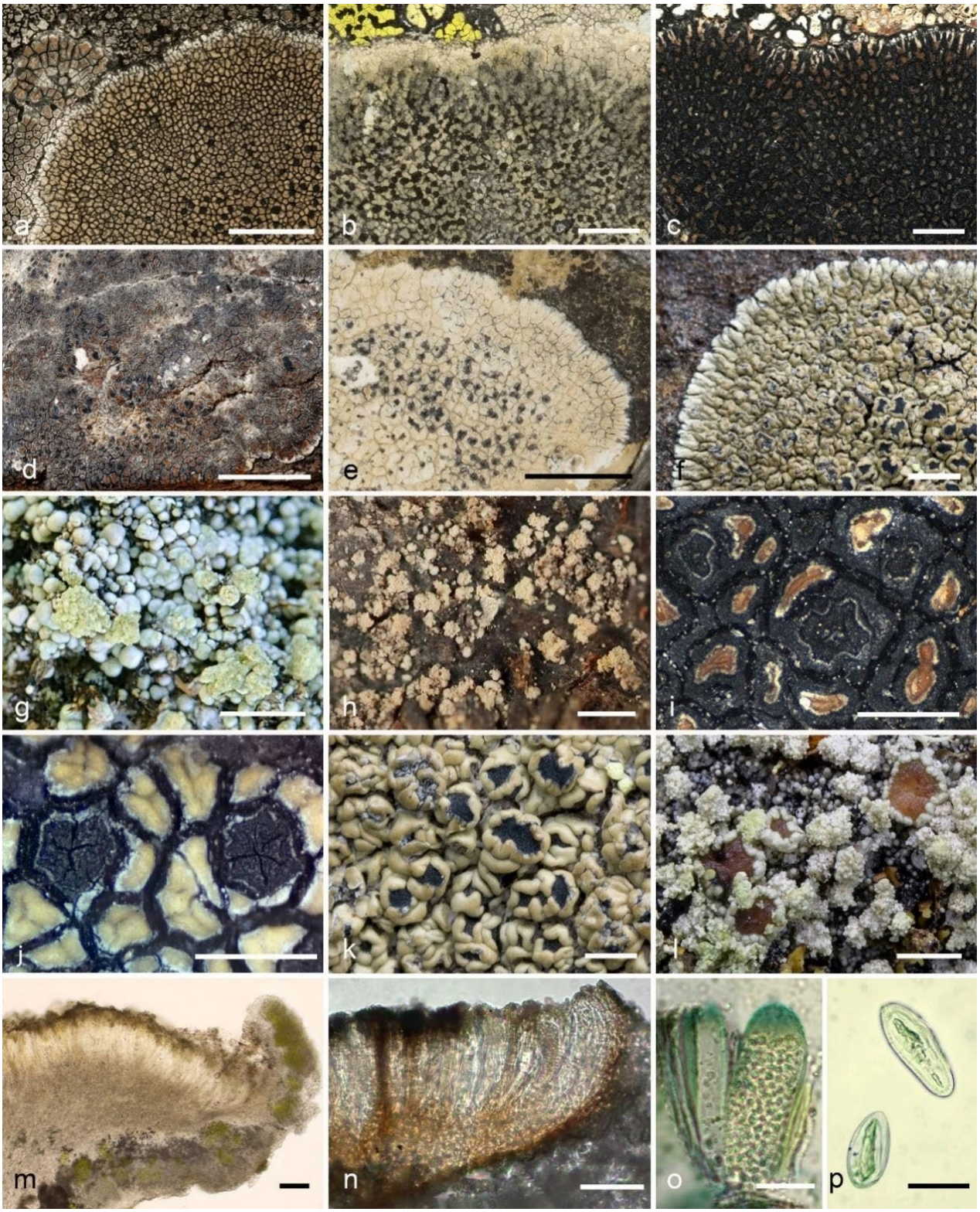


Figure 152 – Sexual morph of *Sporastatiales.* a *Sporastatia testudinea.* b *S. polyspora*. c S. *karakorina.* d *S. asiatica*. e *S. subasiatica*. f *S. crassulata.* g *Toensbergia geminipara.* h *T. leucococca.* i *Thalloconidia* on the prothallus of *S. karakorina.* j *Lecideine apothecia* of *S. testudinea.* k Pseudolecanorine apothecia of *S. crassulata.* l, m *Lecanorine apothecia* of *T. geminipara.* n Ascomata morphology of *Sporastatia.* o Multi-spored asci of *Sporastatia.* p Ascospores of *Toensbergia geminipara*. Scale bars: a, b, d, e, f, g = 5 mm; c, l = 2 mm; h, k = 1 mm; i, j = 0.5 mm; m, n = 50 µm; o, p = 20 µm. Photo: a,b, d, e, f, h, k, Davydov, c, i, W. Obermayer g, l, m, p A. V. Melekhin n, o L. S. Yakovchenko.

Significance

Ecological and economic roles

Representatives of *Sporastatia* are long lived and play an important role in the pedogenetic processes (Favero-Longo et al. 2005). Several species are hosts for lichenicolous fungi or lichens, especially the species *Rhizocarpon pusillum*, *R. asiaticum*, and *Miriquidica invadens* (Poelt 1990, Rambold & Triebel 1992, Davydov et al. 2012, Hafellner et al. 2014). *Toensbergia leucococca* and *T. blastidiata* are locally common members of epiphyte communities on bark of trees, and *Toensbergia geminipara* is not abundant but widespread species in Arctic and mountain tundra's on mosses and plant debris (Brodo 1984, Chambers et al. 2009, Coppins 2009).

Chemical diversity

Species of *Sporastatiales* demonstrate quite uniform secondary chemistry. Species of *Sporastatia* sometimes produce orcinol depsides (gyrophoric and lecanoric, acids), and *Toensbergia* – benzyl esters: all species alectorialic acid and *T. geminipara* in addition barbatolic acid (Brodo 1984, Moberg 1986, Spribille et al. 2020).

Other relevant data and future recommendations

Sporastatia lives in places with a harsh climate and is characterized by slow growth. Growth rate for *Sporastatia testudinea* in the Swiss Alps is estimated to be 1 to 2 cm per 100 years (Haeberli et al. 1979). At the same time, the thalli have a clear edge contrasted by the prothallus and it is easy to measure. All this makes *Sporastatia* species suitable for lichenometry. *Sporastatia testudinea* has been used in lichenometric studies (Haeberli et al. 1979, Lewkowicz & Hartshorn 1998).

Teloschistales D. Hawksw. & O.E. Erikss., Systema Ascomycetum 5(1): 183 (1986)

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Lecanoromycetidae*

Introduction & History

Teloschistales is a lichenized group with cosmopolitan distribution and shows diverse morphological characters and lifestyles (Gaya et al. 2015). *Teloschistales* was established by Eriksson & Hawksworth (1986c). Kärnefelt (1990) accepted two families within *Teloschistales*, *Letrouitiaceae* with a single genus *Letrouitia*, and ten genera (*Apatoplaca*, *Caloplaca*, *Cephalophysis*, *Fulgensia*, *Ioplaca*, *Seirophora*, *Teloschistes*, *Xanthodactylon*, *Xanthoria* and *Xanthope*) were placed in *Teloschistaceae*. Miadlikowska et al. (2006) proposed two suborders *Teloschistineae* and *Physciineae* within *Teloschistales* and found a sister clade relationship between them. *Teloschistineae* comprised *Letrouitiaceae*, *Megalosporaceae*, and *Teloschistaceae* whereas *Physciineae*, comprised *Caliciaceae* and *Physciaceae* and this classification has been accepted in further studies (Hibbett et al. 2007, Lumbsch & Huhndorf 2007, Kirk et al. 2008a). Gaya et al. (2012) reinvestigated this group and restricted *Teloschistales* to *Teloschistiineae* and resurrected the order *Caciliales* for the *Physciineae*. In addition, *Brigantiaeaceae* was accepted under *Teloschistales* that was previously placed in *incertae sedis* in *Lecanoromycetidae* (Lumbsch & Huhndorf 2010). Further, they proposed a suborder *Letrouitineae* for *Brigantiaeaceae* and *Letrouitiaceae* which recovered as sister clades while *Teloschistaceae* and *Megalosporaceae* were restricted for *Teloschistineae*. Kraichak et al. (2018b) synonymized *Letrouitineae* under *Brigantiaeaceae* based on temporal band approach that was further accepted by Lücking (2019) and Wijayawardene et al. (2022a). However, this classification was overlooked in the study of Dombrowski et al. (2022) who reinvestigated *Letrouitineae* as a separate family. *Teloschistales* presently comprises three families namely, *Brigantiaeaceae*, *Megalosporaceae* and *Teloschistaceae* with one genus *Malcolmiella* and placed in *Teloschistales* genus *incertae sedis*. Among them, *Teloschistaceae* is the largest family and the total number of accepted species is underestimated.

General description

The members are characterized by crustose, foliose or fruticose thalli that appear as yellow to orange color (anthraquinone pigments), apothecial ascomata, unbranched paraphyses, unitunicate asci with an apical thickening, and mostly hyaline polarilocular ascospores (Kärnefelt 1989, Kirk et al. 2008a).

Sexual morph: *Thallus* crustose, foliose or fruticose, yellow to orange color. *Ascomata* apothecial. *Paraphyses* unbranched. *Asci* Brigantiaea-type, Letrouitia-type, Megalospora-type, Teloschistes-type, with an apical thickening. *Ascospores* aseptate, 1-transverse septate, muriform, cells, locules present. Asexual morph: conidiophore, conidia present (Fig. 153).

Families included in *Teloschistales*

Brigantiaeaceae Hafellner & Bellem. (= *Letrouitiaceae* Bellem. & Hafellner)
Megalosporaceae Vězda ex Hafellner & Bellem.
Teloschistaceae Zahlbr.

Teloschistales genera *Incertae sedis*
Malcolmiella Vězda

Evolution

Gaya et al. (2015) found that *Letrouitineae* likely diverged 162 MYA in a warm and arid environment and the members are mostly shade tolerant, crustose, epiphytic on bark, and had anthraquinones present in the thallus and apothecia. Habitat switches from shaded bark to exposed rocky substrates during the late Cretaceous period, allowing the members of *Teloschistaceae* to the production of both vegetative structure (thallus) and fruiting body (apothecia) of anthraquinones, secondary metabolites known to protect against UV light. Thus, anthraquinone evolution, appears interlinked with the evolutionary success of *Teloschistales* (Gaya et al. 2015). Llewellyn et al. (2023) studied the production of anthraquinones and UV protectant secondary metabolites in various fungi including *Teloschistales* using metagenomic sequencing and found that metabolite diversification occurs via re-shuffling existing enzyme genes with novel accessory genes rather than biosynthetic gene cluster gains/losses or de novo gene evolution.

Justification of order and problems

Growth form, type of cortical layer and presence of rhizines and spore type have been used to delimit the genera of *Teloschistaceae*. However, the limitations such as intermediate growth forms present in the genera *Caloplaca* from *Xanthoria*, present in all types of cortical layers within *Caloplaca* and the heterogeneous nature of *Fulgensia* render the generic delineation of the family (Hafellner & Poelt 1979, Arup et al. 2013). Many *Teloschistaceae* species are poorly studied or undescribed, including cryptic and semicryptic species. Thus, the estimation of total number is challenging (Vondrak et al. 2009, Arup et al. 2013). The phylogenetic relationship among *Teloschistales*, *Caliciales*, and *Lecanorales* was inconsistent with different gene markers. Thus, further protein-coding genes and data matrices with broad data are needed to resolve the relationships among these three orders (Gaya et al. 2012).

Letrouitiaceae is a less studied group among other families and it is important to study the evolution of anthraquinone pigment production for a clear understanding of the evolution of the family. Suborder *Letrouitineae* is mostly reported in the tropics whereas *Teloschistineae* is common in temperate areas. However, *Letrouitineae* is less diverse than *Teloschistineae* even though the tropics have higher biodiversity (Turner 2004, Dowle et al. 2013). However, *Letrouitia*, make up the most diverse group of lichens in the tropics (Lücking et al. 2009). Therefore, to understand biodiversity patterns, it is crucial to study the diversification differences of *Teloschistales* (Dombrowski 2022).

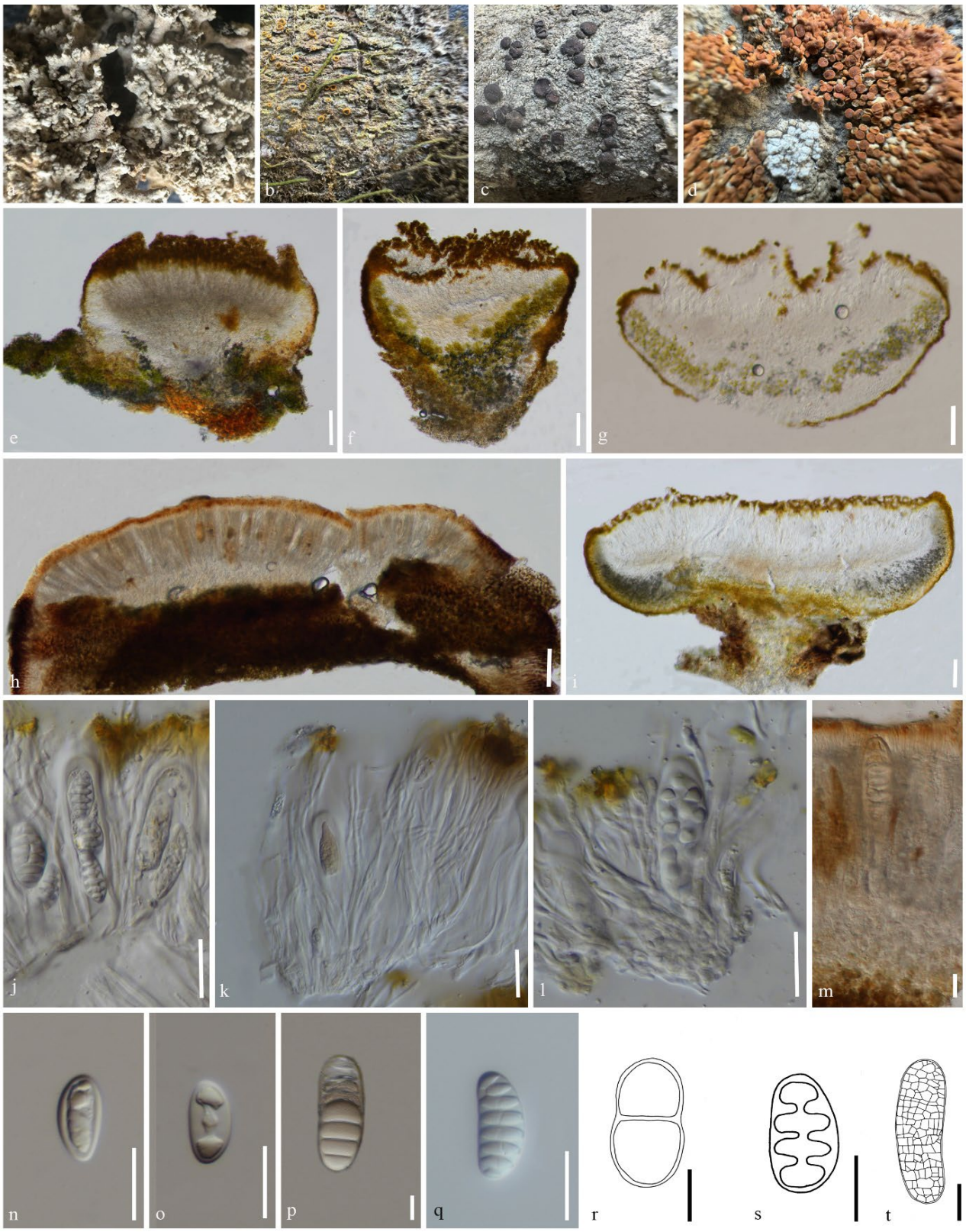


Figure 153 – Morphology of *Teloschistales.* a–d Thallus morpholgy (a *Teloschistes* sp., b *Lentoroutia* sp., c *Megalospora* sp., d *Fulgensia* sp.). e–i Section of apothecia (e *Caloplaca* sp., f *Fulgensia* sp., g *Xanthoria* sp., h *Megalospora* sp., i *Lentoroutia* sp.). J–m Asci and Paraphyses (j, k *Lentoroutia* sp., l *Fulgensia* sp., m *Megalospora* sp.). n–f Ascospores (n, o *Caloplaca* sp., p *Megalospora* sp., q *Lentoroutia* sp., r *Megalospora sulphurata*, s *Austroblastenia pauciseptata*, t *Megalospora occidentalis*) (Redrawn from Kantvilas & Lumbsch 2012). Scale bars: e–i = 100 µm, j–t = 20 µm.

Significance

Ecological and economic roles

Teloschistaceae are distributed worldwide and mainly occur on rocks and the growth form ranges from crustose to fruticose while *Brigantiaeaceae* and *Megalosporaceae* are mostly epiphytic and crustose and are primarily reported in the tropics (Gaya et al. 2012). The taxa are mainly reported as lichenized and often favor nutrient-rich substrates. *Caloplaca*, *Catenarina*, *Flavoplaca*, *Gyalolechia*, *Pachypeltis*, *Shackletonia*, *Sirenophila* and *Variospora* are reported as lichenicolous fungi and several members of the genera such as *Teloschistes* also harbor lichenicolous fungi (Diederich et al. 2018). *Caloplaca nivalis* was reported as a pathogen on *Andreaea* sp. and *Grimmia* sp. (Søchting et al. 2008, Lestari et al. 2023).

Chemical diversity

Anthraquinones are toxic metabolites that are produced in large quantities in crystals in the thallus cortex and reproductive structures of *Teloschistales* (Gaya et al. 2015). Søchting et al. (2014) found 7-chlorocatenarin produced in the newly established genus *Catenarina*.

Thelenellales Lumbsch & Leavitt, Index Fungorum 375: 1 (2018)

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Ostropomycetidae*

Introduction

Thelenellales was recently established by Kraichak et al. (2017) to accommodate a single family, *Thelenellaceae* based on the temporal band approach. The taxa form crustose thallus with trebouxioid photobiont, perithecial ascomata with fused, pale involucrellum, clavate, 2–8-spored, nonamyloid asci with thick-walled, transversely septate to muriform and hyaline ascospores (Kraichak et al. 2017). The order comprised three genera *Aspidothelium* and *Chromatochlamys* with *Thelenella* as the generic type.

History

The generic type *Thelenella* was described by Nylander (1855). The genus was later subsumed under *Microglaena* (Zahlbruckner 1907, 1926). Mayrhofer (1987) established a new family *Thelenellaceae* following the suggestion of Eriksson (1981). Mayrhofer & Poelt (1985) distinguished *Chromatochlamys* from *Thelenella* based on the presence of periphysoids in the ostiole and a recessed ocular chamber in the ascus apex. Subsequently, Mayrhofer (1987) suggested separating these genera based on the presence or absence of an ocular chamber without considering periphysoids character. Harris (1995) noted the differences in paraphysoids and questioned the presence of an ocular chamber in several *Thelenella* specimens also noted differences in the paraphysoids of these two genera. However, Harris (1995) did not unite these genera due to limited specimens available for *Chromatochlamys* and raised concerns regarding the use of paraphysoids characters for generic-level classification. Fryday & Coppins (2004) also expanded the generic concept of *Thelenella* to include *Chromatochlamys* within *Thelenella* based on morphological investigation.

Aspidothelium was described with *Aspidopyrenium* (Vainio 1890) and they differ in spore septation and paraphyses and the genus was placed in *Verrucariaceae.* Later, both genera were synonymized by Santesson (1952) and placed in *Strigulaceae*. Spegazzini (1919) synonymized *Patellonectria* under *Aspidothelium*. Malme (1928) synonymized *Porinopsis* under *Aspidothelium* and suggested the close morphological association to *Thelenella* and *Porina*. *Aspidothelium* was treated as a synonym of *Thelenella* due to the different modes of ascospore separation with fusiform ascospores despite these two genera sharing similar ascus types. However, *Aspidothelium* was retained as a distinct genus based on sessile and exposed perithecia and unusual ascospores (Lücking 1998).

Räsänen (1943) informally included this genus in *Aspidotheliaceae*. Eriksson (1981) formally recognized *Aspidothelium* under *Aspidotheliaceae* which was further accepted by David & Hawksworth (1991). Harris (1995) treated *Aspidotheliaceae* under *Thelenellaceae* which was further accepted by Aptroot et al. (2008a) while several authors retained *Aspidotheliaceae* as a distinct family (Eriksson 2005, Kirk et al. 2008b, Lumbsch & Huhndorf 2010). Nelsen et al. (2017) initially provided the molecular data for *Aspidothelium* and accepted the synonymy of *Aspidotheliaceae* with *Thelenellaceae*.

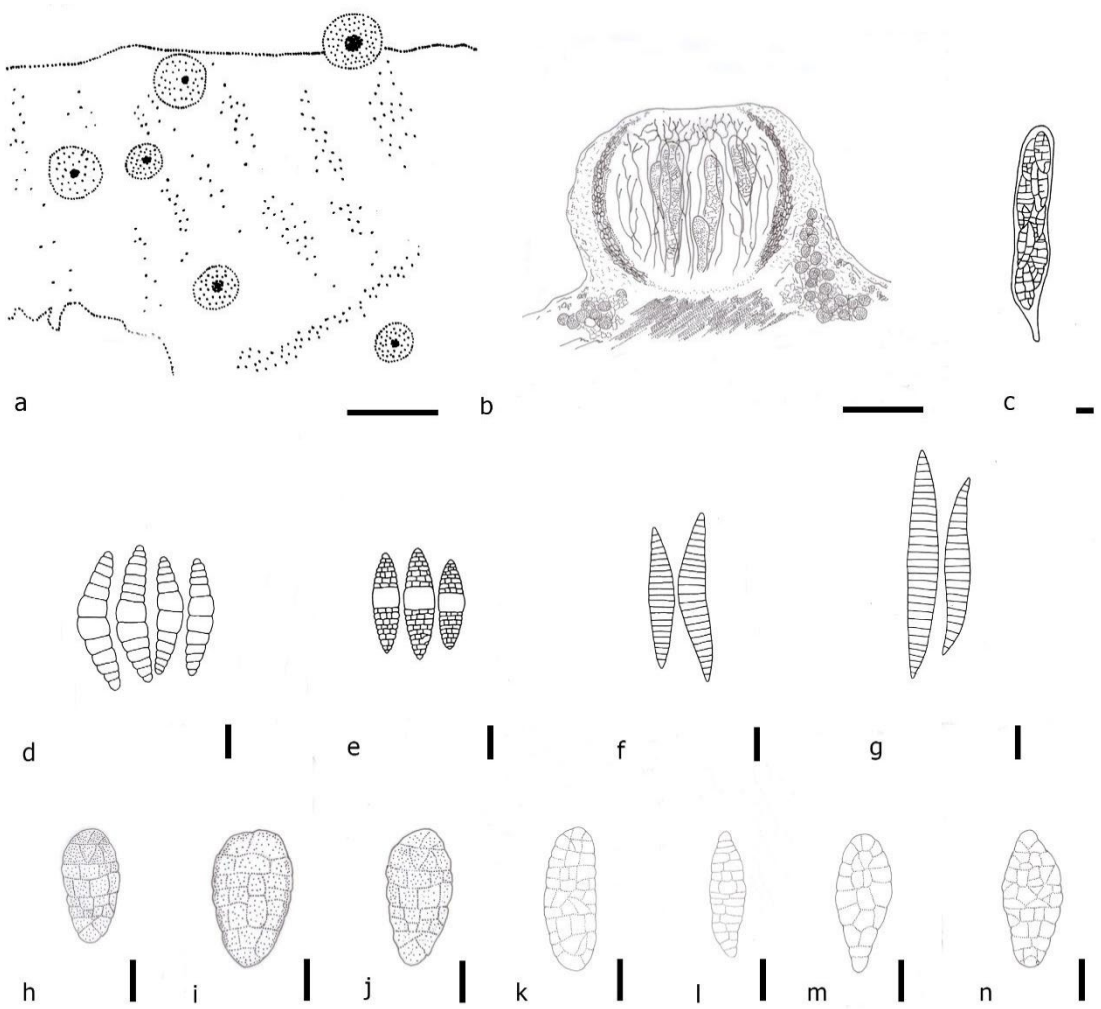


Figure 154 – Morphology of *Thelenellales*. a Perithecia of *Aspidothelium cinerascens*. b Transverse section of *Thelenella melanospora*. c Ascus of *Aspidothelium glabrum*. d–n Ascospores (d Transversely septate ascospores of *A. arachnoideum*. e Ascospores of *A. mirabile*. f Fusiform, transversely septate ascospores of *A. fugiens*. g Transversely septate ascospores of *A. papillicarpum*. h–j *T. melanospora*, k *T. justii*. l–n *T. modesta*) (redrawn from Etayo & Mayrhofer 2003, Flakus 2009, Nelsen et al. 2017). Scale bars: a = 1000 µm, b = 10 µm, c–n = 10 µm.

General description

Ascospore size is an important feature in identifying many species of *Thelenella* species. Immature ascospores are frequently smaller than the values reported in published accounts and overmature ascospores are frequently much narrower. Thus, measuring a sufficient number of ascospores are essential to determine the typical size range. It is also important to count the number of transverse and longitudinal septa. The size of septation is important at the generic level classification of *Thelenellaceae* species (Nelsen et al. 2017).

Sexual morph: *Thallus* crustose. *Photobiont* chlorococcoid, trentepohlia, trebouxioid. *Ascomata* perithecoid, involucrellum mostly less differentiated. *Paraphyses* branched or unbranched and anastomosing with simple or branched periphysoids thick-walled. *Asci* bitunicate, more or less well-developed, KI– ocular chamber, (two- to four-) eight-spored, thick-walled asci with a inamyloid tholus. *Ascospores* hyaline, submuriform to muriform, transversely septate ascospores. Asexual morph: *Pycnidial* conidiomata, black filiform conidiospores with filiform conidia (adapted from Nelsen et al. 2017) (Fig. 154).

Families included in *Thelenellales*

Thelenellaceae O.E. Erikss. ex H. Mayrhofer

Justification of order and problems

The length of ascospores is mainly used for species-level identification of *Thelenella*. However, the length may vary with maturity. Thus, careful observation with a sufficient number of ascospores is necessary to determine the size range (Morse 2016).

Significance

Ecological and economic roles

The taxa are reported as corticolous, foliicolous, muscicolous, and saxicolous species (Nelsen et al. 2017). *Aspidothelium* members are mostly foliicolous and few species are corticolous and rarely saxicolous and the taxa are confined to the tropics (Nelsen et al. 2017). The type species of *Thelenella*, *Thelenella modesta* is included in the Italian red list of epiphytic lichens as "Near-threatened" (Nascimbene et al. 2013).

Chemical diversity

No relevant studies are available for the chemical diversity of *Thelenellales*.

Other relevant data and future recommendations

Thelenella taxa are poorly known and some distinctions between species remain uncertain. Thus, broad sampling to characterize the range of morphological and ecological variability among members with measurements and distributional information is important to define the members (Morse 2016). The traditional anatomical, morphological, and ecological characterization of the genera of *Thelenellaceae* is not well-resolved due to aberrant taxon sampling. Additional molecular sampling especially for the type *Thelenella modesta* is essential (Nelsen et al. 2017).

***Turquoiseomycetales* Crous, Fungal Systematics and Evolution 3: 121 (2019)**

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Incertae sedis*

Introduction and History

Turquoiseomycetales was introduced to accommodate a single family (*Turquoiseomycetaceae*), a genus (*Turquoiseomyces*) and a species (*T. eucalypti*) isolated on leaves of *Eucalyptus leptophylla* from Australia. The species was identified with conidia surrounded by tissue with a green-blue discoloration. Its appearance differs from normal foliicolous coelomycetes on *Eucalyptus* (Crous et al. 2019a). The species also formed a greenish-grey colony on MEA. The sexual morph of the species is unknown. The order formed a distinct lineage in *Lecanoromycetes* and basal to *Lecanorales* and *Umbilicariales* in the LSU phylogenetic analysis. However, the subclass placement of this order remains unresolved (Crous et al. 2019a). Wijayawardene et al. (2020, 2022a) accepted this order within *Lecanoromycetes*.

General description

The order is characterized by pycnidial conidiomata, solitary to aggregated, globose, dark brown. Conidiophores are extensively branched, septate, tightly aggregated. Conidiogenous cells appear as ampulliform to subcylindrical with pale green-brown color. Conidia are subcylindrical and guttulate with medianly 1-septate.

Sexual morph: Unknown. Asexual morph: *Conidiomata* pycnidial, solitary to aggregated, globose, dark brown, opening by irregular rupture. *Conidiophores* lining the inner cavity, subcylindrical, extensively branched, septate, tightly aggregated, 10–25 × 3–4 µm, pale green-brown, finely roughened, subcylindrical. *Conidiogenous cells* ampulliform to subcylindrical, pale green-brown, finely roughened, terminal and intercalary, 5–10 × 3–4 µm, proliferating percurrently. *Conidia* solitary, subcylindrical, guttulate, smooth-walled, medianly 1-septate, apex swollen with mucoid cap, base somewhat tapered, truncate, reflective, 1.5–2 µm diam, straight to flexuous, (50–) 55–60(–80) × 3(–4) µm (adapted from Crous et al. 2019a, Fig. 155).

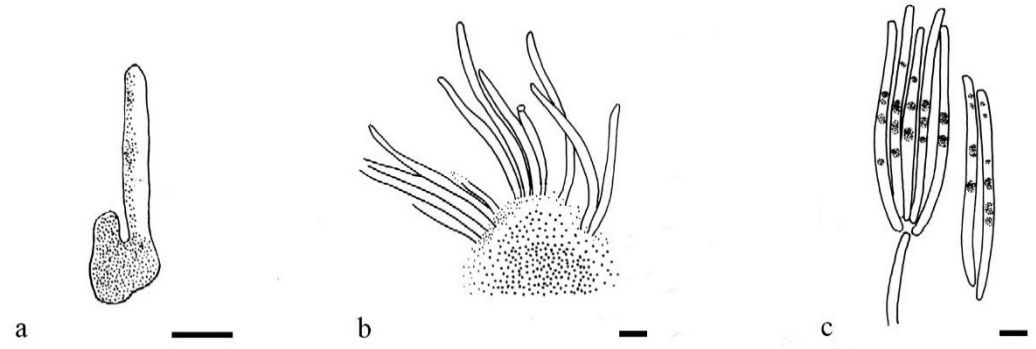


Figure 155 – Morphology of *Turquoiseomyces eucalypti*. a, b Conidiogenous cells giving rise to conidia (redrawn from Crous et al. 2019a). c Conidia. Scale bars: a–c = 10 µm.

Families included in *Turquoiseomycetales*

Turquoiseomycetaceae Crous

Evolution

No relevant studies are available for the evolutionary studies of *Turquoiseomycetales*.

Justification of order and problems

Crous et al. (2019a) placed this order in *Lecanoromycetes* solely based on the LSU gene region. However, both nuclear and protein coding based phylogenetic analysis can provide better taxonomic resolution of the order.

Significance

Ecological and economic roles

Turquoiseomycetales is isolated on leaves of *Eucalyptus leptophylla* from Australia (Crous et al. 2019a).

Chemical diversity

No relevant studies are available for the chemical diversity of *Turquoiseomycetales*.

***Umbilicariales* J.C. Wei & Q.M. Zhou, Mycosystema 26(1): 44 (2007)**

See *Umbilicariales* Lumbsch, Hestmark & Lutzoni, [May] 2007 (*Index of Fungi* **7**: 915), an isonym [Art. 6.3 Note 2].

Subphylum : *Pezizomycotina*
Class : *Lecanoromycetes*
Subclass : *Umbilicariomycetidae*

Introduction

Umbilicariales is a relatively small lichenized order in *Ascomycota* which comprises ca. 200 species from 13 genera and four families. The delimitation of the order has significantly changed over the last decade. Morphologically and ecologically different lichen families have been shown to belong to this order: *Elixiaceae* (Lumbsch et al. 2004b), *Ophioparmaceae* (Miądlikowska et al. 2006, Zhou & Wei 2007, Bendiksby & Timdal 2013), *Fuscideaceae* (Reeb et al. 2004, Miądlikowska et al. 2006, 2014, Bylin et al. 2007), and *Ropalosporaceae* (Bylin et al. 2007, although without strong statistical support). *Umbilicariales* belong to subclass *Umbilicariomycetidae* and has a relatively old phylogenetic age, in molecular clock analysis (Prieto & Wedin 2013) *Umbilicariales* branched off from the main lineages of *Lecanoromycetes* prior to the major diversification of the latter. Poelt (1973) suggested *Umbilicariaceae* belongs in a separate suborder *Umbilicariineae* within *Lecanorales*. Wei & Jiang (1993) recognized the family *Umbilicariaceae* as a member of the *Lecanorales* but pointed out that the Umbilicaria-type ascus structure is a special category in the order. Molecular phylogenetic studies showed that *Umbilicariaceae* clustered outside of *Lecanorales* (Stenroos & DePriest 1998, Kauff & Lutzoni 2002, Peršoh et al. 2004). Reeb et al. (2004) suggested a new order of *Umbilicariales* for the *Fuscideaceae–Umbilicariaceae* group. Consequent phylogenetic studies specify the genera and families to be included (Lumbsch et al. 2004b, Wedin et al. 2005b, Miadlikowska et al. 2006, Bylin et al. 2007). Three families, *viz*. *Umbilicariaceae*, *Ophioparmaceae* and *Elixiaceae* form a well-supported group in phylogenetic analyses of different set of DNA markers, whereas the position of *Fuscideaceae* and *Ropalosporaceae* remains obscure (Bylin et al. 2007, Bendiksby & Timdal 2013, Miądlikowska et al. 2014). The taxonomic conclusion of the most comprehensive phylogenetic analysis of *Lecanoromycetes* (Miądlikowska et al. 2014) was "in addition to the *Umbilicariaceae*, *Ophioparmaceae*, and *Elixiaceae*, the families *Fuscideaceae* and *Ropalosporaceae* should be considered as members of the *Umbilicariales* or as separate orders in the *Umbilicariomycetidae*." A more comprehensive selection of *Fuscideaceae* and *Ropalosporaceae* is needed to make the final conclusion on the phylogenetic position of these families. Nevertheless, *Fuscideaceae* and *Ropalosporaceae* accepted as members of *Umbilicariales* in recent classifications (Lücking et al. 2017, Wijayawardene et al. 2017a, 2020, 2022b). We also accept *Fuscideaceae* and *Ropalosporaceae* within *Umbilicariales sensu lato* pending further studies.

The formal description of *Umbilicariales* was made by two scientific groups independently. Zhou & Wei (2007) basing on their SSU DNA, previous studies (Kauff & Lutzoni 2002, Lumbsch et al. 2004b) as well as morphological investigations, described *Umbilicariales* for *Umbilicariaceae* and *Rhizoplacopsidaceae*. The latter family included a single species which was soon synonymized with *Boreoplaca ultrafrigida* (Davydov & Wei 2009). The type of the order was incorrectly proposed as *Umbilicariaceae* but legitimate and automatically typified by the generic name (see Art. 10.10 and 16.1(a)). Hibbett et al. (2007) based on previous phylogenetic studies (Reeb et al. 2004, Miadlikowska et al. 2006, Hofstetter et al. 2007) proposed *Umbilicariales* Lumbsch et al. [isonym, art. 6.3 Note 2] with the type *Umbilicaria* and example genera *Umbilicaria* and *Lasallia*.

Umbilicariales represent a group characterized mainly by their phylogenetic relationship since they do not present striking common morphological characters between families except a similar ascus type. The angular shape of apothecia or the presence of sterile hyphal or paraphysal elements within the hymenial layer, which is characteristic of *Umbilicaria*, also found in *Xylopsora* and *Elixia*. The taxa are distributed worldwide with most occurring on siliceous rock, mostly in polar or mountain regions, or on wood and bark mostly in temperate forests predominantly in the Holarctic (Llano 1950, Timdal 1984, Rogers & Hafellner 1988, Ekman 1993, Wei & Jiang 1993, Fryday 2008, Davydov & Wei 2009, Zhang et al. 2018e). Two genera endemic to Australia were also described (Kantvilas & McCarthy 2003, Kantvilas & Lumbsch 2009).

History

Umbilicaria, the type genus of *Umbilicariales*, is most diverse and corresponds to the family *Umbilicariaceae* before molecular-phylogenetic (phylogenomic) methodology was implemented into the taxonomical investigations. *Umbilicariaceae* in the previous sense was recognized as a well-

defined group of lichens by earlier lichenologists. Linnaeus (1763) united seven species of his genus *Lichen* under the heading *Lichenes umbilicati* to emphasize their mode of attachment by 'umbilicus'. Hoffmann (1789) accepted this group as the genus *Umbilicaria*. Acharius (1803) circumscribed *Gyrophora* by the presence of striated (gyrose) apothecial discs and assigned 15 species to this genus. Furthermore, he placed two species of *Umbilicaria* with plane discs into *Lecidea*.

The classification of the family has been repeatedly changed, taxa were distinguished on the basis of various morphological and anatomical features of the thallus (Minks 1900, Frey 1933, 1949), fruit bodies (Acharius 1803, Scholander 1934, Llano 1950, Wei & Jiang 1993), or ascospores (Koerber 1855, Elenkin & Savicz 1910, Frey 1931, 1933, 1936, Savicz 1950, Imshaug 1957) also detailed in the review of the main studies in Llano (1950) and Davydov (2007). The lichen family *Umbilicariaceae* was long considered to be composed of two genera, *Umbilicaria* and *Lasallia*, together comprising about 100 species of mostly umbilicate growth habit (Savicz 1950, Poelt 1962, Wei & Jiang 1993). Clarifying the relationships among *Umbilicariaceae* species was achieved by molecular phylogenetic analyses (Niu & Wei 1993, Ivanova et al. 1999, Romeike et al. 2002, Ott et al. 2004, Krzewicka et al. 2009, Davydov et al. 2010, 2019, 2020, Hestmark et al. 2011, McCune & Curtis 2012, McCune et al. 2014, Davydov 2022, Davydov & Masson 2022). Molecular phylogenies based on multiple markers (Miadlikowska et al. 2014) supported the paraphyletic status of *Umbilicaria*. Bendiksby & Timdal (2013) extended the family circumscription by including the two new genera *Fulgidea* and *Xylopsora*. *Fulgidea* and *Xylopsora* were described to accommodate species previously belonging to the polyphyletic *Hypocenomyce* (Timdal 1984, 2001). Davydov et al. (2017) provided multigene phylogenetic analyses of 79 taxa of *Umbilicaria* and *Lasallia* and reconstructed the evolution, distribution, and structural or functional coupling of the phenotypic traits in *Umbilicariaceae*, they synonymized *Lasallia* and *Umbilicaria* and suggested the new classification includes eight subgenera in *Umbilicaria*.

Wirth & Vézda (1972) described the genus *Fuscidea* for well-defined *Lecidea cyathoides* group (= *Lecidea rivulosa*-group by Magnusson 1925). Hafellner (1984) based on the similarities in ascus apex introduced the family *Fuscideaceae* for *Fuscidea* and *Maronea*, the genus with multi-spored asci introduced by Massalongo (1856b) and revised by Magnusson (1934). Kantvilas & McCarthy (2003) placed *Hueidea* to *Fuscideaceae* based on the similarity of the ascus type. This placement was accepted by Eriksson et al. (2006) based on the fuscidea-type asci as the diagnostic character for the family, but no molecular phylogenetic evidence was obtained. The generic composition of *Fuscideaceae* changed several times (Lumbsch & Huhndorf 2007, Tehler & Wedin 2008) and according to Lücking et al. (2017) *Fuscideaceae* accommodates *Fuscidea*, *Hueidea*, *Maronea* and *Orphniospora*.

The genus *Ropalospora* was circumscribed by Massalongo (1860) and raised to the monogeneric family *Ropalosporaceae* by Hafellner (1984). Then it was synonymized to *Fuscideaceae* (Ekman 1993, Eriksson et al. 2006), but was later reinstalled based on mtSSU DNA phylogeny and tentatively placed in *Umbilicariales* (Bylin et al. 2007). Zahradníková (2017) showed results of 5-gene phylogeny and suggested again to synonymize *Ropalosporaceae* with *Fuscideaceae* (unpublished). Major progress in clarifying the relationships of *Umbilicariales* within *Lecanoromycetes* was achieved by molecular phylogenetic analyses over the last decades. Early molecular-phylogenetic studies based on a single DNA marker showed that *Umbilicariaceae* clustered outside of *Lecanorales* (Stenroos & DePriest 1998, Kauff & Lutzoni 2002, Peršoh et al. 2004). Lumbsch et al. (2004b) found in the study based on LSU and mtSSU data that *Elixia flexella* (*Elixiaceae*) formed a well-supported monophyletic group within the family *Umbilicariaceae*. Reeb et al. (2004) suggested in the study based on LSU, SSU, and RPB2 DNA markers a new order of *Umbilicariales* for the *Fuscideaceae–Umbilicariaceae* group. Wedin et al. (2005b) obtained phylogenetic signals for the clustering of *Umbilicariaceae* and related genera (including *Hypocenomyce scalaris*, *'Hypocenomyce' friesii*, *Elixia*, *Boreoplaca*, *Fuscidea*, and *Ophioparma*). With time the number of genera and species as well as ribosomal and protein-coding markers included in phylogenetic analyses increased. Miadlikowska et al. (2006) suggested the order or subclass status for *Umbilicariaceae* (*Umbilicaria* and *Lasallia*), *Ophioparmaceae* (*Ophioparma*,

Hypocenomyce, and *Boreoplaca*) and *Fuscideaceae* (*Fuscidea* and *Maronea*) based on the phylogenetic analysis of ribosomal DNA (LSU, SSU, and mtSSU) and protein-coding genes (RPB1, RPB2). Bylin et al. (2007) tested monophyly of *Fuscidea*, *Maronea* and *Ropalospora* based on mtSSU and suggested to include *Ropalosporaceae* to *Umbilicariales* in addition to *Fuscideaceae*, but showed low bootstrap support of this composition of *Umbilicariales* in the phylogenetic tree. Bendiksby & Timdal (2013) raised *Umbilicariales* to formally described subclass *Umbilicariomycetidae*. Mentioned authors improved species number in their analyses based on ITS, LSU, and mtSSU DNA regions and accepted *Umbilicariaceae*, *Ophioparmaceae*, and *Elixiaceae* within *Umbilicariales*. The clade *Fuscideales* was treated as *incertae sedis* within *Lecanoromycetes*, but authors mentioned that asci in *Umbilicaria* revealed a type similar to the fuscidea-type, i.e. with amyloid layers lining both the inside and outside of the ascus wall near its apex.

Miadlikowska et al. (2014) significantly improved their previous phylogeny by including sequences of new species and markers and accepted *Umbilicariomycetidae* with five families. *Umbilicariaceae*, *Ophioparmaceae*, and *Elixiaceae* clearly belong to *Umbilicariales*, and *Fuscideaceae* and *Ropalosporaceae* considered to be members of *Umbilicariales* or separate orders in the *Umbilicariomycetidae*. Based on mentioned phylogenetic study, classification has been accepted in recent systems of *Lecanoromycetes* (Lücking et al. 2017, Wijayawardene et al. 2017a, 2020, 2022b).

General description

Representatives of four families of *Umbilicariales* have various appearance and anatomical traits, but share similar ascus types, i.e. amyloid inner and outer layer with an inamyloid layer in between (fuscidea-type and umbilicaria-type). All species lack cephalodia. *Umbilicariales* taxa form various growth forms which are crustose, subsquamulose, squamulose, peltate, or umbilicate foliose. Crustose species may have prothallus, but it differs with genus as well as species. Chlorococoid green algae, *Apatococcus* and *Trebouxia* are commonly found as photobionts (Beck 1999, Romeike et al. 2002, Sadowska-Des 2014, Zahradníková et al 2017a).

The shape of the ascomata can vary and mostly form disc-shaped ascomata. The angular shape of apothecia characteristic of *Umbilicariaceae*, is also appeared in *Xylopsora* and *Elixia* (Frey 1931, 1933, Henssen 1970). The presence of excipular tissue within the hymenial layer is typical of *Umbilicariaceae*, resulting in the formation of four major apothecial types (Scholander 1934, Llano 1950). Apothecia are mostly sessile to stipitate but can be immersed in *Fuscideaceae* (Ekman 1993, Fryday 2008) and *Elixiacerae* (Kantvilas & Lumbsch 2009). The apothecial type in *Umbilicariales* is usually lecideoid. Thalline (proper) margin is common in *Maronea* (Harris 2006) and *Ophioparma* (Rogers & Hafellner 1988). Ragged, incomplete, 'thalline margin' comprised of abraded, adhering remnants of thallus develops in *Meridianelia*; proper margin barely evident. Apothecia of *Umbilicaria* in addition to excipulum proprium often have a pseudoexcipulum, mostly formed by the upper thallus cortex, or composed by the pseudoexcipulum in the basal and by an excipulum proprium in the upper part (Henssen 1970). Frey (1936) classifies such apothecia as 'superlecideoid,' and Wei & Jiang (1988) as 'sublecanorine.'

The structure and pigments of true excipulum and epihymenium vary between the genera (Henssen 1970, Timdal 1984, 1994, 2001, Ekman 1993, Kantvilas & McCarthy 2003, Kantvilas & Lumbsch 2009, Bendiksby & Timdal 2013). Paraphyses are usually simple or moderately branched and septate (Wei & Jiang 1993, Timdal 1994), whereas paraphyses of *Meridianelia* are highly branched, anastomosing and entangled, with tapered apices. *Elixia* has capitate paraphyses with a sharply delimited pigment zone in the top of the apical cell. Swollen apices of paraphyses are also characteristic of *Fuscidea* (Fryday 2008). Asci can be rhombic to clavate, prototunicate, fuscidea-type or umbilicaria-type, with an amyloid inner and outer layer with an inamyloid layer in between (Janex-Favre 1974, Wei & Jiang 1993, Bendiksby & Timdal 2013). Asci are mostly 8-spored but can be one or two-spored in *Umbilicaria* (Llano 1950, Davydov et al. 2010) or multi-spored in *Maronea* (Massalongo 1856b, Harris 2006).

Genera of *Umbilicariales* are characterized by wide range of ascospore types. Ascospores are mostly ellipsoidal and range from aseptate to multi-septate, submuriform or muriform. Ascospores color, size, and septation were used in the genera and species delineation of *Umbilicariales* (Wei & Jiang 1993, Ekman 1993, Kantvilas & McCarthy 2003, Harris 2006, Fryday 2008, Kantvilas & Lumbsch 2009, Davydov et al. 2010). Simple ascospores in some species are constantly curved (*Fuscidea*, Fryday 2008) or nodulose (*Umbilicaria*, McCune et al. 2014). Ascospores in *Ophioparma* and *Ropalospora* are spirally arranged in ascus, fusiform, transversely multiseptate, and colorless (Rogers, Hafellner 1988, Ekman 1993). Most deviant ascospores in the order – plurilocular with very narrow and inconspicuous channels – are characteristic of *Hueidea* temporarily placed to *Fuscideaceae*. Such ascospores are typical for *Teloschistales*. Many species of the *Umbilicaria* develop rather characteristic mitosporic dispersal units, so-called 'thalloconidia,' which were shown to be highly species-specific (Hasenhüttl & Poelt 1978, Hestmark 1990). However, the possession of thalloconidia is also found in various lichen families (Hasenhüttl & Poelt 1978, Poelt & Obermayer 1990). Thus, it is not considered a distinctive character within *Umbilicariales*. A wide range of vegetative propagules can be produced by some species within *Umbilicariales*. That are soredia, parasoredia, schizidia, isidia, lobules, and thallyles (Timdal 1984, Wei & Jiang 1993, Kantvilas & Lumbsch 2009, Davydov et al. 2017). Umbilicaria-type pycnidia is observed in some genera within *Umbilicariales* (Vobis 1980). Conidia are mostly ellipsoid to bacilliform or rod-shaped in *Ophioparma* (Smith et al. 2009).

Sexual morph: *Thallus* crustose, subsquamulose, squamulose, peltate, or umbilicate foliose. *Prothallus* present or absent. *Cephalodia* absent. Photobionts *Chlorococcoid*, *Apatococcus* and *Trebouxia*. *Ascomata* apothecial, mostly sessile to stipitate, mostly disc-shaped and black, concave to plane, or plain to convex, proper margin or its derivate present or usually absent. *Pruina* absent or present. *Hypothecium* hyaline to pigmented. *Excipulum* well or poorly developed, usually with colorless inner part. *Hymenium* hyaline to light brown, usually not inspersed with oil droplets, comprising unbranched to sparingly branched or highly branched paraphyses and asci. *Paraphyses* sometimes without ок with pigment cap at the tips. *Epihymenium* present. *Asci* rhombic to clavate, prototunicate, Fuscidea-type or *Umbilicaria*-type, with amyloid inner and outer layer with a inamyloid layer in between, one, two, eight to multi-spored. *Ascospores* ellipsoid to oblong, simple, 1-septate to muriform, sometimes slightly constricted at the septum, hyaline to dark brown. Asexual morph: *thalloconidia*, as well as vegetative soredia, parasoredia, schizidia, isidia, lobules, thallyles (Figs. 156, 157, 158).

Families included in *Umbilicariales*

Elixiaceae Lumbsch
Fuscideaceae Hafellner
Ophioparmaceae R.W. Rogers & Hafellner
Umbilicariaceae Chevall.

Evolution

Umbilicariales has a relatively old phylogenetic age, in molecular clock analysis (Prieto & Wedin 2013). *Umbilicariales* branched off prior to the major diversification of *Lecanoromycetes*. Bendiksby & Timdal (2013) suggest that the presence of four clades containing species occur on burnt wood in the *Umbilicariales sensu stricto* (*Elixia*, *Fulgidea*, *Hypocenomyce*, and *Xylopsora*) may be explained as a plesiomorphy in this order, in which case the saxicolous genera *Boreoplaca* and *Umbilicaria* have evolved from ancestors growing on burnt wood. The distribution of the diagnostic morphological and chemical traits against the molecular phylogenetic topology in *Umbilicaria* (Davydov et al. 2017) revealed the following patterns of evolution: 1) Rhizinomorphs were gained at least four times independently. 2) Asexual reproductive structures, i.e. thalloconidia and lichenized dispersal units, appear more or less mutually exclusive. Two major ontogenetic types of thalloconidial development (thallobred versus rhizinobred) exist, reflecting their non-homologous origin. Both types of thalloconidial formation were gained multiple times. 3) The apothecial type is

a relatively variable trait because the main types of apothecia switched several times in evolution. Multiple evolutionary changes from the gyrodiscs to leiodiscs, by reduction of carbonized hymenial structures, seem likely. 4) Ascospore characters, such as spore number per ascus, spore size, and septation type and degree are strongly correlated. Eight aseptate small ascospores per ascus represent a plesiomorphic trait.



Figure 156 – Thallus morphology of *Umbilicariales.* a–j *Umbilicaria* sp. k *Xylopsora friesii.* l *Boreoplaca ultrafrigida.* m *Elixia flexella.* n *Hypocenomyce scalaris.* o *Ophioparma* sp. p *Fuscidea*

sp. r *Maronea* sp. s *Ropalospora* sp. t *Orphniospora* sp. (Photo: a-s: Davydov & Yakovchenko, t: F. Schumm). Scale bars: a, f, g, h, i, m = 500 µm, b, c, d = 1 cm, e, j, k, n, o, p, r, s, t = 1 mm, l = 2 mm.

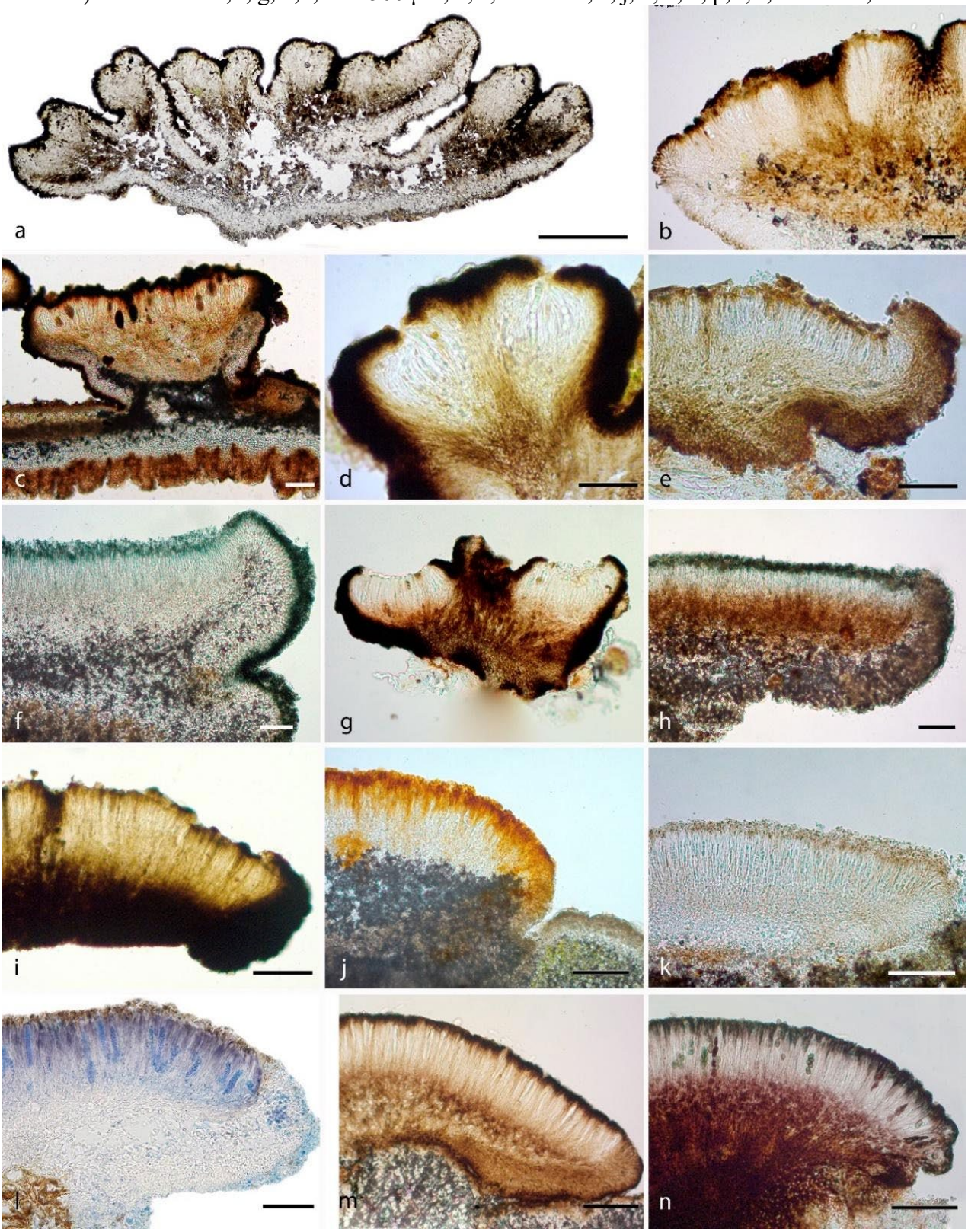


Figure 157 – Ascomata morphology of *Umbilicariales*. a–d *Umbilicaria* sp. e *Xylopsora friesii*. f *Boreoplaca ultrafrigida*. g *Elixia flexella*. h, i *Hypocenomyce* sp. j *Ophioparma* sp. k *Fuscidea lightfootii*. l *Maronea* sp. m *Ropalospora* sp. n *Orphniospora* sp. (Photo: a, l: F. Schumm. b-k, m, n: Davydov & Yakovchenko. For *Hueidea* see Kantvilas & McCarthy (2003)). Scale bars: a, c, j, l, m, n = 100 µm, b, d, e, f, g, h, i, k = 50 µm.

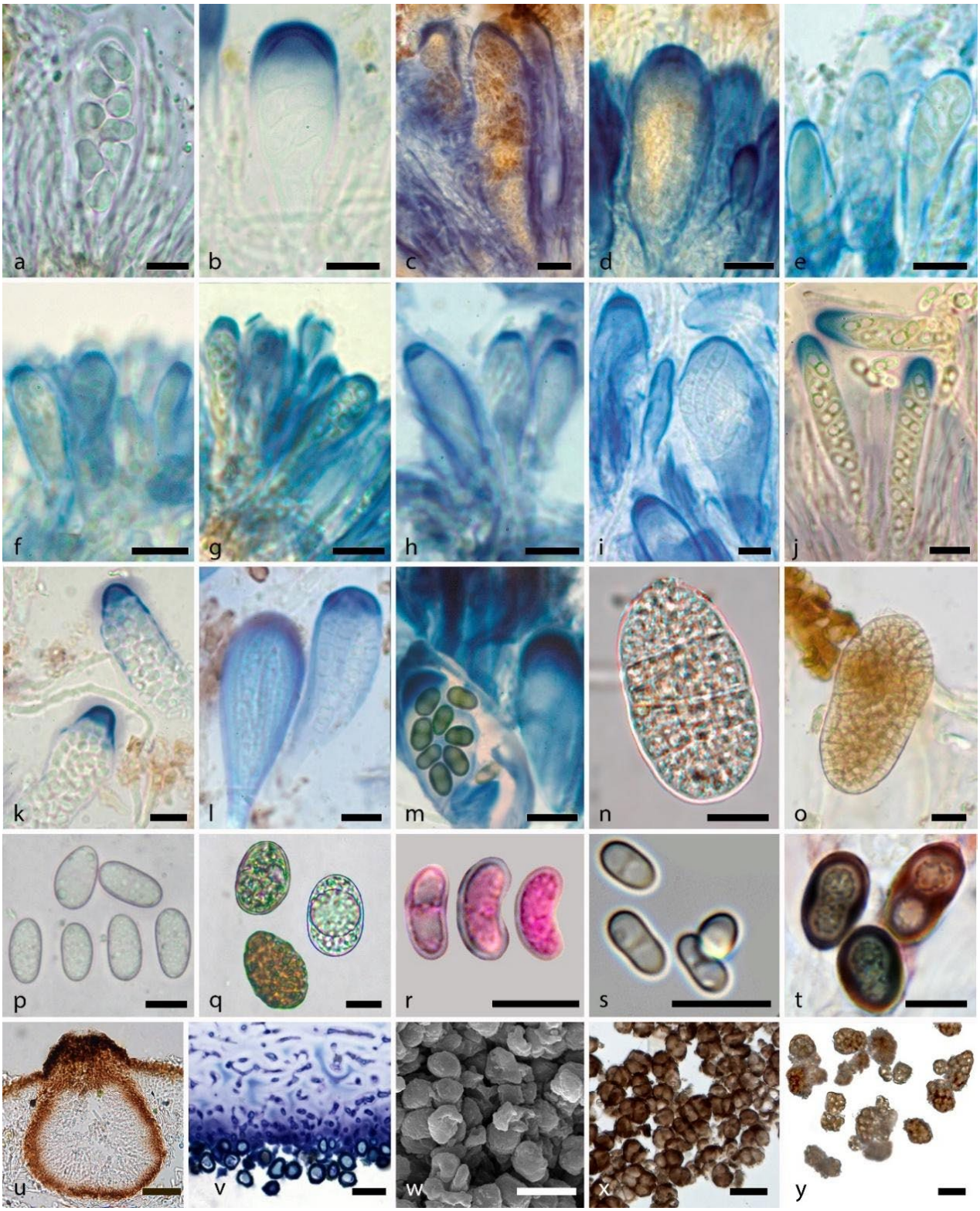


Figure 158 – Asci, ascospores and thalloconidia morphology of *Umbilicariales.* a–d, n, o, p, q *Umbilicaria* sp. e *Boreoplaca ultrafrigida*. f *Xylopsora friesii*. g *Elixia flexella*. h *Hypocenomyce* sp. i *Ophioparma* sp. j *Fuscidea lightfootii*. k *Maronea* sp. l *Ropalospora* sp. m *Orphniospora* sp. r *Fuscidea* sp. s *Maronea* sp. t *Orphniospora* sp. u Pycnida of *Umbilicaria*. v, w, x, y *Thalloconidia* of *Umbilicaria* **(**Photo: a-q, u-y Davydov & Yakovchenko, r, s, t: F. Schumm.). Scale bars: a, b, e–l, n–t, v, w, x = 10 µm, c, d, m, y = 20 µm, u = 50 µm.

Justification of order and problems

The close association of *Umbilicariaceae* with *Elixiaceae* and *Ophioparmaceae* were supported by shared morphological characteristics in the ascoma and asci and strong phylogenetic support (Zhou & Wei 2007, Bendiksby & Timdal 2013, Miadlikowska et al. 2014). Reeb et al. (2004), Bylin et al. (2007), and Miadlikowska et al. (2006, 2014) suggested the close relationship of *Fuscideaceae* and *Ropalosporaceae* to *Umbilicariales sensu stricto* or its affiliation to the order (= *Umbilicariales sensu lato*). However, broad taxon sampling with multigenes is important to clarify the phylogenetic relationship between *Umbilicariales* and these two families. The most comprehensive data was collected by Zahradníková (2017) and Zahradníková et al. (2017b, 2018) who nevertheless considers *Fuscideaceae* as family *incertae sedis* within *Umbilicariomycetidae*.

Significance

Ecological and economic roles

The taxa are distributed worldwide with most occurring on noncalcareous rock, mostly in polar or mountain regions, or on wood and bark mostly in temperate forests predominantly in Holarctic (Llano 1950, Timdal 1984, 2001, Rogers & Hafellner 1988, Ekman 1993, Wei & Jiang 1993, Fryday 2008, Davydov & Wei 2009). Two genera endemic to Australia were described in the last decades (Kantvilas & McCarthy 2003, Kantvilas & Lumbsch 2009). Some species produce primary production in extreme low temperature environments such as polar and alpine regions (*Umbilicaria*) or inhabit substrates "difficult" for other fungi, such as burned wood (*Fulgidea*, *Hypocenomyce*, *Xylopsora*).

Romeike et al. (2002) showed relatively high diversity of *Trebouxia* in the investigated *Umbilicaria* species in Antarctic. Sadowska-Des et al. (2014) found that *Umbilicaria pustulata* is associated with at least five species of *Trebouxia* and most of them are shared with other lichen-forming fungi. *Umbilicaria esculenta* is well-known in Eastern countries as edible lichens named "Iwatake" in Japan, "Sheakki" in Korea, and "Shi-er" in China (Yoshimura 1993). The species is also used in medicine (e.g., Hirabayashi et al. 1989, Yoshimura 1993 [and references in that paper], Kim & Lee 2006, Wu et al. 2014b, Xu et al. 2014). Several species of *Umbilicaria* and *Ophioparma* are used in traditional medicine at least in Asia and America (Wang & Qian 2013, Crawford 2015).

Chemical diversity

Species of *Umbilicariales* are associated with a wide range of chemical production mostly belong to following classes: orcinol depsides (crustinic, divaricatic, gyrophoric, hiascic, isohyperlatolic, lasallic, lecanoric, ovoic, perlatolic, and umbilicaric acids), meta-depsides (secicaic and submerochlorophaeic acids), depsido-depsones (friesiic acid), β-orcinol depsides (atranorin), β-orcinol depsidones (stictic and norstictic acids), β-orcinol metadepside (thamnolic acid), benzyl ester (alectorialic acid), antraquinones, aliphatic acids, fatty acids, terpenes and usnic acid (Elix 2014). Secondary metabolism of *Umbilicariaceae* has been studied rather extensively since Nylander (1869). The main compounds in *Umbilicaria* are gyrophoric and lecanoric acids (Narui et al. 1996a). Some species of *Umbilicaria* produce in addition anthraquinones, atranorin, crustinic, hiascic, lasallic, norstictic, ovoic, stictic and umbilicaric acids (Huneck et al. 1993, Huneck & Yoshimura 1996, Narui et al. 1996a, b, Cohen 2002). *Fulgidea* produce alectorialic and thamnolic acids, and *Xylopsora* – friesiic and thamnolic acids (Bendiksby & Timdal 2013). Within *Ophioparmaceae*, genera *Boreoplaca* and *Hypocenomyce* contain lecanoric acid (Timdal 1984, 1994), and *Ophioparma* produces orcinol depsides, aliphatic acids, and occasionally depsidones and terpenes, in addition five quinonoid naphthopyranones, *i. e.* ophioparmin, 4-methoxyhaemoventosins, and 4-hydroxyhaemoventosin, anhydrofusarubin lactone, and haemoventosin were isolated from the fruiting bodies of *Ophioparma ventosa* (Le Pogam et al. 2016). Within *Elixiaceae*, *Meridianella* contains protolichesterinic acid (Kantvilas & Lumbsch 2009). In *Fuscideaceae*, species of *Fuscidea* may contain alectorialic, divaricatic, fumarprotocetraric, and norstictic acids (Fryday 2008), *Ropalospora* contains atranorin, gyrophoric, norstictic, perlatolic, isohyperlatolic, usnic acids and anthraquinones (parietin), (Ekman 1993, Elix 2014), *Maronea* – divaricatic, secicaic, and

submerochlorophaeic acids (LaGreca 2006), *Orphniospora* can produce anthraquinones and fatty acids (McCune 2017).

Thus, families within *Umbilicariales* have as common secondary metabolites, as specific ones. However, most chemical substances are not exclusive to *Umbilicariales*. The presence or absence of a compound in the phenotype cannot fully address evolutionary questions. Fungal secondary metabolites genes are organized in biosynthetic gene clusters, contiguous genomic regions (Keller et al. 2005, Calcott et al. 2018), and a chemical phenotype is determined not only by the presence of genes required for the production of a compound but by the expression of the entire pathway leading to the compound.

Other relevant data and future recommendations

Poelt & Nash (1993) emphasized that most species in *Umbilicariaceae* "consists of individuals that exhibit a series of developmental stages". Similar to vascular plants these ontogenetic stages can be roughly divided into juvenile, mature and senescent stages. The definiteness of the boundaries of an individual thallus in *Umbilicaria* makes it a useful model taxon for the study of phenotypic variation (Larson & Carey 1986), strategies of reproduction (Hestmark 1992, Gregersen et al. 2006), population ecology and ontogenesis (Topham 1982, Sletvold & Hestmark 1997, Ramstad & Hestmark 2001, Cao et al. 2015), elemental composition of thallus (Bargagli et al. 2000), metabolic activity (Scott & Larson 1986, Valladares et al. 1996, 1998, Sancho et al. 1997, 2003, Schroeter et al. 2011, Raggio et al. 2016), climatic niche modeling (Rolshausen et al. 2017). Species of *Umbilicaria* also model taxa for recent genome investigations (Merges et al. 2021, Dal Grande et al. 2018, 2022, Singh et al. 2021, 2022).

Umbilicaria include lichen species which are able to be photosynthetically active at subzero temperatures. *Umbilicaria aprina* is a species with a distinct preference for high alpine and high arctic and antarctic habitats. It has been shown that *Umbilicaria aprina* in the continental antarctic is able to gain a significant CO_2 uptake at temperatures in the field down to -17 °C. Photosynthetic activity and re-hydration from the snow at subzero temperatures are of great ecological for primary production in extreme environments such as polar and alpine regions where metabolic activity is severely limited by water availability and low temperatures (Schroeter & Scheidegger 1995). Australian endemic genera *Hueidea* and *Meridianelia* lack molecular data, and molecular-phylogenetic studies of *Fuscideaceae* included only a limited number of species and need further studies for their generic classification and support their placement in *Umbilicariales*.

***Leotiomycetes* O.E. Erikss. & Winka, Myconet 1(1): 7 (1997)**
***Chaetomellales* Crous & Denman, Persoonia 39: 423 (2017)**

Subphylum : *Pezizomycotina*
Class : *Leotiomycetes*

Introduction

Chaetomellales is a relatively small order, containing a single family, *Chaetomellaceae* with five genera, and 76 species (Johnston 2022, Wijayawardene et al. 2022a). Asexual structures are predominant with many species producing complex conidiomata, either pycnidia or sporodochia, or both. Sexual morphs are rarely observed but are apothecial where known. All taxa have been isolated from living or dead plant matter or soil. *Chaetomella* is the most speciose genus (with 26 species), followed by *Sphaerographium* (23), and *Pilidium* (23). *Synchaetomella* (3) and *Xeropilidium* (1) are the least represented.

History

The type genus of this clade, *Chaetomella*, was described by Fuckel (1867) (for which a formal type species was designated by Clements & Shear (1931)). *Pilidium* was first erected as a genus by Kunze & Schmidt (1823). Due to similarities including the production of black, ellipsoid to reniform pycnidia and their substrata, Rossman et al. (2004) suspected an affinity between selected

Chaetomella and *Pilidium* and provided the first phylogenetic evidence that these genera were closely related. Their analysis also supported the close phylogenetic relationship with *Leotiomycetes*. However, the higher level (family, order, class) classifications were not designated at that time. The family was erected by Baral (2016) and the clade was recognized as an independent order by Crous et al. (2017a). In *Chaetomella* and some *Hainesia* species, reproductive structures are usually covered in distinct setae, which are long, dark brown, thick-walled, septate, with clavate to acuminate apex, straight to curled (Punithalingam & Spooner 1997, Verkley 2002, Rossmann et al. 2004, Decock et al. 2005, Crous et al. 2017a, Marin-Felix et al. 2017, Pärtel et al. 2017, Ekanayaka et al. 2019a, Li et al. 2020).

General description

Species in this group are mostly known from their asexual stage while sexual morphs are uncommon (Pärtel et al. 2017) and reported in *Chaetomella*, *Pilidium* and *Xeropilidium* (Rossmann et al. 2004, Pärtel et al. 2017).

Sexual morph: *Ascomata* apothecial, sessile to substipitate, developing beneath the host epidermis, erumpent. *Asci* 8-spored, unitunicate, cylindrical-clavate, inamyloid, arising from croziers. *Ascospores* hyaline, ellipsoid to fusoid, aseptate. *Paraphyses* simple, branched or not. Ectal excipulum of *textura angularis*, globulosa, prismatica or porrecta, medullary excipulum of *textura prismatica* to *porrecta* (Ekanayaka et al. 2019a). Asexual morph: dimorphic, with pycnidial and sporodochial stages present. *Pycnidia* sessile, subglobose, darkly pigmented, with walls composed of a *textura angularis*, and usually open by fissures. *Sporodochia* sessile to long-stalked, ochraceous to brown. *Conidia* cylindrical to ellipsoidal, straight to curved, usually with acute ends, with 0–1 septa, arising from phialides (adapted from Crous et al. 2017a, Ekanayaka et al. 2019a) (Fig. 159).

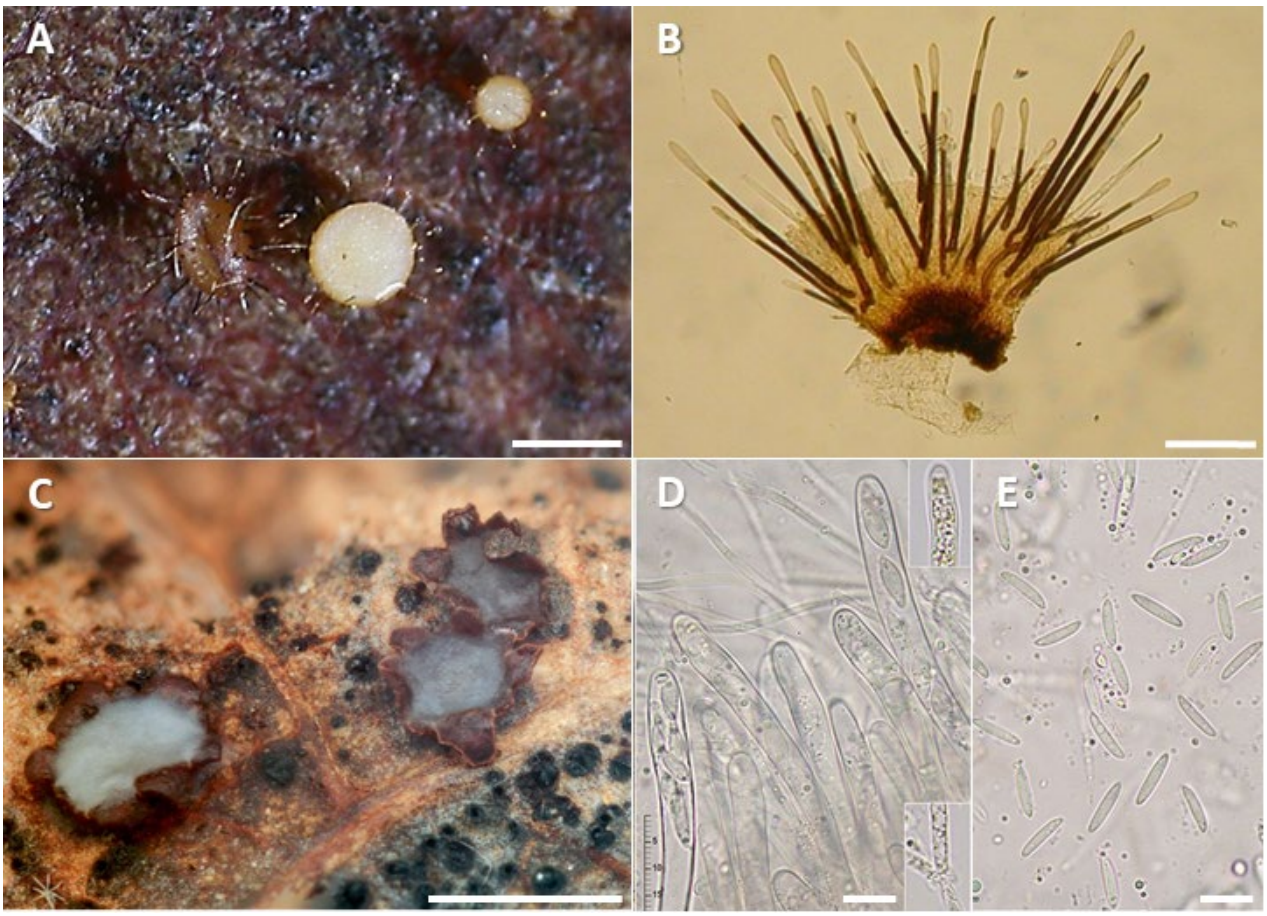


Figure 159 – Morphological characteristics of *Chaetomellales*. A *Chaetomella oblonga*, pycnidium (left), apothecia (right). B *Chaetomella oblonga* apothecium. C Pycnidia of *Pilidium acerinum*. D Asci of *Chaetomella oblonga*, croziers (bottom right). E Conidia of *Chaetomella oblonga* (Photos:

A, B – Hans-Otto Baral; C – Dragiša Savić; D, E – Enrique Rubio.). Scale bars: A = 500 μm, B = 100 μm, C = 1000 μm, D, E = 10 μm.

Families included in *Chaetomellales*

Chaetomellaceae Baral, P.R. Johnst. & Rossman

Justification of order and problems

Regardless of which markers are used (Johnston et al. 2019b), molecular phylogenetic studies support *Chaetomellales* as an independent clade within *Leotiomycetes*, although how it is related to other orders within the class varies considerably based on taxon and loci sampling (Quijada et al. 2022, Barreto et al. 2023). The morphology and life history strategies employed by members of this order also support the distance relationship to *Leotiomycetes* (Baral 2016). The prominent production of pycnidia and sporodochia are unusual in this class (Quandt & Haelewaters 2021).

Based on the recommendations of Johnston et al. (2014b) in accordance with the change in the botanical code of nomenclature (ICBN), all species in *Discohainesia*, *Hainesia*, and *Sclerotiopsis* should be transferred to *Pilidium*. However, only *Discohainesia* has been formally addressed, thus far. Future nomenclatural studies should formalize these changes in *Hainesia* and *Sclerotiopsis*. All species of lichenicolous *Hainesia* have been incorporated into *Epithamnolia* (*Leotiales*), including one species that is listed as *Hainesia* on MycoBank (*H. lecanorae*) (Suija et al. 2017).

Significance

Ecological and economic roles

Chaetomellales is an order of essentially plant-associated and soil-dwelling fungi. Most species are decomposers of dead plant tissues, but some are endophytes such as *Chaetomella endophyitica* (Suwannarach et al. 2018) whereas several species are plant parasites. *Chaetomella raphigera*, originally described growing on rose twigs by Swift (1930), now known to be a pathogen causing brown spot/ tan-brown rot disease on leaves and fruits of several plants (Rossmann et al. 2004), including cultivated plants such as pomegranate (*Punica granatum*) (Gajbhiye et al. 2016), *Cuphea* spp. (Singh et al. 1999), *Eucalyptus urophylla* × *E. grandis* (Cao et al. 2021), and *Rosa chinensis* (Zhang et al. 2014). Species of *Pilidium* are commonly found as plant pathogens, causing leaf spots, root lesions, and tan-brown rot of fruits in a wide range of hosts (Marin-Felix et al. 2017).

Chemical diversity

Chaetomella species produce a range of chemicals with potential applications. Kao et al. (2019) and Yoneda et al. (2014) found that the enzyme β-glucosidase D2-BGL, a cellobiose degrader produced by *Chaetomella raphigera*, has potential for use in the biofuels industry. Several studies have also found different compounds in *Chaetomella* species with potential beneficial health properties. Lingham et al. (1993) and Singh et al. (1993), isolated the molecules chaetomellic acids A and B, which act by inhibiting farnesyl-protein transferase, an enzyme that changes Ras protein into an oncogenic factor. Gangadevi & Muthumary (2009) found another anticancer compound, taxol, a well-known and widely used drug, being produced by *Chaetomella raphigera*. Esumi et al. (2003) reported one *Chaetomella* isolate producing α-glucosidase inhibitor, a drug used to treat Type-2 diabetes.

Other relevant data and future recommendations

Due to its pleomorphic nature, many species in *Chaetomellales* are good examples of complex life cycles in fungi, although little is known about them. Nevertheless, they are good examples of the impacts of the "one fungus = one name" initiative (Hawksworth 2011, Taylor 2011, Johnston et al. 2014b), resulting in many taxonomic imbroglios which can be explored in teaching.

Increased sampling of genetic data is needed to resolve the taxonomic problems within the order, such as the incorporation of *Hainesia* and *Sclerotiopsis* into *Pilidium*, as suggested by Johnston et al. (2014b). Currently, the only sequences available for *Hainesia* species are ones from species

that have already been incorporated into other genera. No sequences for *Sclerotiopsis* are available on GenBank.

Helotiales **Nannf., Nova Acta Regiae Societatis Scientiarum Upsaliensis, Ser. 4, 8 (2): 68 (1932)**

= *Erysiphales* Gwynne-Vaughan
= *Cyttariales* Luttr. ex Gamundí
= *Medeolariales* Korf
Subphylum : *Pezizomycotina*
Class : *Leotiomycetes*
Subclass : *Leotiomycetidae*

Introduction

The taxonomy of *Helotiales* has been revised by molecular phylogenetics, with a switch from a classification based on morphology to one based on molecular phylogeny. Although some strong, highly resolved multi-gene and genome-based phylogenies are now available, missing from these studies are genetic data from many of the named taxa and from type material (only about 20% of the genera have DNA sequences from type material of the type species), and there remains a strong north temperate bias to taxon sampling (Quandt & Haelewaters 2021). Careful consideration of morphology in addition to the relationships suggested by phylogeny is also lacking from many of the phylogenetic studies. For example, Baral and co-authors (e.g., Baral et al. 2015) have shown that features of the paraphyses and asci in the living state are phylogenetically informative, and morphology strongly supported the revision of *Solenopeziaceae* and the division of this taxon into two families, *Solenopeziaceae* and *Tricladiaceae* (Johnston & Baschien 2020).

Helotiales is treated here in the sense of Johnston et al. (2019b) where both the genome scale and multigene phylogenies strongly support the broad *Helotiales* clade. This has consistently been supported in other recent multigene phylogenies (e.g., Partel et al. 2017, Haelewaters et al. 2021c, Mitchell et al. 2022). *Helotiales* is the largest order within *Leotiomycetes*, with 41 families, with the 471 genera making up 74% of those in *Leotiomycetes*, and more than 5000 species making up 79% of the named species (data from Wijayawardene et al. 2022a). Johnston et al. (2019b) estimated that this represents less than 10% of the actual diversity. Tian et al. (2024) introduced the latest family, *Neodictyocheirosporaceae*, to the order. The taxonomic diversity is reflected in a broad range of lifestyles i.e. saprobes, leaf and root endophytes, plant and animal pathogens, mycorrhizas and aquatic hyphomycetes.

History

Helotiales was established by Nannfeldt (1932), as part of his classification of the inoperculate discomycetes. The name was formally validated by Korf & Lizon (2000) following an earlier proposal by Carpenter (1988) to replace the invalid Nannfeldt name with *Leotiales*. The classification of Nannfeldt was widely in use until the mid-1990's, although with some additions to the six families recognised by Nannfeldt (Spooner 1987, Carpenter 1988). Some of the earliest rDNA-based phylogenies showed that cup-shaped ascomata typical of the inoperculate discomycetes have evolved independently several times. For example, the families *Orbiliaceae* and *Geoglossaceae*, accepted in *Helotiales* by Nannfeldt, appeared in early DNA-based phylogenies to be phylogenetically distant from other families he placed in *Helotiales* (Sugiyama 1998, Tehler et al. 2000), and this was clearly demonstrated by Wang et al. (2006b). *Orbiliaceae* is now placed in the class *Orbiliomycetes* (Eriksson et al. 2003a) and *Geoglossaceae* in *Geoglossales*. In contrast, other fungi which lacked cup-shaped ascomata were shown by molecular phylogeny to be closely related to *Helotiales*, including *Erysiphaceae*, the powdery mildews, traditionally placed in its own order *Erysiphales*. As noted by Hibbett et al. (2007), helotialean lineages such as *Erysiphales* and *Cyttariales*, if accepted as separate orders because of their distinctive morphology, result in a paraphyletic *Helotiales*.

Phylogenetic studies also showed that several groups of fungi known only from their asexual state belong in *Helotiales*, including the phialophora-like *Cadophora*, the root endophytic fungi in

Oidiodendron and several genera of aquatic hyphomycetes with their distinctive, multibranched conidia. Several of the aquatic hyphomycete genera are polyphyletic and whether the species that are *Helotiales* are phylogenetically related to the type species of their genera often remains uncertain (Johnston & Baschien 2020).

Johnston et al. (2019b) for the first time presented a phylogeny of *Leotiomycetes* based on genomes, and a second, more taxon rich, analysis based on up to 15 genes per specimen. Although this study has provisos on taxon coverage, on lack of data linked to type specimens, patchy gene coverage for some clades, and on being based solely on DNA-based phylogeny (without considering morphology), the analyses presented provide strongly supported basal clades across *Leotiomycetes* and resolve a clearly defined *Helotiales*. Ekanayaka et al. (2019a) provided family level names for some of the clades recognised by Johnston et al. (2019b) within *Helotiales* but left some unnamed. Hibbett et al. (2007) noted that future studies may accept a more restricted *Helotiales*, with recognition of additional orders based on current helotialean families. Johnston et al. (2019b) discussed the possibility of breaking the monophyletic *Helotiales sensu lato* into a series of smaller monophyletic orders, but to date this has not been followed in subsequent phylogenetic studies. In fact, Haelewaters et al. (2021c) formally placed *Cyttariales* and *Erysiphales* as synonyms of *Helotiales*, accepting both these taxa at the family level within *Helotiales*. The monotypic order *Medeolariales* has only rDNA sequences available; phylogenies based on ITS and on LSU both suggest an isolated position within *Helotiales* (Johnston et al. 2019b, suppl. data fig 2; unpubl. data) but this needs to be confirmed with additional genes. Several new orders have been proposed for *Leotiomycetes* since 2019 but these have been basal to *Helotiales* (Haelewaters et al. 2021c).

General description

Helotiales were traditionally characterised by the small, cup-shaped apothecia of the sexual state, the usually exposed hymenium comprising asci surrounded by sterile paraphyses. In most species, asci open through an apical pore surrounded by an amyloid ring. Some of the plant pathogens are more frequently observed from their asexual state, such as species of *Sclerotinia*, *Botrytis* and *Pezicula*. Following phylogenetic studies, it is now known that many species of *Helotiales* have been detected only from their asexual state, including some of the phialophora-like *Cadophora* spp. many of the aquatic hyphomycetes, the phylogenetically diverse chalara-like species, the mycorrhizal *Gamarada* and *Oidiodendron* species.

The sexual fruiting bodies of some taxa remain closed, historically creating confusion about their phylogenetic relationships. Examples include *Connersia* and *Pleuroascus* (*Pleuroascaceae*, prior to DNA sequencing thought to be *Pseudeurotiaceae* (Kirk et al. 2008a), a family now in *Thelebolales* (Johnston et al. 2019b)), *Myxotrichaceae* (previously *Onygenales* (Kirk et al. 2001)), the powdery mildews *Erysiphaceae* (previously *Erysiphales*), and *Bicornispora* (previously *Coryneliales* (adapted from Checa et al. 1996) (Fig. 160).

Families included in *Helotiales*

Amorphothecaceae Parbery
Arachnopezizaceae Hosoya, J.G. Han & Baral
Ascocorticiaceae J. Schröt.
Ascodichaenaceae D. Hawksw. & Sherwood
Bryoglossaceae Ekanayaka & K.D. Hyde
Calloriaceae Marchand
Cenangiaceae Rehm (= *Hemiphacidiaceae* Korf)
Chlorociboriaceae Baral & P.R. Johnst.
Chlorospleniaceae Ekanayaka & K.D. Hyde
Chrysodiscaceae Baral & Haelew.
Cordieritidaceae Sacc.

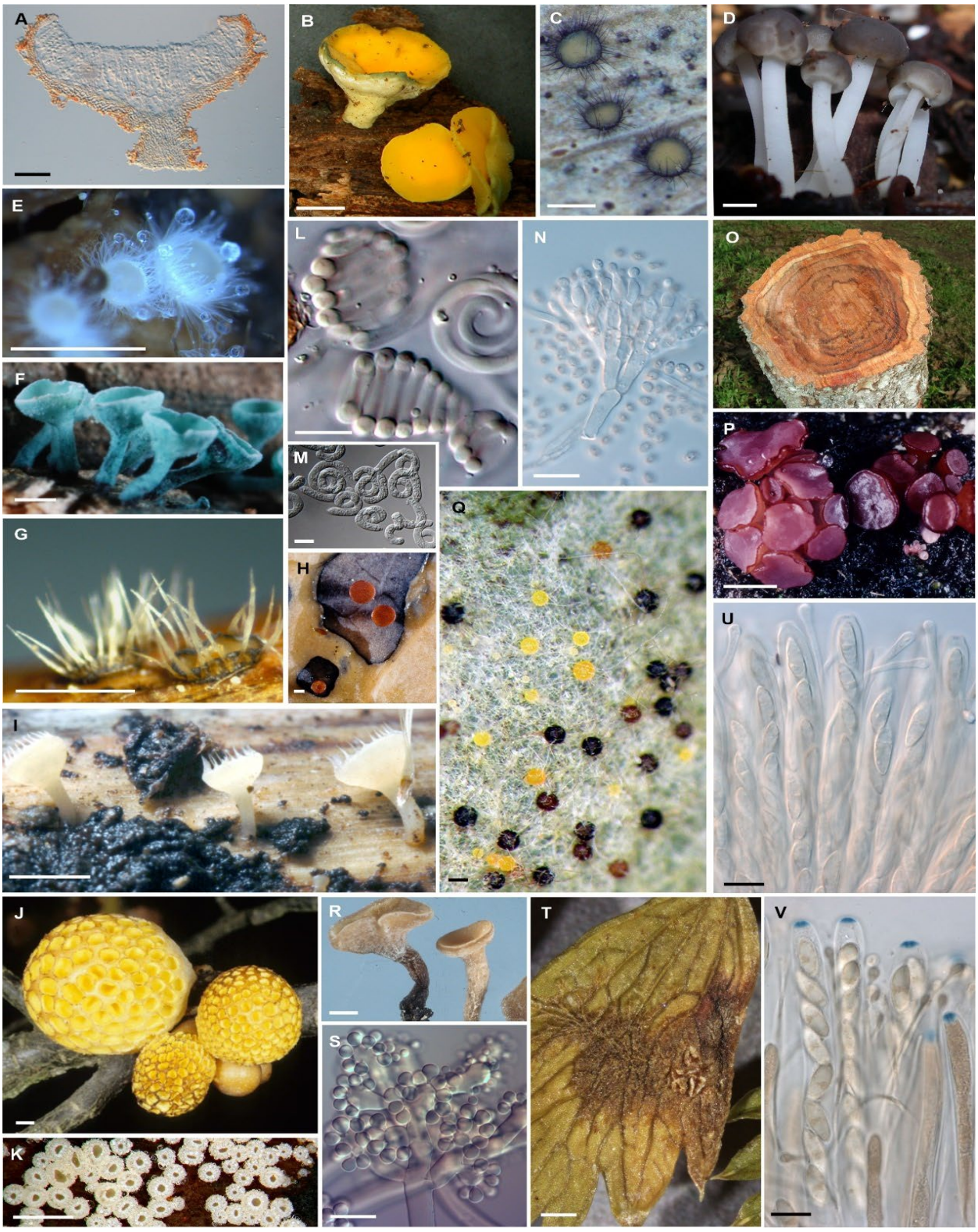


Figure 160 – *Helotiales* showing diversity of macromorphology, typical hymenium, examples of some sexual and asexual states, examples of some lifestyles. A Typical stalked, cup-shaped ascoma in vertical section (‘*Lanzia*’ *ovispora*, *Helotiaceae*, scale = 100 µm). B Glabrous, cup-shaped ascoma (unnamed species and genus, *Helotiaceae*, scale = 1 mm). C Ascoma with dark setae (unnamed *Hymenotorrendiella* sp., *Helotiaceae*, scale = 1 mm). D ‘*Chlorovibrissea’ albofusca* (*Helotiales* incertae sedis, scale = 1 mm). E *Lachnopsis* sp. (*Lachnaceae*, scale = 1 mm). F *Chlorociboria* sp. (*Chlorociboriaceae*, scale = 1 mm). G *Hispidula dicksoniae* (*Helotiaceae*, scale = 1 mm). H *Moellerodiscus coprosmae*, reddish apothecia developing within stromatic patches on host leaf (*Rutstroemiaceae*, scale = 1 mm). I *Cyathicula* sp. (*Helotiaceae*, scale = 1 mm). J *Cyttaria* cf. *gunnii*

(*Cyttariaceae*, scale = 1 mm). K '*Lachnellula' rhopalostylidis* (*Lachnaceae*, scale = 1 mm). L *Helicodendron* sp., aquatic hyphomycete asexual state (*Tricladiaceae*, scale = 10 µm). M *Helicodendron triglitziense*, aquatic hyphomycete asexual state (*Helotiales incertae sedis*, scale = 10 µm). N Asexual state of *Neobulgaria alba* (*Gelatinodiscaceae*, scale = 10 µm). O Vascular staining of *Actinidia* wood from where *Neobulgaria alba* culture was isolated. P *Ascocoryne* sp. (*Gelatinodiscaceae*, scale = 1 mm). Q *Erysiphe* necator, powdery mildew of grape with globose enclosed ascoma (*Erysiphaceae*, scale = 0.1 mm). R-S *Botrytis cinerea* sexual and asexual states (*Sclerotiniaceae*, scales = 1 mm, 10 µm). T *Pseudopeziza* sp. parasitic on *Anisotome aromatica* leaf (*Drepanopezizaceae*, scale = 1 mm). U '*Hymenoscyphus*' *metrosideri*, sterile paraphyses amongst the asci, and ascospores (*Helotiaceae*, scale = 10 µm). V *Ascocoryne* sp., asci with prominent amyloid pore, typical of many *Helotiales* (*Gelatinodiscaceae*, Scale bar = 10 µm).

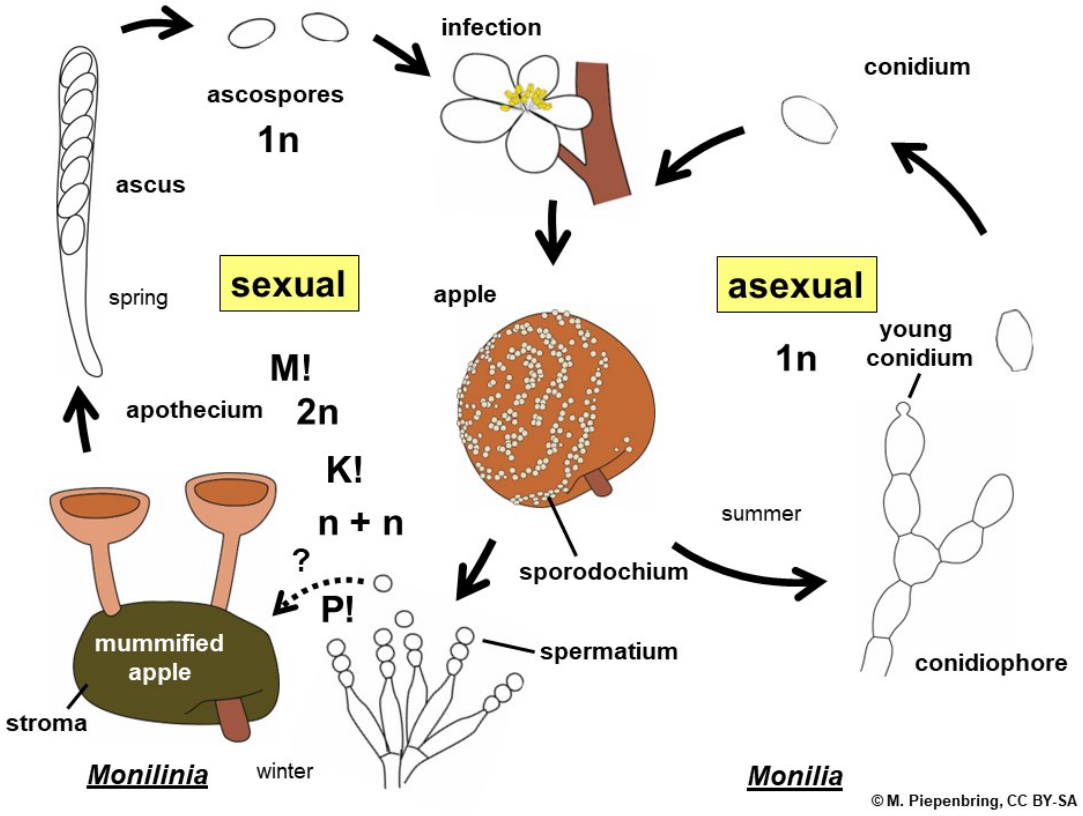


Figure 161 – Sexual and asexual life cycles of *Helotiales* (From Mycological teaching diagrams by Meike Piepenbring (2023)). Abbreviations: 1n = haploid, 2n = diploid, P! = plasmogamy, K! = karyogamy, M! = meiosis. Black and white circles represent haploid nuclei of different mating types, circles of both colors represent diploid nuclei.

Cyttariaceae Lév.
Dermateaceae Fr.
Discinellaceae Ekanayaka & K.D. Hyde
Drepanopezizaceae Baral
Erysiphaceae Tul. & C. Tul.
Gelatinodiscaceae S.E. Carp
Godroniaceae Baral
Hamatocanthoscyphaceae Ekanayaka & K.D. Hyde
Helotiaceae Rehm
Heterosphaeriaceae Rehm
Hyaloscyphaceae Nannf.

Hyphodiscaceae Ekanayaka & K.D. Hyde
Lachnaceae Raitv.
Leptodontidiaceae Hern.-Restr., Crous & Gené
Mitrulaceae Rchb.
Mollisiaceae Rehm (= *Loramycetaceae* Dennis ex Digby & Goos)
Myxotrichaceae Locq. ex Currah
Neodictyocheirosporaceae W.H. Tian, K.D. Hyde & Maharachch.
Neolauriomycetaceae Crous
Patellariopsidaceae Karun., Camporesi & K.D. Hyde
Pezizellaceae Velen. (= *Porodiplodiaceae* Crous; = *Bloxamiaceae* Locq.)
Pleuroascaceae Unter. & Réblová
Pyrenopezizaceae Velen. (= *Ploettnerulaceae* Kirschst.)
Rutstroemiaceae Holst-Jensen, L.M. Kohn & T. Schumach.
Sclerotiniaceae Whetzel
Solenopeziaceae Ekanayaka & K.D. Hyde
Tricladiaceae P.R. Johnst. & Baschien
Vandijckellaceae Sand.-Den.
Vibrisseaceae Korf

Helotiales genera *incertae sedis*
Aeruginoscyphus Dougoud
Algincola Velen.
Aphanodesmium Réblová & Hern.-Restr.
Aquadiscula Shearer & J.L. Crane
Aquapoterium Raja & Shearer
Arachnoscypha Boud.
Ascluella DiCosmo, Nag Raj & W.B. Kendr.
Ascoclavulina Otani
Asterocalycella Höhn. ex R. Kirschner
Belonioscyphella Höhn.
Benguetia Syd. & P. Syd.
Bioscypha Syd.
Blastosporium Z.F. Yu & H. Zheng
Brachyalara Réblová & W. Gams
Brefeldochium Verkley
Bulgariopsis Henn.
Cadophora Lagerb. & Melin
Caesiodiscus Holien & Suija
Cairneyella D.J. Midgley & N. Tran-Dinh
Capillipes R. Sant.
Capricola Velen.
Cashiella Petr.
Cejpia Velen.
Cenangiumella J. Fröhl. & K.D. Hyde
Chloroepilichen Etayo
Chlorospleniella P. Karst.
Chlorovibrissea L.M. Kohn
Chondroderris Maire
Ciliella Sacc. & P. Syd.
Cistella Quél.
Clathrosphaerina Beverw.
Clathrosporium Nawawi & Kuthub.

Coleosperma Ingold
Colipila Baral & Guy García
Comesia Sacc.
Cornuntum Velen.
Coronellaria (P. Karst.) P. Karst.
Criserosphaeria Speg.
Crocicreas Fr.
Crucellisporium M.L. Farr
Crumenella P. Karst.
Cryptohymenium Samuels & L.M. Kohn
Cryptopezia Höhn.
Dactylaria Sacc.
Dawsicola Döbbeler
Dematioscypha Svrček
Dermateopsis Nannf.
Didonia Velen.
Didymascella Maire & Sacc.
Discomycella Höhn.
Durella Tul. & C. Tul.
Encoeliopsis Nannf.
Episclerotium L.M. Kohn
Erikssonopsis M. Morelet
Eustilbum Rabenh.
Filosporella Nawawi
Gloeopeziza Zukal
Godroniopsis Diehl & E.K. Cash
Gorgoniceps (P. Karst.) P. Karst.
Grimmicola Döbbeler & Hertel
Grovesia Dennis
Helicocentralis Sri-indr., Chuaseehar., Boonyuen, K. Yamag., Suetrong & C.K.M. Tsui
Hemiglossum Pat.
Hydrocina Scheuer
Hyphoscypha Bres.
Hysteronaevia Nannf.
Hysteropezizella Höhn.
Involucroscypha Raitv.
Jacobsonia Boedijn
Korfia J. Reid & Cain
Lanceolata Ekanayaka & K.D. Hyde
Larissia Raitv.
Lasseria Dennis
Lemalis Fr.
Leohumicola N.L. Nickersen, Hambleton & Seifert
Libartania Nag Raj
Livia Velen.
Masseea Sacc.
Melanopeziza Velen.
Merodontis Clem.
Microdiscus Sacc.
Miricatena Punith. & Spooner
Mitrulinia Spooner
Monochaetiellopsis B. Sutton & DiCosmo

Mycoarthris Marvanová & P.J. Fisher
Neonematogonum Crous & Akulov
Neosatchmopsis Crous, M.A. Delgado & R.K. Schumach.
Obconicum Velen.
Orbiliopsis (Sacc. & D. Sacc.) Syd. & P. Syd.
Otwaya G.W. Beaton
Pachydisca Boud.
Parencoelia Petr.
Patinellaria H. Karst.
Peltigeromyces Möller
Pezolepis Syd.
Pezomela Syd.
Phacidiella P. Karst.
Phaeofabraea Rehm
Phragmonaevia Rehm
Piceomphale Svrček
Pleoscutula Vouaux
Podophacidium Niessl
Polydesmia Boud.
Polyphilus D.G. Knapp, Ashrafi, W. Maier & Kovács
Populomyces Hern.-Restr.
Potridiscus Döbbeler & Triebel
Pseudohelotium Fuckel
Pseudolachnum Velen.
Pseudomitrula Gamundí
Pseudopeltis L. Holm & K. Holm
Pseudotryblidium Rehm
Psilophana Syd.
Psychrophila M.M. Wang & Xing Z. Liu, nom. inval.
Pteromyces E. Bommer, M. Rousseau & Sacc.
Pubigera Baral, Gminder & Svrček
Radotinea Velen.
Rhizocladosporium Crous & U. Braun
Rhizothyrium Naumov
Rommelaarsia Baral & Haelew.
Roseodiscus Baral
Sageria A. Funk
Sambucina Velen.
Sarcomyces Massee
Sclerocrana Samuels & L.M. Kohn
Scutulopsis Velen.
Scytalidium Pesante
Sorokina Sacc.
Sorokinella J. Fröhl. & K.D. Hyde
Srinivasanomyces S. Rana & S.K. Singh
Stamnaria Fuckel
Stilbopeziza Speg.
Strossmayeria Schulzer
Themisia Velen.
Tovariella Syd.
Trichohelotium Killerm.
Triposporium Corda

Unguicularia Höhn.
Urceolella Boud.
Waltonia Saho
Woodiella Sacc. & P. Syd.
Xeromedulla Korf & W.Y. Zhuang
Zugazaea Korf, Iturr. & Lizoň

Evolution

Helotiales is the most derived of the orders of *Leotiomycetes* (Johnston et al. 2019b) but a lack of genomic data for basal *Leotiomycetes* clades, resulting a lack of support amongst the basal branches of the *Leotiomycetes* phylogeny, means that its relationship to the more basal clades in the class is unresolved (Quandt & Haelewaters 2021). The resolution of evolutionary relationships between families within *Helotiales* needs genome scale data (Johnston et al. 2019b). As genomes become more widely sampled across the order, a series of broad clades may become evident and useable, for example a 'sclerotinioid' clade made up of *Sclerotiniaceae*, *Rutstroemiaceae*, *Cenangiaceae* and *Chlorociboriaceae* (Johnston et al. 2019b). Multigene analyses suggest that *Cordieritidaceae* and *Cyttariaceae* may also belong in this clade (Haelewaters et al. 2021c), but additional genomes are needed to confirm this, and to confirm that such a scheme may be taxonomically useful across *Helotiales*.

Justification of order and problems

Helotiales is treated here in the sense of Johnston et al. (2019b) where both the genome scale and multigene phylogenies strongly support the broad *Helotiales* clade. This has consistently been supported in other recent multigene phylogenies (e.g., Partel et al. 2017, Haelewaters et al. 2021c, Mitchell et al. 2022). However, taxonomic issues within *Helotiales* remain to be resolved, especially in relation to limited taxon sampling.

More genes from more specimens. Although multi-gene phylogenies can be used to reliably determine whether *Leotiomycetes* genera belong in *Helotiales*, relationships within the order remain fluid. Even rDNA-based phylogenies can often place a genus within *Helotiales* reasonably confidently (Johnston et al. 2019b). However, deeper branches in the *Helotiales* phylogeny require multiple genes to resolve, or ideally genomes (Johnston et al. 2019b, Quandt & Haelewaters 2021). One of the larger taxonomically problematic clades contains morphologically and phylogenetically diverse taxa within a clade discussed by Johnston et al. (2019b) as *Stamnaria* lineage/Han Clade 9/*Vandijckellaceae*. This unnamed clade was first recognised by Han et al. (2014) and includes type species of *Calloriaceae* and *Vandijckellaceae*. A careful combination of morphological and phylogenetic analysis is needed to resolve sensible family-level limits within this clade.

Accurately identified specimens. To relate modern phylogenies back to the classical taxonomy of the order requires the specimens being used to be accurately identified, especially those being used to represent the type species of a genus. For older genera, with existing sequencing technologies, this requires either epitypes to be selected, something barely started for *Leotiomycetes*, or absolutely accurate identification of modern specimens. Of the 471 genera listed as *Helotiales* in Wijayawardene et al. (2022a), 110 have DNA sequences from specimens identified as the type species of a genus, 70 of these curated as part of the RefSeq resource in GenBank (data from https://www.ncbi.nlm.nih.gov, accessed 29 August 2022). Only 21 genera of *Helotiales* have species that have been epitypified, of these only four represent the generic type species (data from MycoBank, http://www.mycobank.org, accessed September 2022).

More complete geographic coverage. For historical reasons, most fungal classifications were developed by mycologists based in north temperate regions, and traditionally have largely reflected the diversity of fungi found in those regions (Quandt & Haelewaters 2021). This bias continues largely to this day (Quandt & Haelewaters 2021), although it is changing (Hyde et al. 2020c, 2024b). Within *Helotiales*, there are family level clades with their diversity concentrated in the Northern Hemisphere (e.g., *Sclerotiniaceae*, *Cordieritidaceae*) and others concentrated in the Southern

Hemisphere (e.g., *Cyttariaceae*, *Chlorociboriaceae*) (Wang et al. 2006b). Recent studies in poorly sampled regions have revealed some previously unknown family level clades, for example, species in the genus *Cryptohymenium*, form what is probably the genetic equivalent of a family, basal in *Helotiales*, sister to *Cenangiaceae* and *Cordieritidaceae* (Johnston et al. 2022). This matters because taxon sampling can strongly influence the results of DNA based phylogenetic analyses. If geographic bias results in phylogenetic bias, accurate and stable phylogenies will remain a dream irrespective of advances in sequencing technologies.

Significance

Ecological and economic roles

Helotiales have diverse lifestyles on plants, in soil, water or in the air. This may help explain that they are often amongst the most detected group of Ascomycetes in studies sampling from DNA extracted directly from environmental samples from both soil (Tedersoo et al. 2021, Vašutová et al. 2021) and leaves (Johnston et al. 2017, Wemheuer et al. 2019).

Taxa associated with freshwater are often only known from an asexual morph as “aquatic hyphomycetes". They have been found in marine environments, including sponges in the Antarctic. Mycorrhizas, including those associated with ericoid plants, are formed by some species of *Mollisiaceae*, *Hyaloscyphaceae*, and *Myxotrichiaceae* (Vrålstad et al. 2002, Jaklitsch et al. 2016a). Endophytes have been found in several lineages of *Dermateaceae*, *Gelatinodiscaceae*, *Helotiaceae*, and *Phacidiaceae* (Jaklitsch et al. 2016a). Some of the species isolated from living leaves as endophytes are host-specialised, the same species switching to a saprobic lifestyle after the host leaf has fallen, apothecia developing on the fallen, dead leaf tissue (Johnston et al. 2014a). Five families are exclusively plant pathogenic (*Cyttariaceae*, *Erysiphaceae*, *Drepanopezizaceae*, *Medeolariaceae*, and *Sclerotiniaceae*). Despite this great diversity, the two predominant lifestyles are saprobic and parasitic, with both strategies coexisting in most families. The saprobic lifestyle appears to be the most common, more than half of the families having saprobic members growing on dead or decaying plant material (Jaklitsch et al. 2016a).

Chemical diversity

The wide diversity of lifestyles amongst *Helotiales* suggests a high potential for the production of useful metabolites. Examples include species known to produce clinically important compounds, such as the antifungal echinocandins including pneumocandin B (Vaca & Chavez 2019, Hüttal 2021). *Calycina marina*, a marine species that inhabits decomposing alga, is being studied as a candidate for algal-based biofuel production (Hagestad et al. 2021).

Other relevant data and future recommendations

Resolution of *Helotiales* classification at the family level is important to better understand the relationship between phylogeny and lifestyle. With plant and animal pathogens, putatively mycorrhizal fungi, root and leaf endophytes, and saprobes mixed throughout the *Helotiales* phylogeny, more intensive genome sampling will not only help clarify the classification but also provide data to better understand the genetic basis of differences in lifestyle. Some of the larger genera such as *Hymenoscyphus* and *Cadophora* are known to be polyphyletic, resolution of the taxonomy of genera such as these requires intensive genetic and morphological study along with epitypification of the type species. Families such as *Calloriaceae* and *Vandijckellaceae* remain poorly understood phylogenetically and several clades recognized in current phylogenies remain unnamed. More intensive sampling from under-explored parts of the world may provide the data needed to clarify the phylogeny of the order.

***Lahmiales* O.E. Erikss., Mycotaxon 27: 357 (1986)**

Subphylum : *Pezizomycotina*
Class : *Leotiomycetes*

Introduction

Lahmiales, an order in *Ascomycota*, accommodates only the family *Lahmiaceae* with its sole genus *Lahmia*, which comprises two species (Wijayawardene et al. 2022a). *Lahmiales* was introduced and described by Eriksson (1986) in *Dothideomycetes*, which was then transferred to *Lecanoromycetes* (Raitviir & Spooner 1994), but Baral (2016) suggested including this order in *Leotiomycetes*. According to Baral (2016), *Lahmiales* was placed in *Leotiomycetes* based on the similar ascomatal morphologies shared with *Rhytismatales*. However, it differs from the latter by having bitunicate asci and lacking clypeate stroma. *Lahmia*, introduced by Koerber (1865), accommodated six species (Rehm 1900), among which four were transferred to other genera (Ciferri & Tomaselli 1953, Fries 1961, Timdal 1991), leaving only *Lahmia kunzei* and *L. waghornii* (Species Fungorum 2025). *Lahmia* is mainly distributed on the bark of *Populus* trees in northern Europe and North America and is often associated with *Rhytidiella baranyanyi* (Rehm 1900, Funk 1976, Eriksson 1986, Quandt & Haelewaters 2021).

History

Koerber (1865) initially observed and documented *Lahmia kunzei* and *L. fueistingii*, but the latter was reassigned to *Arthrorhaphis grisea* (Fries 1860, Species Fungorum 2025). Nannfeldt (1932) treated *Lahmia* as a lichenized species in *Lecanorales*, for which Rehm (1896) opposed as the species gave negative results in the iodine test. Koerber (1865) once included *Lahmia* in discolichens, but the excipular cells of *Caliciales* published by Tibell (1984) did not fit with the asci and ascospores characteristics of *Lahmia*. Saccardo listed *Lahmia piceae*, which was then synonymized with *Lahmiomyces piceae* (Ciferri & Tomaselli 1953). *Lahmia plumbina* was listed in Keissler (1930) but then transferred to *Toninia plumbina* (Timdall 1991). Rehm (1900) introduced *Lahmia waghornii*, which is accepted to this date, along with *Lahmia kunzei* (Species Fungorum 2025).

Lahmia was known as *Parkerella* when Funk (1976) found it as a secondary colonizer along with *Rhytidiella baranyanyi*, the fungus causing the cork bark disease on *Populus tremuloides*. Funk (1976) included *Parkerella populi* in *Coronophorales* (*Sordariomycetes*) due to its similarity to *Thaxteria* by having turbinate ascomata, long-stalked asci and 3-septate ascospores. However, Eriksson (1986) pointed out the difference in ascomatal tissues. *Parkerella* was characterized by scleroplectenchymous cells, while *Thaxteria* has pseudoparenchymatous cells; hence, *Parkerella* was believed to be conspecific with *Lahmia kunzei*. Subsequently, Eriksson (1986) established *Lahmiales* and *Lahmiaceae* to accommodate *Lahmia* with *Lahmia kunzei* as the type species.

General description

The sexual morphs of *Lahmiaceae* have perithecial to apothecial ascomata, stalked on various thallus-like structures once thought to be lichenized (Nannfeldt 1932, Eriksson 1986). Their ascomata vary from turbinate to cup-shaped structures (Funk 1976, Rehm 1900, Eriksson 1986), and the ascomatal walls composed of hyphal cells of *textura intricata*. These scleroplectenchymous walls are filled with gelatinous materials and melanized on the hyphal surface (Eriksson 1986). The hamathecium in young ascomata consists of filiform paraphysoids stretched between and above the asci; the upper part of the hamathecium produces paraphyses-like filaments with free, slightly swollen tips (Eriksson 1986). Asci are clavate with a long base and bitunicate, composed of thin exotunicata and endotunicata, which become thickened after ascospore ejection (Eriksson 1986). Ascospores are hyaline, crescent-shaped, and septate (Rehm 1900, Eriksson 1986). The sexual morph is only reported by Funk (1976).

Sexual morph: *Ascomata* perithecial to apothecial, erumpent, turbinate, black, swell in the water, with stipitate. *Excipulum* composed of *textura intricata* to *epidermoidea*. *Hamathecium* comprises filiform paraphysoids between and above the asci, with the uppermost part consisting of paraphyses-like structures with slightly swollen apices. *Paraphysoids* swollen at the tips. *Asci* 8-spored, bitunicate, clavate, amyloid. *Ascospores* crescent-shaped, 1–4-septate, contorted, hyaline (Fig. 162). Asexual morph: Short phialides bearing falcate conidia (adapted from Eriksson 1986).

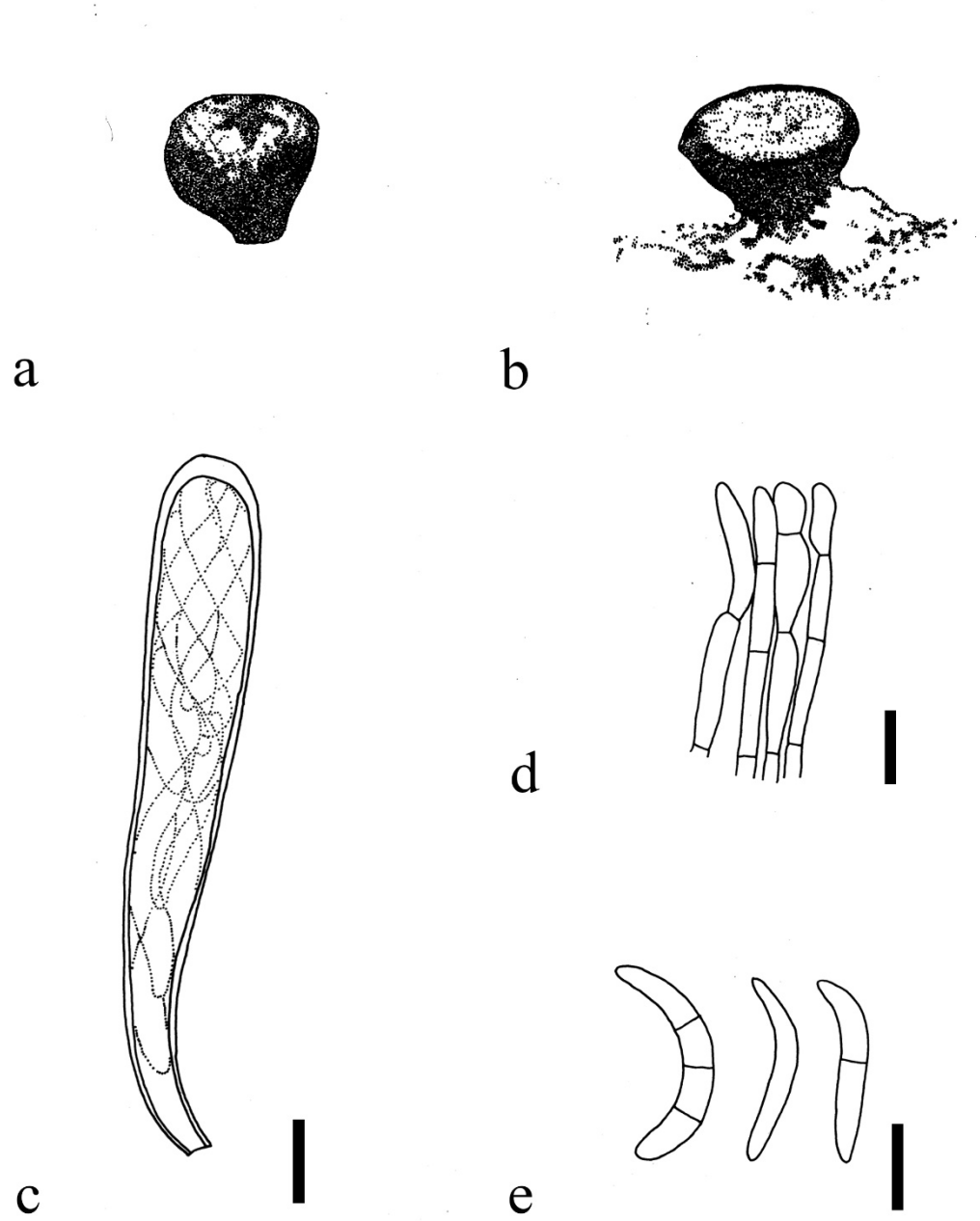


Figure 162 – Morphology of *Lahmia kunzei.* a, b Ascomata. c Ascus. d Tips of paraphysis-like structures. e Ascospores (redrawn from Eriksson 1986). Scale bars: a, b = 35 µm, c–e = 10 µm.

Families included in *Lahmiales*

Lahmiaceae O. Eriksson

Evolution

Eriksson (1986) suggested that *Lahmiales* is a monotypic family based on its distinct morphology. No sequence data of *Lahmia* are available; hence, the phylogenetic evolutionary relationship is unknown.

Justification of order and problems

Lahmia is previously described as a lichenized species due to the presence of ascomata on tissue-like structures similar to those of *Lecanorales* (Nannfeldt 1932) and apical structures similar to *Odontotremataceae* (Raitviir & Spooner 1994). Some mycologists suggested that *Lahmia* should belong to *Dothideomycetes* based on its rubbery ascomata and bitunicate asci (Raitviir &

Spooner1994). Baral (2016) treated this taxon in *Leotiomycetes*, citing the similarities of its ascomatal morphology with *Rhytismatales*, even though *Lahmia* is distinct in having bitunicate asci and lacking clypeate stroma. *Lahmiales* is one of the least studied orders in *Ascomycota*, and the lack of molecular data makes its phylogenetic placement uncertain and ambiguous (Quandt & Haelewaters 2021). New findings are needed to address the phylogenetic and taxonomic issues of this group.

Significance

Ecological and economic roles

Lahmia kunzei have been reported commonly in its sexual morph from Canada, and in association with *Populus* barks (Eriksson 1986), along with *Rhytidiella baranyanyi*, the fungal pathogen causing cork-bark disease on *Populus* (Funk & Zalasky 1975, Funk 1976). However, the role and the impact of *Lahmia kunzei*, (= *Parkerella populi*), was not known ecologically and economically until this date. *Lahmia fuckelii* was another *Lahmia* species which was first described by Rehm (1896) growing on rotten oak and willow trunk in German. However, additional information on ecological and economic roles is unknown since it was first described.

Chemical diversity

The secondary metabolite diversity of *Lahmia* species has been overlooked; hence, there is no data regarding what chemical substances these taxa synthesize.

Other relevant data and future recommendations

Since all reference studies of specimens of *Lahmia* are dated, they have overlooked phylogeny, and chemical diversity. The lack of molecular data for *Lahmia* species leads to uncertain delineation (Quandt & Haelewaters 2021). New collections and investigations on *Lahmia* species are required for better taxonomic and phylogenetic resolution as well as future conservation.

***Lauriomycetales* Hern.-Restr., R.F. Castañeda & Guarro, Studies in Mycology 86: 83 (2017)**

Subphylum : *Pezizomycotina*
Class : *Leotiomycetes*

Introduction

Lauriomycetales is a saprobic order in *Leotiomycetes* with one family, one genus, comprising 11 species to date (Castañeda Ruiz & Kendrick 1990, Crous & Wingfield 1994, Somrithipol et al. 2006, 2017, Somrithipol & Jones 2007, Liu et al. 2015a, Hernandez-Restrepo et al. 2017, Barreto et al. 2023). *Lauriomycetales* was established by Hernandez-Restrepo et al. (2017) based on morphological studies and phylogenetic analyses, with the newly introduced *Lauriomycetaceae* as its type family. *Lauriomycetaceae* was a monotypic family (Castañeda Ruiz & Kendrick 1990, Crous & Wingfield 1994, Somrithipol et al. 2006, 2017, Somrithipol & Jones 2007, Liu et al. 2015a, Hernandez-Restrepo et al. 2017), comprising *Lauriomyces* as the type genus, which was erected by Castañeda Ruiz & Kendrick (1990). Many phylogenetic studies have confirmed *Lauriomycetales* as a monophyletic order in *Leotiomycetes* (Hernandez-Restrepo et al. 2017, Somrithipol et al. 2017, Ekanayaka et al. 2019a, Haelewaters et al. 2021c, Barreto et al. 2023).

History

Hernandez-Restrepo et al. (2017) studied the morphology and phylogenetic relationships of *Lauriomyces* taxa and found similar conidiogenesis and conidia to *Haplographium*, which is phylogenetically distant in *Leotiomycetes* based on the LSU phylogeny. Hence, *Lauriomycetales* and *Lauriomycetaceae* were erected to accommodate *Lauriomyces* (Hernandez-Restrepo et al. 2017). The phylogenetic relationships of *Lauriomycetales* have been studied since the order was established. Based on the LSU phylogeny, Hernandez-Restrepo et al. (2017) showed a fully supported independent lineage for *Lauriomycetales* basal to the *Helotiales*. Somrithipol et al. (2017) relied on the combined phylogeny of SSU, LSU, and 5.8S rDNA sequences to confirm the position of

Lauriomycetales in *Leotiomycetes*. Subsequent studies re-confirmed the results of Hernandez-Restrepo et al. (2017) and recognized *Lauriomycetales* as a basal order in *Leotiomycetes* (Ekanayaka et al. 2019a, Haelewaters et al. 2021c, Barreto et al. 2023).

General description

Sexual morph: Unknown. Asexual morph: *Conidiophores* macronematous, mononematous, developing a complex, branched conidiogenous apparatus at the apex. *Conidiogenous* cells blastic, discrete, hyaline. *Ramoconidia* in 1 or several tiers, hyaline, smooth. *Conidia* in acropetal chains, hyaline, smooth. (adapted from Hernandez-Restrepo et al. 2017) (Figs. 163, 164).

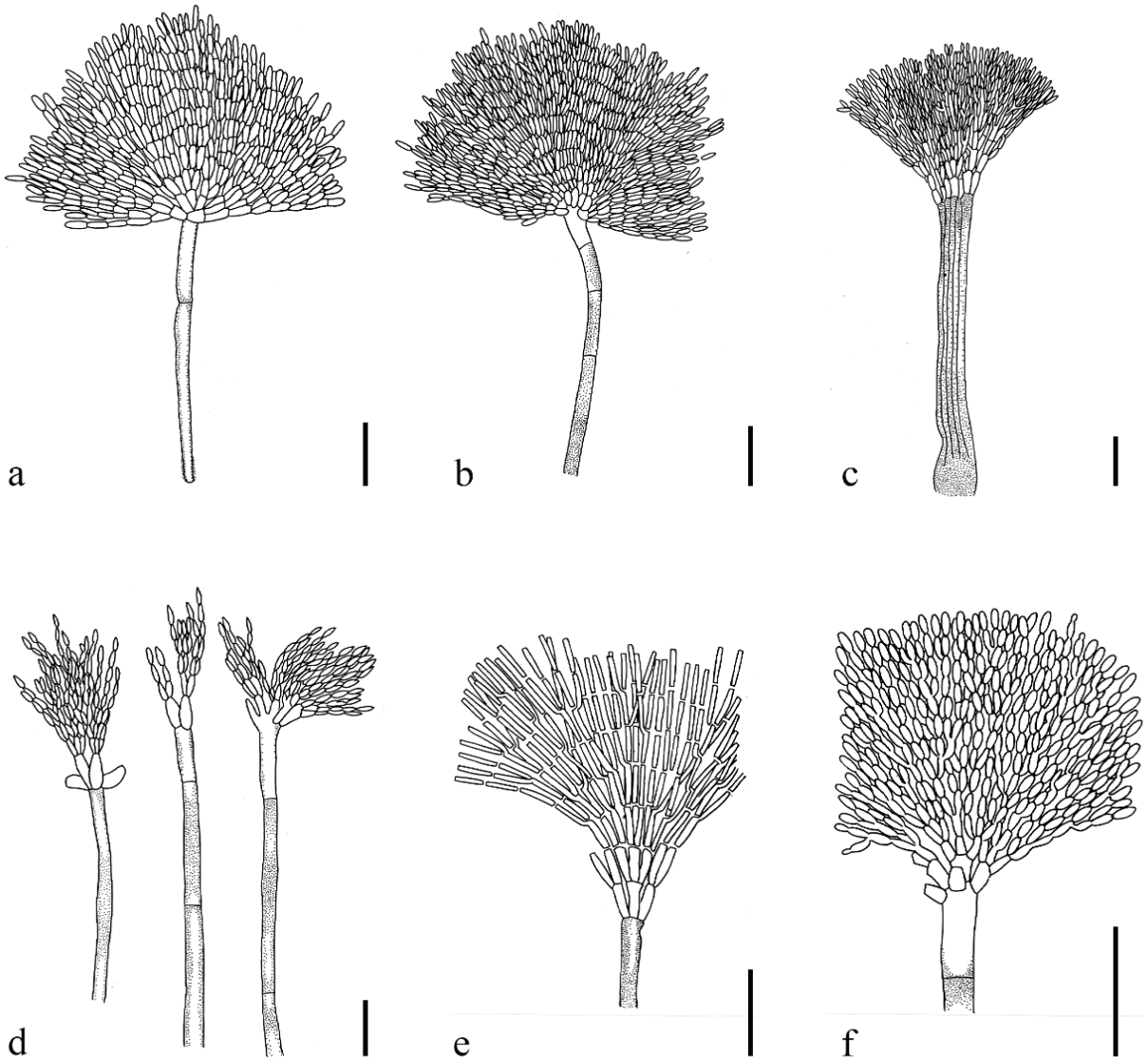


Figure 163 – Conidiophore morphology of *Lauriomycetales.* a *Lauriomyces basitruncatus.* b *L. acerosus.* c *L. synnematicus.* d *L. glumateus.* e *L. cylindricus.* f *L. ellipticus* (drawn or redrawn from Somrithipol & Jones 2007, Liu et al. 2015a, Somrithipol et al. 2017). Scale bars: a–f = 20 µm.

Families included in *Lauriomycetales*

Lauriomycetaceae Hern.-Restr. R.F. Castañeda & Guarro

Evolution

Recent phylogenetic studies showed *Lauriomycetales* as a basal lineage in *Leotiomycetes*, and was an early diverging lineage within *Leotiomycetes* (Ekanayaka et al. 2019a, Haelewaters et al. 2021c, Barreto et al. 2023).

Justification of order and problems

Lauriomyces was lectotypified with *Lauriomyces pulcher* (Castañeda Ruíz & Kendrick 1990). As the sequences are lacking for the type species, Hernandez-Restrepo et al. (2017) constructed their phylogeny with only the sequences from *L. heliocephalus* and *L. bellulus*. Later, many authors also studied the phylogenetic relationships of *Lauriomyces*, but they also lacked the sequences for the lectotype species (Somrithipol et al. 2017, Ekanayaka et al. 2019a, Haelewaters et al. 2021c, Barreto et al. 2023). Therefore, it is necessary to collect fresh specimens and obtain sequences for *Lauriomyces pulcher* to confirm the placement of the type species in the phylogeny.

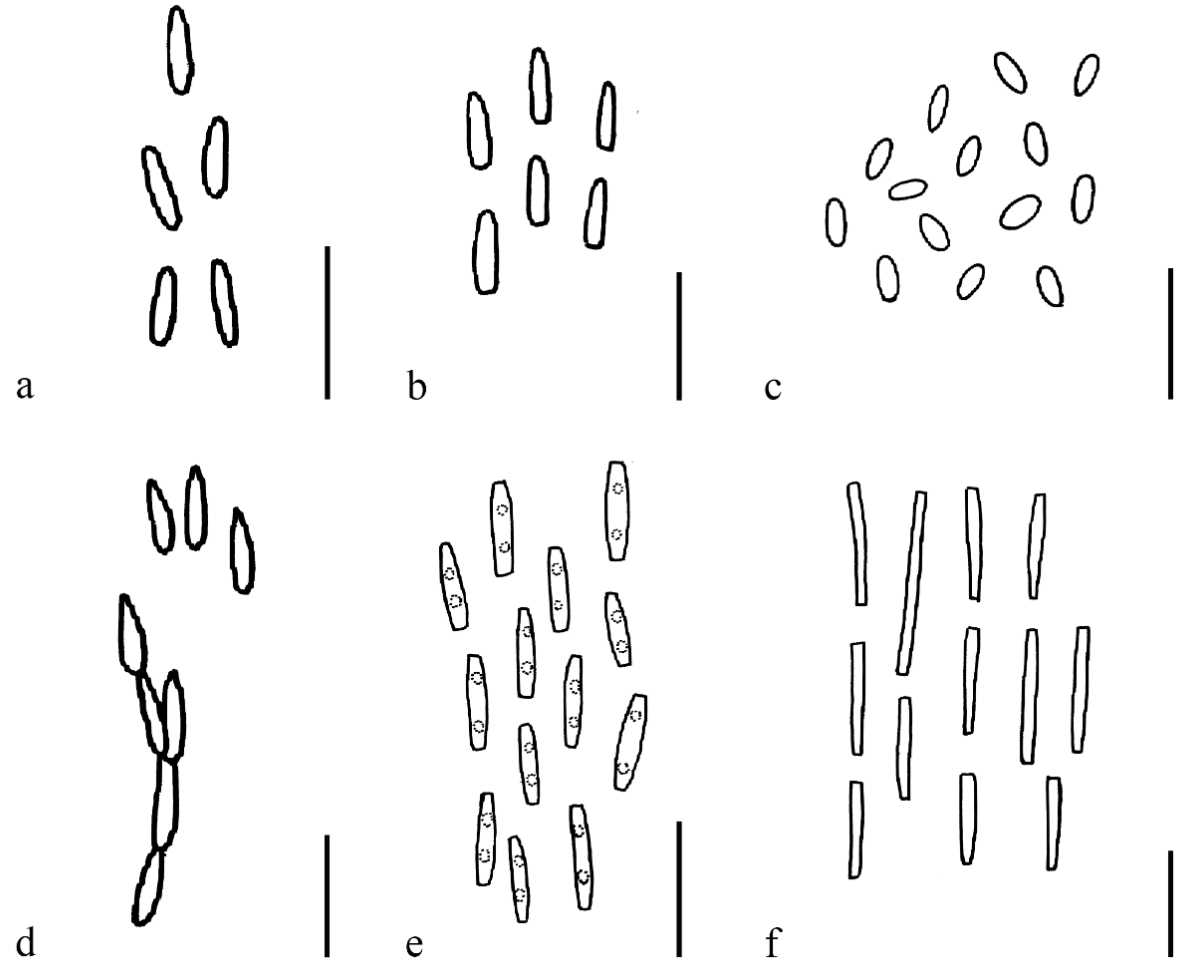


Figure 164 – Conidial morphology of *Lauriomycetales*. a *Lauriomyces acerosus*. b *L. basitruncatus*. c *L. ellipticus*. d *L. glumateus*. e *L. synnematicus*. f *L. cylindricus* (adapted from drawn or redrawn from Somrithipol & Jones 2007, Liu et al. 2015a, Somrithipol et al. 2017). Scale Bars: a–f = 10 µm.

Significance

Ecological and economic roles

Lauriomycetales exhibits a cosmopolitan distribution. Within this order, most species grow mainly on dead leaves of *Coccoloba uvifera*, with some on dicotyledon species. Notably, *L. bellulus* was found on cupules of *Castanea sativa*, while *L. ellipticus* and *L. sakaeratensis* were found on decaying fruits (Castañeda Ruiz & Kendrick 1990, Crous & Wingfield 1994, Somrithipol et al. 2006, 2017, Somrithipol & Jones 2007, Liu et al. 2015a, Hernandez-Restrepo et al. 2017, Quandt & Haelewaters 2021).

Chemical diversity

It has been reported that *Lauriomyces bellulus* SANK 26899 can produce haplofungins, which is a novel inositol phosphorylceramide synthase inhibitor (Ohnuki et al. 2009).

Other relevant data and future recommendations

Lauriomyces bellulus (SANK 26899) was reported to produce haplofungins (Ohnuki et al. 2009). There were comprehensive studies on the taxonomy, secondary metabolites, and their bioactive properties of *L. bellulus* (SANK 26899), specifically haplofungins, their physicochemical properties, and planar structure (Ohnuki et al. 2009). However, the synthesis mechanism of haplofungins and their regulation mechanisms are yet to be discovered.

Leotiales **Korf & Lizoň, Czech Mycology 52(4): 256 (2001)**

Subphylum : *Pezizomycotina*
Class : *Leotiomycetes*
Subclass : *Leotiomycetidae*

Introduction

Leotiales was introduced by Korf & Lizon (2001) for a single-family *Leotiaceae* to accommodate the genera *Calloriopsis*, *Gelatinopsis*, *Gelatinopulvinella*, *Geocoryne*, *Neobulgaria* and *Pezoloma* with the generic type *Leotia*. However, the order name *Leotiales* was originally proposed and invalidly published by Carpenter (1988).

History

Carpenter (1988) proposed *Leotiales* for inoperculate discomycetes based on the illegitimate name *Helotiaceae*, in contravention to Art. 17.1. The name was proposed to replace the ordinal name *Helotiales* Nannf. which was based on the invalid generic name *Helotium* Pers., was a later homonym of the basidiomycete genus *Helotium* Tode (Donk 1962). Korf (1973) adopted *Leotiaceae*, based on *Leotia* Pers., to include discomycetes that were previously placed in *Helotiaceae*. Eriksson (1982) and Eriksson & Hawksworth (1986c) accepted Korf's treatment and accepted the name *Leotiaceae* and rejected *Helotiaceae*. However, this classification was not accepted in Hawksworth et al. (1983b). Korf (1986) formally proposed to reject *Helotium* Tode because it has been widely used for a taxon not including its type, and the family name *Helotiaceae* also proposed not to be used because of the illegitimate generic name *Helotium* Pers. However, the ordinal name lacked either a Latin description or diagnosis or reference to a previously and effectively published Latin description or diagnosis (International Code of Botanical Nomenclature, Art. 36.1). Therefore, the name *Leotiales* was not validly published. Korf & Lizon (2001) found that few genera centered around *Leotia* Pers., which have typically been placed in the *Helotiales*, deserve ordinal recognition, and recognized *Leotiaceae* as a separate family from *Helotiaceae* and established *Leotiales* for *Leotiaceae*. Baral (2016) accepted only *Geoglossaceae* and *Leotiaceae* under *Leotiales*. Further, *Geoglossales* was treated under *Leotiales* without accepting it as a separate order due to morphological similarities between *Geoglossaceae* and *Leotiaceae,* despite they being genetically distinct. *Tympanidaceae* was previously placed in *Phacidiales* and Ekanayaka et al. (2019a) accepted this order under *Leotiales* based on the phylogeny. Johnston et al. (2019b) provided a detailed phylogenetic classification with broad taxon sampling of *Leotiomycetes* and accepted *Leotiaceae*, and *Tympanidaceae* with a newly established family *Mniaciaceae* which was introduced for *Mniaecia* lineage which formed a sister clade relationship to the extant families of *Leotiales*. *Lichinodiaceae* was established to accommodate a single lichenized genus *Lichinodium* by Prieto et al. (2019) in a separate order *Lichinodiales* in *Leotiomycetes*. Quandt & Haelewaters (2021) suggested the possibility of combining the order under *Leotiaceae*. Subsequently, Haelewaters et al. (2021c) combined this order under *Leotiales*. The order presently accommodates four families including *Leotiaceae*, *Lichinodiaceae*, *Mniaciaceae*, and *Tympanidaceae* with eight genera treated under *Incertae sedis*.

General description

Leotiales comprised inoperculate discomycetes and was characterized by apothecial ascomata, ectal excipulum composed of *textura intricata* to *textura porrecta* immersed in a copious gel in the outermost layer, outermost layer sometimes restricted to a basal pad of gel at the base of the stipe or only part way up the flanks of the apothecia, inner layer of thin-walled hyphae or a cellular tissue not in a gel, and a medullary layer of hyphae again immersed in a gel and the asexual morph is reported in Pycnidial or Hyphomycetous states (Ekanayaka et al. 2019a).

Sexual morph: *Ascomata* clavate-stipitate, gelatinous or not, with light to dark colors, with an elongate or pileate fertile part, opening in the prohymenial phase. *Stipe* smooth or densely covered with squamules. *Ectal excipulum* in stipe of *textura porrecta*, crystals absent. *Paraphyses* consistently without VBs (refractive vacuolar bodies). *Asci* with conical apex, mostly with a large amyloid ring or inamyloid, exceptionally entire ascus wall amyloid. *Ascospores* ellipsoid to vermiform, homo- to heteropolar, 0- to multiseptate, hyaline or brown, smooth, always with a high lipid content, without sheath, not easily germinating. Asexual morph: *Pycnidial* or hyphomycetous. *Pycnidia* uni- or multilocular. *Hyphomycetes* synnematal. *Conidiogenesis* phialidic. *Conidia* hyaline, ellipsoid, filiform, cylindric or allantoid, sometimes curved and 0–3-septate (adapted from Groves 1954, Funk 1979, Ekanayaka et al. 2019a) (Fig. 165).

Families included in *Leotiales*

Leotiaceae Corda
Lichinodiaceae M. Prieto, M. Schultz, Olariaga & Wedin
Mniaeciaceae Baral
Tympanidaceae Baral & Quijada

Leotiales genera *incertae sedis*
Alatospora Ingold
Aotearoamyces P.R. Johnst., J.A. Cooper & Quijada
Calyptrozyma Boekhout & Spaay
Flagellospora Ingold
Gorgomyces M. Gonczol & Revay
Mycosymbioces J.L. Frank
Pallidophorina S. Bien & Damm
Scolecoleotia H.B. Jiang, Phookamsak & K.D. Hyde
Variabilispora S. Bien, C. Kraus & Damm

Evolution

The evolution of *Leotiales* needs further study. Verkley (1994) studied the ultrastructural morphology of the ascus apical apparatus in *Leotia lubrica* and some *Geoglossaceae*. The small fruiting bodies were dominant in pathogens such as *Tympanidaceae* and *Mniaeciaceae*, but large fruiting bodies evolved in ectomycorrhizal lineages such as *Leotia* (Johnston et al. 2019b).

Justification of order and problems

In the recent outline, several genera were included and excluded from *Leotiales*. A monotypic genus *Mycosymbioces* was introduced to accommodate a mushroom parasite *M. mycenophila* and was treated under *Rhytismatales* genera *incertae sedis* (Wijayawardene et al. 2022a) and is accepted under *Leotiales* genera *incertae sedis* based on ITS sequence data. *Claussenomyces* was accepted under *Tympanidaceae* and is treated under *Leotiomycetes* genera *incertae sedis* in Wijayawardene et al. (2022a). Additional genes and taxa, and careful consideration of morphology, are needed to develop a stable classification

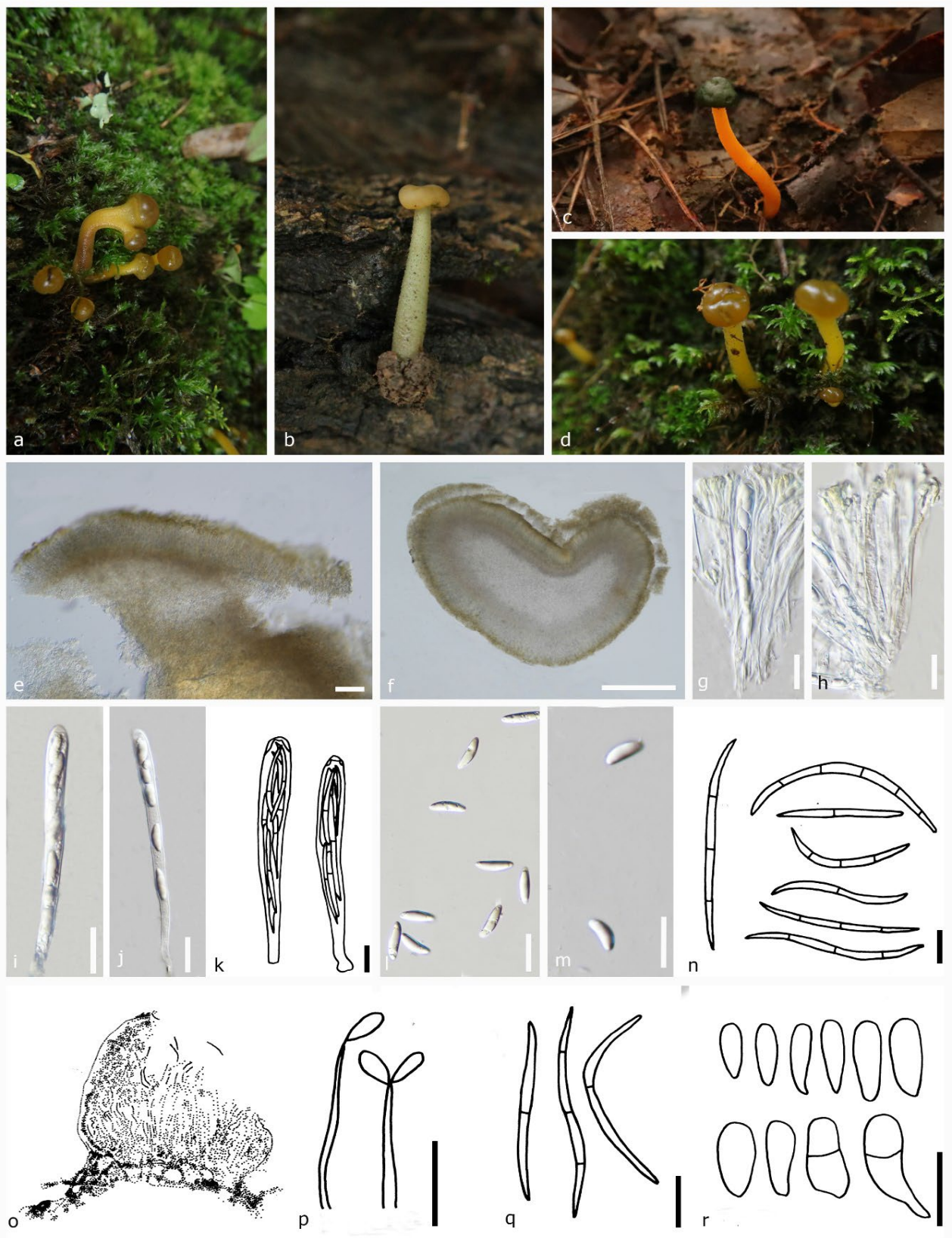


Figure 165 – Ascomata morphology of *Leotiales* (a–d *Leotia* sp.). Vertical section through ascoma (*Leotia* sp.). Paraphyses (*Leotia* sp.). i–k Asci (i, j *Leotia* sp., k *Duvandiella alni*). Ascospores (l, m *Leotia* sp., k *Duvandiella alni*). o Conidiomata (*Gelatinosporium griseo-lanatum*). p Conidiophore *Mycosymbioces mycenophila*. q Conidia and Conidiospores (q *Duvandiella alni*, r *Mycosymbioces mycenophila*) (redrawn from Groves 1954, Funk 1979, Edwards et al. 2020). Scale bars: e = 100 µm, f =500 µm, g–m = 20 µm, k, n, q = 10 µm, O x 150.

Significance

Ecological and economic roles

The taxa are reported as saprobe, pathogens, liverwort parasites, lichenized and mycorrhizal fungi (Quandt & Haelewaters 2021, Lestari et al. 2023). The discomycetous species *Mniaecia jungermanniae* has been reported as a pathogen on *Cephalozia*, *Diplophyllum* and *Scapania* from Belgium (Raspé & Sloover 1998, Pressel & Ducket 2011) and *Pragmopora pithya* is reported as a pathogen on Douglas fir from the USA (Funk 1975).

Chemical diversity

The chemical diversity of *Leotiales* is poorly studied.

Marthamycetales P.R. Johnst. & Baral, IMA Fungus 1(no. 1): 16 (2019)

Subphylum : *Pezizomycotina*
Class : *Leotiomycetes*

Introduction

Marthamycetales was erected by Johnston et al. (2019b), belonging to the class *Leotiomycetes*, based on a 15 concatenated multi-gene phylogenetic reconstruction. Apothecia of *Marthamycetales* usually grow immersed and erumpent, forming irregular slits from the epidermis of the substrate (Baral 2015, Johnston et al. 2019b). The flat and colorful hymenial surfaces are exposed with granular exudate. Based on the phylogenetic analysis of LSU sequences and morphologies of two ascospore types, *Marthamycetaceae* taxa were divided into two clades: taxa with cylindric-ellipsoid ascospores and taxa with filiform ascospores (Corda 1842b, Fuckel 1869, DiCosmo et al. 1983b, Sherwood-Pike 1987, Baral 2015, Johnston & Park 2019).

History

Marthamycetales consists of a single family, *Marthamycetaceae*, comprising nine genera *viz*. *Cyclaneusma*, *Mellitiosporium*, *Mellitiosporiella*, *Marthamyces*, *Naemacyclus*, *Propolina*, *Propolis*, *Phragmiticola* and *Ramomarthamyces* with 79 species (Baral 2015, Hyde et al. 2024b). Among the *Marthamycetaceae* genera, the clade comprising three genera in *Rhytismatales*, namely *Propolis*, *Marthamyces* and *Mellitiosporium*, are recognized as propoloid fungi, based on immersed ascomata under the epidermis of the substrate. *Cyclaneusma* and *Naemacyclus* were placed in *Helotiales* based on the phylogenetic analysis of the LSU sequences (Hustad & Miller 2011, Lantz et al. 2011, Baral 2015). The oldest genera of *Marthamycetaceae*; *Propolis* and *Mellitiosporium*, were introduced by Corda (1842b). Other species were transferred from *Stictis*. *Stictis versicolor* was transferred to *Mellitiosporium* and designated as its type (Corda 1842b). Even though *Mellitiosporium versicolor* was identified as a synonym of *Propolis farinosa*, Dennis (1982) showed *Mellitiosporium versicolor* to be a separate species from *P. farinosa* using the LSU phylogeny (Lantz et al. 2011). *Stictis phacidioides* was introduced into *Propolis* but was subsequently transferred to *Marthamyces* (Corda 1842b, Sherwood 1977a, DiCosmo et al. 1983a, b, Minter 2003, Lantz et al. 2011). The generic name *Propolis* with the type species *Propolis farinosa* and *Propolomyces* were disputed until it was concluded that the type species of both genera was the same fungus, and the latter was synonymized under *Propolis*, confirming the type status of *P. farinosa* (Sherwood 1977a, DiCosmo et al. 1983b, Lantz et al. 2011). Subsequently, some members of *Propolis* with long and thin-walled, filiform ascospores were transferred to an individual genus *Marthamyces* in *Rhytismataceae* despite the presence of two similar genera (*Naemacycltus* and *Cyclanesma*) (Minter 2003). Based on the phylogenetic analysis of LSU sequence data, *Cyclanesma*, *Marthamyces* and *Naemacycltus* clustered with the type species of *Propolis* (*Propolis farinosa*) and *Mellitiosporium* (*Mellitiosporium versicolor*) (Hustad & Miller 2011, Lantz et al. 2011). Subsequently, Baral (2015) introduced *Marthamycetaceae* to accommodate seven genera, namely *Cyclaneusma* and *Naemacyclus*, which were transferred from *Helotiales*. *Marthamyces*, *Mellitiosporium* and *Propolis* were transferred from *Rhytismataceae*. *Mellitiosporiella*, *Phragmiticola* and *Propolina* were transferred from

Phacidiaceae. *Marthamyces* was designated as the type genus. Baral et al. (2015) suggested that *Marthamycetaceae* should be treated as a separate group based on the LSU and mtSSU phylogenetic analyses (Hustad & Miller 2011, Lantz et al. 2011). Because *Marthamycetaceae* was placed basal to *Helotiales*, a new monophyletic order, *Marthamycetales* was introduced to accommodate the family. Some members of *Marthamyces sensu stricto* were transferred to the genus *Ramomarthamyces* based on phylogenetic analysis rather than the propoloid form (Johnston & Park 2019, Johnston et al. 2019b). Karakehian et al. (2023) suggested that the names *Mellitosporium*, *Mellitosporiella* and *Mellitosporium versicolor* should be conserved.

General description

Members of *Marthamycetales* are called 'propoloid fungi' because of their propoloid paraphyses (Lantz et al. 2011, Baral 2015, Johnston et al. 2019b). *Marthamycetales* genera are divided into two clades according to the shape of their ascospores (cylindric-ellipsoid and filiform). Cylindric-ellipsoid ascospores usually appear in five genera (*Mellitiosporium*, *Mellitiosporiella*, *Phragmiticola*, *Propolis* and *Propolina*) (Baral 2015). Ascospores of *Propolis* are small ellipsoid or kidney-shaped cylindric, and lack septa (Chlebická 2014), whereas *Mellitiosporiella* and *Phragmiticola* have 3-septate, cylindric ascospores. Furthermore, *Phragmiticola* is distinguished from these others by having a prominent gelatinous sheath surrounding the spores (Sherwood-Pike 1987) and amyloid apical rings similar to *Phacidiaceae* (Baral 2015). *Mellitiosporium* can be distinguished by its unique muriform ascospores (usually having multiple horizontal septa and longitudinal septa) (Corda 1842b, Baral 2015). *Propolina* is distinguished by its multi-spored asci (Baral 2015). Filiform ascospores with single to multiple septa appear in four genera, namely *Cyclaneusma*, *Marthamyces*, *Naemacyclus* and *Ramomarthamyces*. The apices of ascospores in *Cyclaneusma*, and *Ramomarthamyces* are covered with gelatinous sheaths at both ends, but the apices of *Marthamyces* are only partially covered (DiCosmo et al. 1983b, Minter 2003, Baral 2015, Johnston & Park 2019). Therefore, spore morphology can be an important basis for identification in this family. Ascomata of *Marthamycetales* are usually immersed under the epidermis of the host, which covers the ascomatal splits irregularly and the flaps of the host tissue folding back, exposing the whole hymenium (Corda 1842b, Minter 2003, Chlebická 2014, Baral 2015, Gu et al. 2015, Raymundo et al. 2016, 2022, Johnston & Park 2019). Species of *Cyclaneusma* and some members in *Ramomarthamyces* have one longitudinal split and turn it back as two flaps (DiCosmo et al. 1983b). The intra-hypodermal of immature ascoma usually comprises the decomposed host cells and partial hypogenetic clypeus-like hyphae and forms 'hyphal bridges' at the margin where the hymenium is exposed (DiCosmo et al. 1983b, Johnston & Park 2019). The disc color can also be used as a basis for species identification, but no clear demarcation is found among the genera. The surface of the hymenium in most genera is covered with a layer of white, pale yellow, or yellow crystalline, but sometimes not obvious, such as in *Propolis occulta*, *P. strobilina* and *Ramomarthamyces tuku* (Chlebická 2014, Gu et al. 2015, Raymundo et al. 2016, 2022, Johnston & Park 2019). Furthermore, the propoloid paraphyses of *Marthamyces* can be differentiated from the distinctly branched paraphyses of *Ramomarthamyces* (Johnston & Park 2019).

Sexual morph: *Ascomata* apothecial, circular, angular, suborbicular to elongate, generally scattered, rarely coalescing, immersed under the epidermis of the substrate, cleistohymenial development, erumpent, covering host tissue, splitting irregularly and becoming lobes or tooth-shaped flaps of tissue folding back to expose the hymenial surface, lobes sometimes white-fimbriate; *Hymenium* white, cream or blue-green-grey, rarely yellow or orange-rose, exterior pale to dark, with its surface covered by pruinose. *Ectal excipulum* usually comprised of two layers, the outer layer near the host tissue, comprised of isodiametrical cells or broad tangled hyphae, dark color, crystals sometimes present in lobes, the inner layer comprised of tangled hyphae and often entirely covered with hyaline periphysiods. *Paraphyses* filiform, densely septate, apically flexuous propoloid or branched, covered by granular exudate. *Asci* 8-spored, rarely polysporous, clavate or cylindric, rounded or conical apex, undifferentiated, thick or thin-walled, J-, and croziers present. *Ascospores* ellipsoid to cylindrical or filiform, transversely single to 7-septate, rarely up to 13 septa, rarely

longitudinal forming muriform, straight or curved, hyaline or pale brown, with a gelatinous hat at both ends or absent, lipid content low to high. Asexual morph: *Conidiomata* developing within the leaves, immersed in the host, host tissue darker than surroundings, globose, with a round pore. *Conidiomatal wall* comprised of thin-walled, tangled hyphae, inner layer comprised of lining elongated and periphysoid-like cells. *Conidiophore* subcylindrical, branched and septate, hyaline, bearing several conidiogenous cells. *Conidiogenous cells* cylindric, slightly tapering towards the barely differentiated apical conidiogenous locus. *Conidia* filiform (Fig. 166).

Families included in *Marthamycetales*

Marthamycetaceae Baral, Lantz, Hustad & Minter

Evolution

In immersed ascomata, the host epidermal splitting is believed to cause a break at the apex of the asci to release ascospores. Some ascospores with a gelatinous sheath or hats at both ends were once placed in *Rhytismataceae* despite the absence of a blackened clypeus (a feature that appears in *Rhytismataceae* but not unique to *Rhytismataceae*) (Fuckel 1869, DiCosmo et al. 1983b). The presence of mycelial bridges resembles the members of *Phacidiaceae sensu stricto* (Dennis 1982, DiCosmo et al. 1983b). With the advent of molecular techniques and further morphological analysis, 'propoloid fungi' were considered as members of *Rhytismataceae*, and several genera were clustered basal to the *Helotiales* (DiCosmo et al. 1983b, Hustad & Miller 2011, Lantz et al. 2011). *Marthamyces* and *Propolis* were regarded as *incertae sedis* within the *Leotiomycetes* (Lantz et al. 2011, Baral 2015, Johnston & Park 2019). To date, they are placed in a single order *Marthamycetales*. The phylogenetic analysis of 15 genes shows that *Marthamycetales* is located basal in *Leotiomycetes* (Johnston & Park 2019, Johnston et al. 2019b).

Justification of order and problems

Due to the presence of immersed ascomata, some genera of *Marthamycetaceae* were initially placed in *Patellariaceae* (*Patellariales*) in *Dothideomycetes* and *Phacidiaceae* (*Phacidiales*) in *Leotiomycetes* (Corda 1842b, Fuckel 1869). The close associations of genera in *Marthamycetaceae* with *Rhytismataceae* and *Phacidiaceae* were discussed for many years (DiCosmo et al. 1983b, DiCosmo et al. 1984, Minter 2003, Hustad & Miller 2011, Lantz et al. 2011, Chlebická 2014, Baral 2015). Despite some morphological evidence showing their homology, phylogenetic analyses from 2011 to 2020 confirmed the independence of *Marthamycetaceae* in *Leotiomycetes* (Hustad & Miller 2011, Lantz et al. 2011, Baral 2015, Gu et al. 2015, Johnston & Park 2019, Johnston et al. 2019b, Raymundo et al. 2022). Some species in *Marthamycetaceae* live as parasites. Phylogenetic analysis showed that this parasitic lifestyle evolved more than once in this family (Johnston & Park 2019).

Significance

Ecological and economic roles

Taxa in *Marthamycetaceae* are mainly distributed in tropical and temperate regions (Central Europe, East and South Asia, North and South America and some islands of the South Pacific). Most occur on fallen leaves of a wide range of plants (*Arbutus uva-ursi*, *Avicennia germinans*, *Carex firma*, *Dendrobium cunninghamii*, *Dracophyllum* sp., *Eucalyptus* sp., *Fagus grandifolia* subsp. *mexicana*, *Fissistigma* sp., *Hakea lissosperma*, *Metrosideros collina*, *Orites acicularis*, *Pinus radiata*, *Pinus maritima*). They are also found on dead branches (*Annona squamosa*, *Juniperus communis*, *Nothofagus antarctica*), culms (*Panicum proliferum*), ferns (*Pteris aquilina*), grass (*Cyperus* sp., *Juncus* sp., *Rosmarinus* sp. and *Urtica dioica*) and pine cones and vines (*Lonicera* sp.) (Tilak et al. 1967, DiCosmo et al. 1983b, Minter 2003, Johnston 2006, Gu et al. 2015, Raymundo et al. 2016, 2022, Johnston & Park 2019). Most taxa in *Marthamycetaceae* are saprobic on some hosts; several groups affect pine trees, especially 6–20-years-old trees (Bulman 1993). An aerial survey has shown several outbreaks of diseases caused by *Marthamycetaceae* spp. in New Zealand (Bulman 1993).

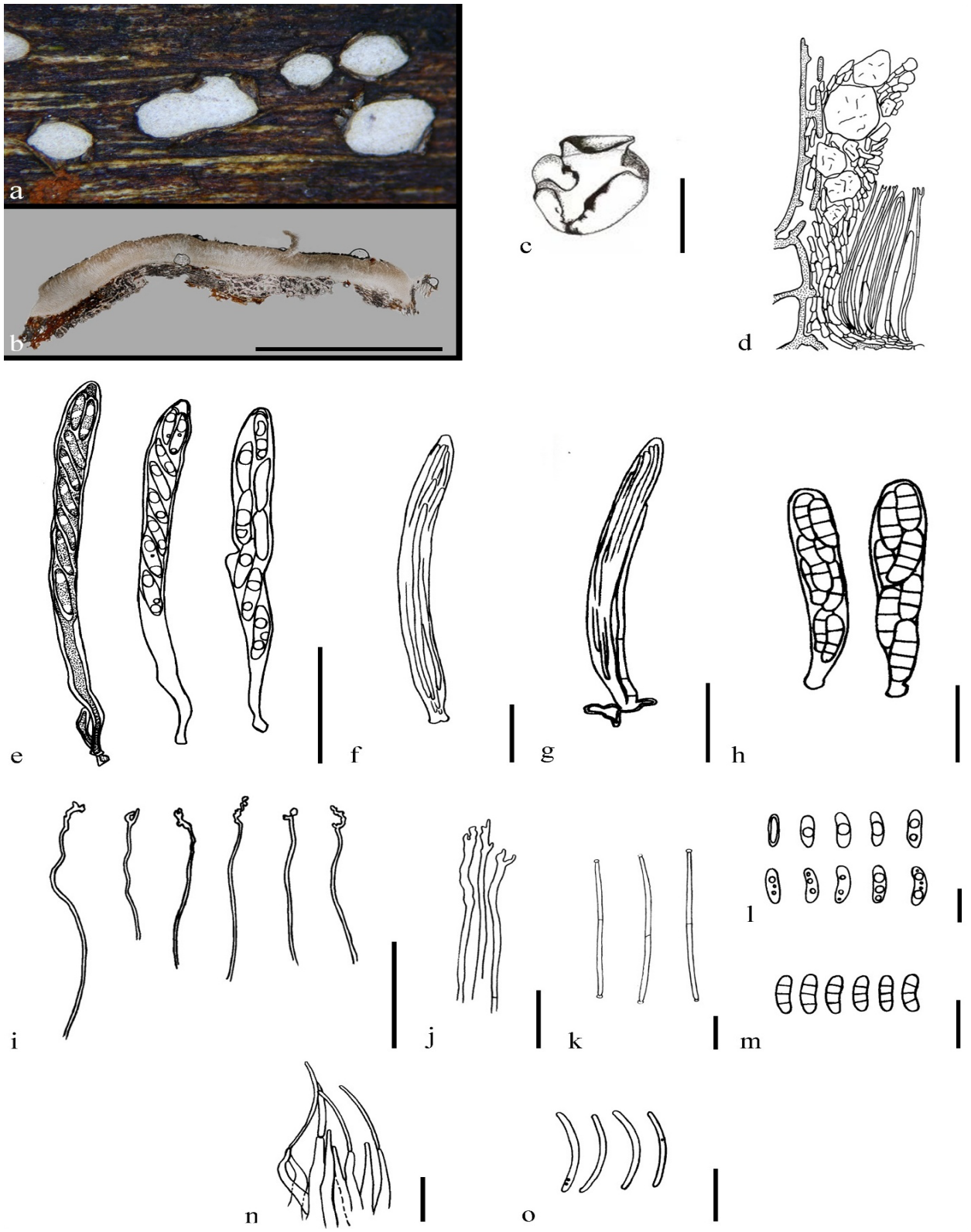


Figure 166 – Morphology of *Marthamycetales*. Morphology of *Propolis farinosa* (redrawn from Crous et al. 2019d, Sherwood 1977a) (a–b, e, i, l). a Ascomata. b Vertical section of an ascoma. e Asci. i Paraphyses. l Ascospores. Morphology of *Mellitiosporiella pulchella* (ERD-5771, https://www.centrodeestudiosmicologicosasturianos.org/?p=309) (h, m). h Asci m Ascospores. Sexual and asexual of *Marthamyces emarginatus* (redrawn from Crous et al. 2019d, Sherwood 1977a) (c–d, f–g, j–k, n–o). c Ascomata. d Excipulum. f–g Asci. j Paraphyses. k Ascospores. n Conidiophores giving rise to conidia. o Conidia. Scale bar: b = 800 µm, c = 150 µm, d ≈ ×750, e = 50 µm, f–h, l–m = 20 µm, i = 40 µm, j–k, n–o = 10 µm.

Cyclaneusma spp. are the main cause of the infection, with the degree of infection spread being related to the climate of the previous winter (Bulman 1993). *Marthamyces* and *Cyclaneusma* are pathogens on the leaves of a wide range of plants as well as on the needles of pine trees. Examples are the foliar diseases caused by *M. harakeke*, *M. culmigenus* and two species in *Cyclaneusma* (Johnston & Park 2019). Most taxa in *Naemacyclus* and *Propolis* are reported as saprobes on dead stems or branches (Minter 2003, Chlebická 2014, Gu et al. 2015, Raymundo et al. 2016, Johnston & Park 2019). This suggests that some members can survive by breaking down lignin, cellulose and other components.

Chemical diversity

No relevant studies are available for the chemical diversity of *Marthamycetales*.

Other relevant data and future recommendations

Sequence data are unavailable for three genera, namely *Mellitiosporiella*, *Propolina* and *Phragmiticola*. Therefore, their placements rely solely on morphological evidence (Baral 2015). To date, the species richness of *Marthamycetales* is low, although some species are widely distributed. Molecular data of *Rhytismataceae* in NCBI showed that some of its species may belong to *Marthamycetaceae*; however, these issues need further investigation (Johnston & Park 2019).

***Medeolariales* Korf, Mycotaxon 15: 232 (1982)**

Subphylum : *Pezizomycotina*
Class : *Leotiomycetes*

Introduction

Medeolariales is a monotypic order that accommodates *Medeolariaceae* and the monotypic genus *Medeolaria* in *Leotiomycetes* (LoBuglio & Pfister 2010, 2013, Quandt & Haelewaters 2021). The order *Medeolariales* was erected by Eriksson (1982), who designated *Medeolariaceae* and *Medeolaria* as the type family and genus. However, Eriksson (1982) placed *Medeolariales* in the *Ascomycota* without a clear taxonomic position because of their lack of ascomatal tissue, ascus types and their parasitic lifestyle. Later, LoBuglio & Pfister (2010) transferred *Medeolariales* into *Leotiomycetes* based on the combined phylogenetic tree of SSU, LSU, and ITS sequences data. With the development of molecular studies, Ekanayaka et al. (2019a) used phylogenetic analyses inferred from 482 taxa of *Leotiomycetes* based on the combined LSU, SSU, ITS, TEF and RPB2 sequence data to transfer the *Ascocorticiaceae*, *Ascodichaenaceae*, *Dermateaceae*, and the *Coleophoma-Parafabraea* clade into *Medeolariales*. In contrast to Ekanayaka et al. (2019a), many studies have shown *Medeolariales* to be a monotypic order (Haelewaters et al. 2021c). *Medeolariales* are obligate parasitic phytopathogens with limited occurrence in the northeastern US (Pfister 1984, LoBuglio & Pfister 2010).

History

Medeolaria was introduced by Thaxter (1921), and placed it into *Protodiscineae* based on the thorough and well-documented description of *Medeolaria farlowii*. Korf (1973) treated *Medeolaria* as the only member of the family *Medeolariaceae* in *Medeolariales*. Eriksson (1982) formally introduced *Medeolariales* and *Medeolariaceae*, based on *Medeolaria* as the type species, and indicated that *Medeolariales* belonged to *Ascomycota* due to its lack of ascomatal tissue, an indistinct ascus apical apparatus, and parasitism. LoBuglio & Pfister (2010) classified *Medeolariales* in *Leotiomycetes*. Ekanayaka et al. (2019a) indicated that *Medeolariales* included *Ascocorticiaceae*, *Ascodichaenaceae*, *Dermateaceae*, the *Coleophoma-Parafabraea* clade, and *Medeolariaceae* based on the morphological evidence and phylogenetic analysis based on combined ITS, LSU, SSU, TEF, and RPB2 loci. However, Haelewaters et al. (2021c) showed that *Dermateaceae* belonged to *Helotiales* based on their best-scoring ML tree of *Leotiomycetes* reconstructed from the concatenated 15 locus dataset. At present, most authors maintain the traditional classification, *Medeolariales* as a

monotypic order with *Medeolariaceae* as type family (Quandt & Haelewaters 2021, Wijayawardene et al. 2022a).

General description

Sexual morph: *Ascomata* apothecial, irregularly organized, reduced, erumpent in host tissue. *Excipulum* reduced or unclear. *Paraphyses* filiform, simple, flexuous, septate below, brownish. *Asci* 8-spored, cylindrical to clavate, inamyloid, with apical dehiscence. *Ascospores* fusiform to naviculate, with a dark outer wall layer with striations (LoBuglio & Pfister 2010, 2013, Ekanayaka et al. 2019a) (Fig. 167). Asexual morph: Undetermined.

Families included in *Medeolariales*

Medeolariaceae Korf

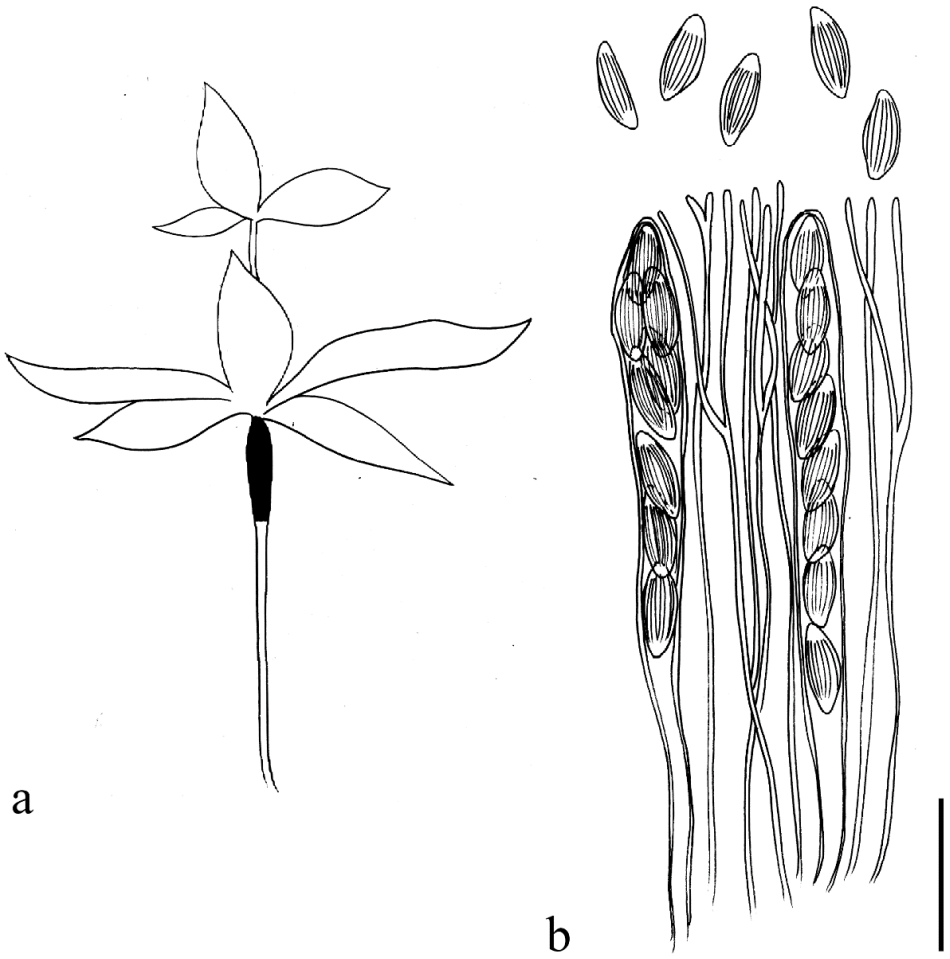


Figure 167 – Morphology of *Medeolaria farlowii.* a Ascomata. b Asci, paraphyses and ascospores (drawn or redrawn from Lobuglio & Pfister 2013). Scale bars: a, b = 50 µm.

Justification of order and problems

Ekanayaka et al. (2019a) accepted *Ascodichaenaceae*, *Dermateaceae*, and *Coleophoma-Parafabraea* clade under *Medeolariales* based on the combined LSU, SSU, ITS, TEF and RPB2 sequence data and the similar morphology of *Ascocorticiaceae* into *Medeolariales*. In contrast to this, many researchers (Haelewaters et al. 2021c, Wijayawardene et al. 2022a) showed that some important taxa were missing in Ekanayaka et al. (2019a), which may lead to topological changes in the phylogenetic analyses. Therefore, it is imperative to enhance the sequencing of crucial taxa in addition to re-evaluating other groups using a broader range of evidence, encompassing morphology, ecology, and chemical profiles beyond solely relying on phylogenetics. The current state of

classification underscores the urgency and importance of delving deeper into the categorization of Leotiomycetes.

Significance

Ecological and economic roles

The only member of *Medeolariales*, *Medeolaria farlowii* (Quandt & Haelewaters 2021), is a presumed obligate phytopathogenic parasite of *Medeola virginiana* (LoBuglio & Pfister 2010). Disease symptoms of *M. farlowii* include shortened internodes and swollen tissues, with brown and woolly characters (Thaxter 1921, LoBuglio & Pfister 2010, Lestari et al. 2023). Infected plants were visible with lesions on stems, rhizomes and tubers, and infections spread throughout plants. However, symptoms at the onset of the disease remain unclear (Lobuglio & Pfister 2013). The order has a limited occurrence in the northeastern US (Pfister 1984, LoBuglio & Pfister 2010).

Chemical diversity

No relevant studies are available for the chemical diversity of *Medeolariales*.

Other relevant data and future recommendations

Though there are reports on pathogenic *Medeolariales* taxa (Pfister 1984, LoBuglio & Pfister 2010, 2013), no research has been found on their pathogenesis and virulence factors. Therefore, further research is required on the pathogenicity of *Medeolariales* taxa, and further fresh specimens are required to confirm the taxonomic status of this species.

***Micraspidales* Quijada & Tanney, Fungal Systematics and Evolution 5: 104 (2019) [2020]**

Subphylum : *Pezizomycotina*
Class : *Leotiomycetes*

Introduction

Micraspidales in *Leotiomycetes* comprises only three species assigned to its only genus, *Micraspis*, which belongs to *Micraspidaceae*, the sole family in *Micraspidales* (Quijada et al. 2020). The taxa of *Micraspidaceae* are characterized by shining, black, orbicular to elliptic apothecia with an irregular longitudinal slit, ectal excipulum arranges in *textura epidermoidea* and inamyloid, 4–8-spored asci (Quijada et al. 2020). The taxa are distributed in Canada, Denmark, Ireland, Russia, the UK and the USA, and most occur on needle leaves of *Picea* spp., the wood of *Picea sitchensis* and cones of *Pinus sylvestris* (Darker 1963, Dennis 1971, Graddon 1984, Popov 2007, Quijada et al. 2020).

History

Studies on *Micraspis* began when Darker (1963) found a foliar disease caused by a fungus in Ontario, Canada. The disease symptoms were similar to those caused by *Phacidium* (*Lophophacidium hyperborium*) except for the color of affected needles, which differs from the usual. Darker then described the specimen as a novel species, *Micraspis acicola*, based on both asexual and sexual morphs are found on needles (Darker 1963). *Micraspis acicola* was placed in *Phacidiaceae*, citing its similarities with apothecia of *Phacidium*, except for the absence of irregular teeth and amyloid asci. Darker (1963), then assigned *Micraspis* in the family 'Cryptomyceten'*sensu* von Höhnel, *Phacidiales* (Höhnel 1917b).

Based on the absence of amyloid ascal tip and vertically oriented covering layer, *Micraspis* was reassigned to *Tympaneae* (Korf 1973, DiCosmo et al. 1983c, 1984). Baral (2016) placed *Micraspis* in *Tympanidaceae* (*Phacidiales*) based on asexual morph characters, especially the formation of microconidia from phialides and septate macroconidia. A study documented a multi-gene phylogenetic tree of *Leotiomycetes* by Johnston et al. (2019b), including several genera of *Tympanidaceae* (the family which formerly accommodated *Micraspis*), but *Micraspis* sequences were not included in the analysis. Quijada et al. (2020) resolved taxonomic issues on *Micraspis* by

providing a multi-gene phylogenetic tree, confirming the previously identified distinct characters; hence, *Micraspis* was placed in the new family, *Micraspidaceae,* in the new order *Micraspidales*.

General description

Micraspidaceae taxa form apothecia, which are scattered or in small clusters, sessile, orbicular or erumpent, irregularly elongate, developing inside the host, closed at first, and then open by tearing up stromatic covering layer into rectangular lids. The shape of the apothecia can be round, irregularly ellipsoid, or elliptical (Quijada et al. 2020). Excipulum cells are composed of dark cells of *textura epidermoidea* to *textura angularis*, often faintly separated between ectal to medullary excipulum. Asci are cylindrical clavate, and the ascal size differentiates *Micraspis tetraspora* from the other two *Micraspis* species (Quijada et al. 2020). Some of the ascospores of *Micraspis tetraspora* are aborted; hence, the asci sometimes bear four ascospores. In general, the ascospores of *Micraspis* are cylindrical fusoid to clavate-ellipsoid and 1–5-transverse septate (Quijada et al. 2020). The asexual morph is pycnidial, scattered, dark brown to black, with phialidic conidiogenous cells bearing filiform, falcate, and fusiform to allantoid conidia.

Sexual morph: *Apothecia* arising singly or in small cluster, orbicular to irregularly elongate, elliptical, subcuticular or erumpent, developing inside the superficial layers of the host tissues, opening by longitudinal slits when mature forming rectangular lids. *Ectal excipulum* 20–120 µm thick, thicker at the upper flank and thinner near the margin or in the lower flanks, comprises cells of *textura epidermoidea* to *textura globosa–angularis* at the margin and flanks. *Medullary excipulum* mostly restricted beneath the hymenium, 20–100 µm thick, composed of a loose network of narrow hyphae (plectenchymatous tissue), brownish to hyaline *textura globosa* to *textura angularis*. *Paraphyses* cylindrical with uninflated to slightly medium clavate, straight or slightly sinuous, no more than 5-septate, simple or branched at the below of the apical cell. *Asci* cylindric-clavate, 4–8-spored, inamyloid, arising from croziers. *Ascospores* bi- or triseriate, cylindrical fusoid to clavate-ellipsoid, hyaline, rounded to obtuse at both ends, sometimes with one end extremely wider than the other, straight or slightly curved, with 1–3(–5) transverse septa at maturity, smooth or with tiny sparse guttules, germinating at both ends. Asexual morph: *Pycnidia* immersed, subcuticular to partly subepidermal, unilocular to multilocular or convoluted, scattered, dark brown to black, shining, outline elliptical to circular or irregular, raised to pulvinate, opening by a single longitudinal or several radial splits. *Conidiophores* lining all inner surfaces of conidioma, simple or branched, sometimes septate, subcylindrical, tapering toward apex, hyaline, smooth, frequently reduced to conidiogenous cells. *Conidiogenous cells* enteroblastic, phialidic, integrated or discrete, determinate or indeterminate, simple or unbranched, hyaline, smooth, aperture minute, collarette inconspicuous. *Conidia* filiform to falcate or fusiform to allantoid, 0–2(–3)-septate, hyaline, smooth or guttulate (adapted from Quijada et al. 2020, Fig. 168).

Families included in *Micraspidales*

Micraspidaceae Quijada & Tanney

Evolution

Micraspis is recently placed in *Micraspidaceae*, *Micraspidales* based on the multi-gene phylogeny and morphology by Quijada et al. (2020), and also relates to the *Trizodia* clade in *Leotiomycetes*. However, further evolution studies are required to confirm the placement of this genus in *Leotiomycetes*.

Justification of order and problems

The placement of *Micraspis* has been uncertain since 1963, and some mycologists, based only on the morphologies, tried to assign this genus to several existing families such as *Phacidiaceae* (Darker 1963), *Tympaneae* (DiCosmo et al. 1983c, 1984) and *Tympanidaceae* (Baral 2016). *Micraspis* is similar to *Phacidiaceae* members based on subcuticular, blackish, circular to elongate with longitudinal slit apothecia (Darker 1963). However, they differ from *Phacidiaceae* by having inamyloid asci and the lack of an irregular teeth-covering layer on apothecia; hence, DiCosmo et al.

(1984) reassigned it to *Tympaneae*. Baral (2016) placed *Micraspis* in *Tympanidaceae* (*Phacidiales*) based on the formation of blastic-phialidic microconidia from ascospore germination. A multi-gene phylogeny of *Leotiomycetes* by Johnston et al. (2019b) included several members of *Tympanidaceae* (*Phacidiales*) but none from *Micraspis* species. Quijada et al. (2020) employed multi-gene phylogeny, including the sequences from *Micraspis acicola* and *M. strobilina*, along with morphological affirmation and transferred *Micraspis* species into the newly established *Micraspidaceae* (*Micraspidales*), resolving previous taxonomic issues related to the genus.

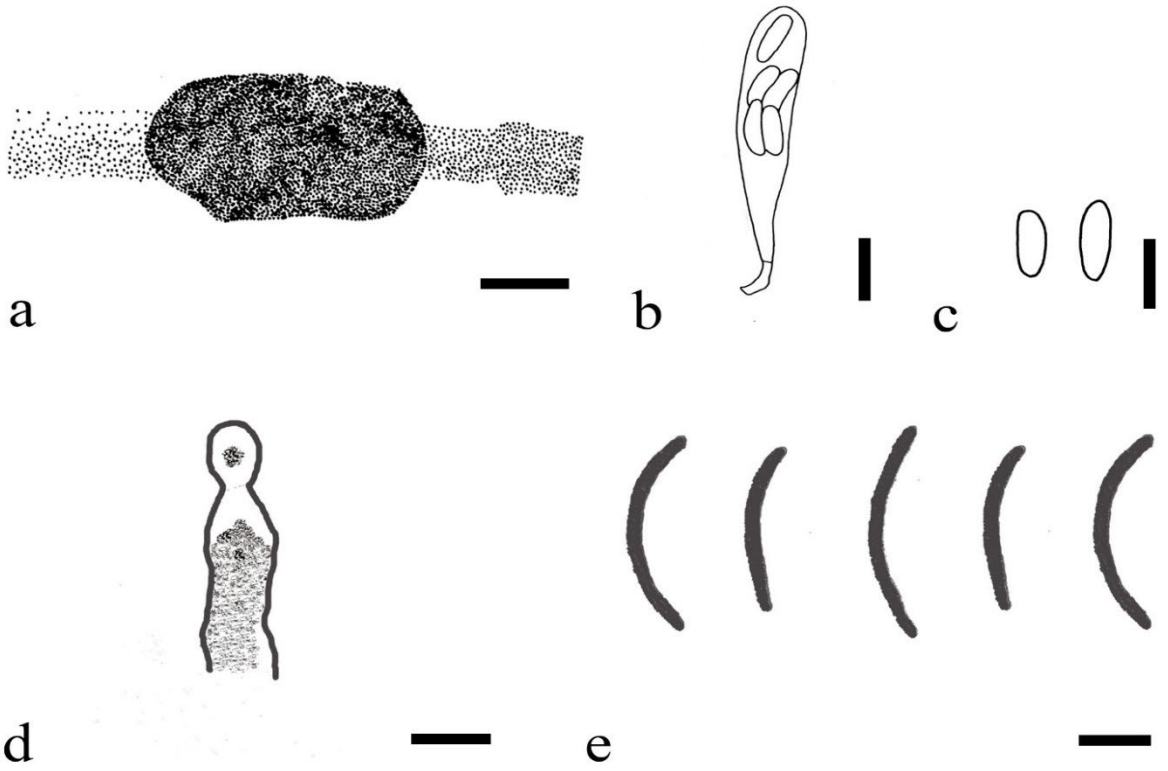


Figure 168 – Sexual and asexual morph of *Micraspis*. a An ascoma of *M. tetraspora*. b Ascus of *M. tetraspora*. c Ascospores of *M. tetraspora*. d Conidiogenous cells and conidiophore of *M. acicola*. e. Conidia of *M. acicola.* (redrawn from Quijada et al. 2020). Scale bars: a = 500 µm, b, e = 10 µm, c, d = 5 µm.

Significance

Ecological and economic roles

Micraspis acicola has been reported in association with needle leaves of *Picea* spp. as endophytes and pathogens in Canada (Quijada et al. 2020). *Micraspis strobilina* was found on fallen cones of *Pinus sylvestris* and was common in the UK, while *M. tetraspora* is native to North America and found on decorticated wood of *Picea sitchensis,* which became an essential timber commodity after being introduced in the UK (Graddon 1984, Quijada et al. 2020). Further studies on the economic and ecological values are expected.

Chemical diversity

The secondary metabolite diversity of *Micraspis* species has been overlooked; hence, there is no data regarding what chemical substances these taxa synthesized.

Other relevant data and future recommendations

Prior to Quijada et al. (2020), molecular data were only available for *Micraspis acicola* in unpublished studies. Subsequently, many endophytic isolations of *M. acicola* from *Picea* spp. were

conducted, which can be used in resolving taxonomic issues of *Micraspis* (Quijada et al. 2020). However, further comprehensive studies on evolution, ecology or other applications are required. *Micraspis strobilina* is the other *Micraspis* species for which molecular data are available besides *M. acicola*. *Micraspis strobilina* is ubiquitous in the UK; hence, further studies on evolution and ecology are required. Apart from the aforementioned species, *Micraspis tetraspora* lacks sequence data. The current taxonomic placement of these species in *Micraspidales* was mainly based on morphological affinities from three specimens (Quijada et al. 2020). Hence, more explorations are vital to discover additional specimens for further studies on this genus.

Phacidiales **C.E. Bessey, University of Nebraska Studies 7: 298 (1907)**

Subphylum : *Pezizomycotina*
Class : *Leotiomycetes*

Introduction

The members of *Phacidiales* are mostly saprobic, but sometimes parasitic, and are characterized by branching septate mycelium, which bears mostly open spore fruits (apothecia) (Bessey 1907). The morphological circumscription of the order has changed over time, leading to extensive changes in the classification of the order. Most of the genera treated under *Phacidiales* were transferred to different orders, including *Asterinales*, *Diaporthales*, *Helotiales*, *Ostropales*, *Rhytismatales*, *Triblidiales* and *Xylariales*, with several genera treated as *incertae sedis* (Quijada et al. 2018).

History

The ordinal name *Phacidiales* was initially used by Bessey (1907) to accommodate *Triblidiaceae*, *Stictidaceae*, and *Phacidiaceae* to accommodate six genera with the generic type *Phacidium*. Later, Höhnel (1917b) accepted six families, including *Schizothryrieen*, *Leptopeltineen*, *Dermopeltineen*, *Phacidiaceen*, *Phacidiostromaceen* and *Cryptomyceteen* with 52 genera. However, the count was reduced in further studies by accepting 32 genera with three families *viz*, *Rhytismataceae*, *Cryptomycetaceae* and *Phacidiaceae* (Korf 1973). *Phacidiales* was treated under *Rhytismatales*, *Leotiales* and *Helotiales* (Hawksworth et al. 1983b, 1995, Kirk et al. 2001, Eriksson 2005, 2006, Lumbsch & Huhndorf 2007, 2010) until Crous et al. (2014a) resurrected this as a separate order. Crous et al. (2014a) circumscribed *Phacidiaceae* and the order which formed a sister clade to *Helotiales*. Previously Wang et al. (2006b) found that the representatives of *Phacidiales* including *Bulgaria inquinans* and *Phacidiophicnes pyri* clustered outside of *Helotiales*. Crous et al. (2014a) treated *Bulgariaceae* as a synonym of *Phacidiaceae* and the family remains as heterogenous.

Baral (2016) restricted the order to *Phacidiaceae* with two additional families, *Tympanidaceae*, and *Helicogoniaceae,* based on their genetic similarities. However, Ekanayaka et al. (2019a) accepted only *Phacidiaceae* under *Phacidiales* which was recovered as sister to the *Thelebolales-Leotiales* clade. Suija et al. (2017) added a lichenicolous genus based on morphological similarities and phylogenetic relationships. The genus formed a close clade to *Epiglia gloeocapsae* and was placed as *incertae sedis* in *Phacidiales*. However, Quijada et al. (2018) found this genus in the *Mniaecia* clade, and the authors treated *Phacidiaceae*, *Helicogoniaceae* and *Tympanidaceae* with *Mniaecia* under *Phacidiales*. Consequently, Johnston et al. (2019b) established a new family for *Mniaecia* and placed it under *Leotiales* along with *Tympanidaceae* and accepted only *Phacidiaceae* and *Helicogoniaceae* within *Phacidiales*. The classification of Johnston et al. (2019b) has been accepted further and presently 22 genera are assigned to two families *Helicogoniaceae* and *Phacidiaceae* whereas the familial placement of *Coma* remains uncertain which is placed in *incertae sedis* (Wijayawardene et al. 2022a).

General description

The sexual members characterized by apothecia that open in the prohymenial to mesohymenial phase with paraphyses lacking vacuolar bodies asci, with or without amyloid ring and ascospores

with variable lipid content (Baral 2016). Exceptionally, *Helicogonium* species form ascogenous hyphae without ascomata (Kimbrough 1981). The asexual morph is characterized by a phialidic, acropleurogenous type of conidiogenesis and hyaline, mainly aseptate to 1-septate conidia (Crous et al. 2014a, Jaklitsch et al. 2016a).

Sexual morph: *Ascomata* absent or present, apothecial if present, circular, 0.25–1.5 mm in diam, (sub-)sessile, immersed, erumpent or superficial, covering layer often thick and stromatic, opening in the mesohymenial phase or prohymenial phase, semiglobose to pulvinate, light- or dark-colored, often ± gelatinous, margin smooth, usually by splitting into teeth or lobes with ± adhering host tissue. *Hymenium* pale cream to black, closing on drying (or with a large gelatinous water storage tissue, Bulgaria); exterior light brown to black. *Ectal excipulum* of *textura prismatica-angularis*, *textura porrecta* or brown angular cells, cells oriented at varying angles, inner layer of marginal lobes entirely covered by more hyaline, often immersed in ± abundant, hyaline to brownish gel, short to long periphysoids embedded in gel; sometimes with crystals. *Paraphyses* cylindrical to slightly lanceolate, straight or curved, apically flexuous, curled, inflated or not, simple or rarely branched; embedded in some hyaline, brownish or lilaceous mucilage or exudate, without VBs. *Asci* clavate, cylindric-clavate, with or without amyloid ring, sometimes opening by an apical slit, with or without croziers. *Ascospores* (4–)8 per ascus, homo- or sometimes heterosporous, subglobose, ellipsoid, fusoid, clavate, cylindric clavate, cylindrical or filiform, hyaline or brown, 0–1(–3)-septate, lipid content low or high, with or without budding conidia. Asexual morph: hyphomycetous, or pycnidial, conidiogenesis monoblastic, annelidic, or phialidic without collarette, conidia small, ellipsoid, cylindrical or fusoid, partly with funnel-shaped, sometimes apical appendage (Fig. 169).

Families included in *Phacidiales*

Helicogoniaceae Baral
Phacidiaceae Fr.

Phacidiales genera *incertae sedis*
Coma Nag Raj & W.B. Kendr.

Evolution

Helicogoniaceae differs from *Phacidiaceae* in the absence of amyloid rings in the asci. The frequency of amyloid rings in the apparently older clade *Geoglossaceae* suggests that ascus amyloidity is a plesiomorphy in the *Phacidiales* (Baral 2016). *Helicogonium* is considered phylogenetically derived from *Helotiales* but with a loss of ability to form apothecia (Baral 1999).

Justification of order and problems

Helicogonium species are poorly explored due to their inconspicuous appearance on the host and their irregular and unpredictable occurrence (Baral 1999, Baral & Kutorga 2010). Many *Phacidiaceae* endophyte sequences, which are available in GenBank are unidentified (Stefani & Bérubé 2006, U'Ren et al. 2010). Endophytic life history strategies among *Phacidiaceae* species are more widespread than previously recognized. Saprotrophic and opportunistic pathogenic fungi may asymptomatically infect host tissue until optimal conditions for extensive colonization and reproduction arise (Tanney & Seifert 2018).

Significance

Ecological and economic roles

The taxa are reported as saprobes and parasites worldwide, but mainly in temperate regions (Baral 2016). *Bulgaria inquinans* occurs on the bark of fallen trunks and branches and on living trees. This species is considered as saprobic and possibly a facultative plant pathogen (Crous et al. 2014a). *Helicogonium* species live as parasites in hymenia of other Ascomycetes and Basidiomycetes where

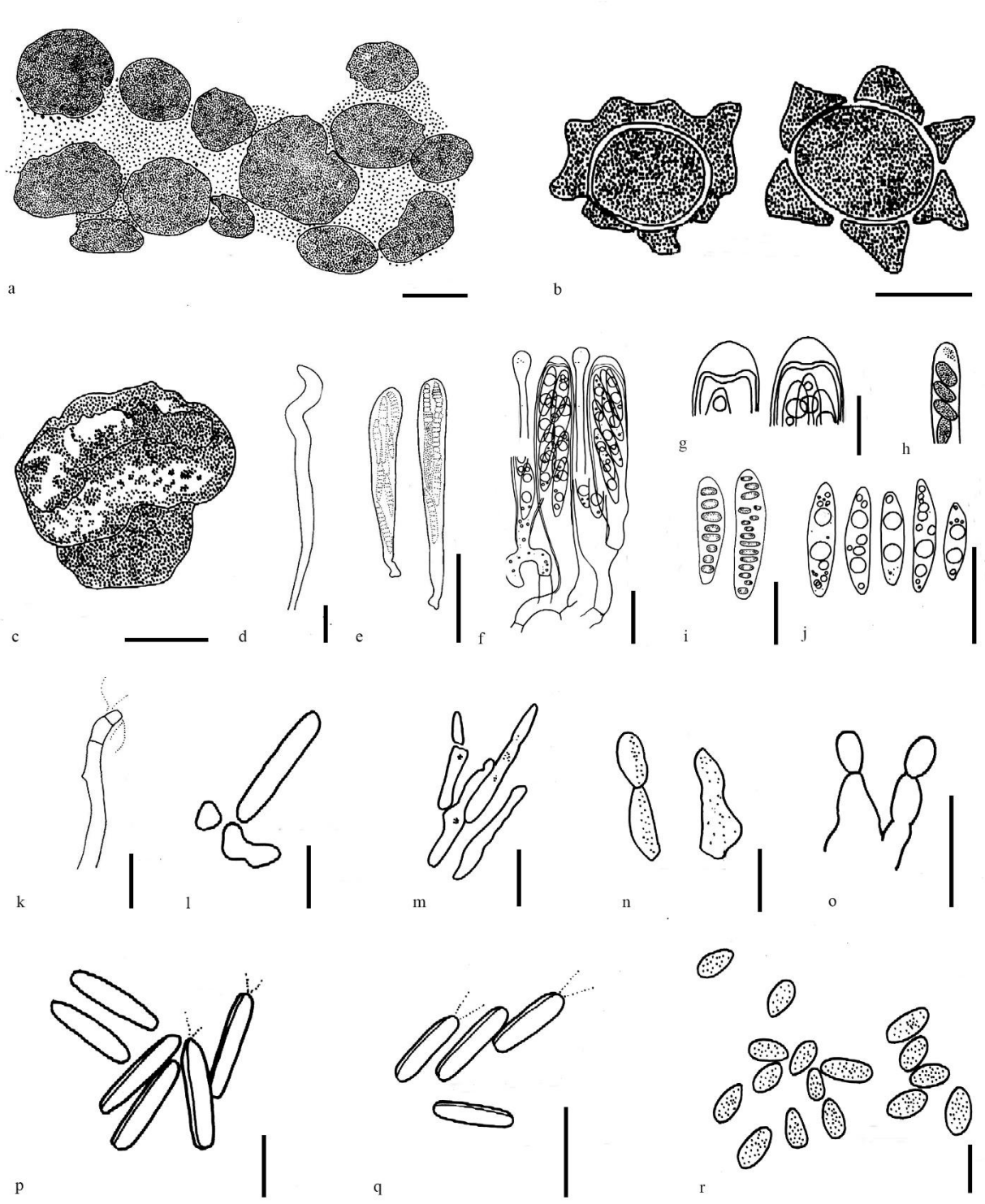


Figure 169 – Morphology of *Phacidiales*. a–c Ascomata on substrate (a *Aotearoamyces nothofagi*, b *Phacidium lacerum*, c *Bulgaria inquinans*). d Paraphyses (*Aotearoamyces nothofagi*). e, f Asci (e *A. nothofagi*, f *Helicogonium fusisporum*). g, h Ascus apices (g *Helicogonium fusisporum*, h *Bulgaria inquinans*). i, j Ascospores (i *Aotearoamyces nothofagi*, j *Helicogonium fusisporum*). k Vegetative hyphae of *Aotearoamyces nothofagi*. l, m Conidiogenous cells (l *Phacidium calderae*, m *P. molleriana*). n, o Conidiogenous cells giving rise to conidia (n *Pseudophacidium ledi*, o *Allantophomopsiella pseudotsugae*). p–r Conidia (p *Phacidium calderae*, q *P. molleriana*, r *Pseudophacidium ledi*) (redrawn from Baral HO, Kutorga 2010, Crous et al. 2014a, Quijada et al. 2018).

they suppress the formation of the host's meiosporangia (Baral 1999). The taxa are reported from a diverse group of plant hosts, particularly within *Ericaceae*, *Pinaceae*, and *Rosaceae* (DiCosmo et al. 1984, Funk 1985, Farr & Rossman 2016). They can also occur as endophytes in asymptomatic conifer needles (Koukol et al. 2012, Tanney & Seifert 2018).

Chemical diversity

An organic extract of *Bulgaria inquinans* yielded three azaphilones, *viz*. bulgarialactones A, B and C (131–133) (Degenkolb & Vilcinskas 2016).

Rhytismatales M.E. Barr ex Minter, Systema Ascomycetum 5(1): 182 (1986)

Subphylum : *Pezizomycotina*
Class : *Leotiomycetes*

Introduction

Rhytismatales is an order of mostly plant-associated Ascomycetes with a global distribution and comprises over 800 species assigned to 59 genera (Lantz et al. 2011, Wang et al. 2023b, Guo et al. 2024). They can be found on diverse vascular plants, but they are most prevalent on conifers, grasses, and members of *Ericales* (Lantz et al. 2011, Lin 2012, Wang et al. 2023b, Guo et al. 2024). Numerous species of *Rhytismatales* are pathogens and cause diseases of economically important tree species, e.g., in China, Europe, North America, and India (Weir 1916, Darker 1932, Minter et al. 1978, Cannon & Minter 1986, Minter & Miller 1993, Lin 2012). Well known taxa include species of *Rhytisma* causing tar spots on *Acer* spp. and several needle-cast pathogens in the genus *Lophodermium* (Lantz et al. 2011, Wang et al. 2023b).

Most species of *Rhytismatales* have immersed apothecia. A layer of black stromatic tissue (clypeus) often covers and surrounds the apothecia at an early developmental stage. Later, hymenia are exposed by a longitudinal split or several more or less irregular splits at maturity, to allow the liberation of the ascospores. *Rhytismatales* is a monophyletic group, but the classification of families within it is very complex. *Rhytismatales* presently comprises three families, namely *Cudoniaceae*, *Triblidiaceae* and *Rhytismataceae sensu lato*. The family *Rhytismataceae* was described by Chevall (1826) and presently includes 64 genera with *Rhytisma* as type genus (Wijayawardene et al. 2018, Wang et al. 2023b, Guo et al. 2024). The family *Cudoniaceae* was introduced by Kirk et al. (2001) with two genera, namely *Cudonia* and *Spathularia* with distinct and more or less club-shaped fruiting bodies (Ge et al. 2014). *Triblidiaceae* only contains the genus *Triblidium* and is distinct by muriform ascospores without cell wall color reactions in iodine-based reagents (Lv et al. 2019). *Cudoniaceae* and *Triblidaceae* are nested within *Rhytismataceae sensu lato* which is thereby paraphyletic (Lantz et al. 2011, Ge et al. 2014, Karakehian et al. 2019, Lv et al. 2019). Wang et al. (2023b) proposed a new concept for the family of *Rhytismataceae sensu stricto* within the *Rhytismataceae sensu lato*.

History

Although the order *Rhytismatales* was formally established rather late (Hawksworth & Eriksson 1986), its research history can be traced back to a long time ago (Terrier 1942, Teng 1963, Darker 1967, Korf 1973, Dennis 1978, DiCosmo et al. 1984). Species of *Rhytismatales* and related taxa were first accommodated in *Phacidiales*. Initially, which was divided into six families including *Hypodermataceae* based on the depth of embedding of ascomata (Höhnel 1917b). At present, *Phacidiales* is treated as a synonym of *Rhytismatales* (Kirk et al. 2001). Darker (1932) published a monograph on *Hypodermataceae* on conifers and criticized the classification system proposed by Höhnel (1917b). The system proposed by Darker (1932) is considered as the foundation of the modern classification of *Rhytismataceae* (Cannon & Minter 1986). Nannfeldt (1932) studied 58 genera in the order *Phacidiales* proposed by Höhnel (1917b), as well as about 30 others, more or less closely related genera. After moving incongruent taxa elsewhere and treating many genera as synonyms, the family *Phacidiaceae* was reduced to 14 genera. Terrier (1942) further studied *Phacidiaceae* based on Nannfeldt's classification and divided them into three families:

Hypodermataceae, *Rhytismataceae*, and *Phacidiaceae sensu stricto*. A revision of the genera in *Hypodermataceae* published by Darker (1967) provided detailed and accurate descriptions of the genera and species in temperate regions, especially species on conifers. The morphology of ascomata and ascospores are considered to be taxonomically significant: Bacilliform ascospores and filiform ascospores are used to distinguish species of *Meloderma* and *Lophodermium*; Ascomata oriented along nerves can be used to distinguish species in *Isthmiella* Darker and *Bifusella* Höhn. (see below). Many new genera were established mainly on the basis of these characteristics in this revision.

Hawksworth et al. (1983b) informally treated *Rhytismatales* as an order, which included four families: *Ascodichaenaceae*, *Cryptomycetaceae*, *Hypodermataceae* and *Rhytismataceae*. They transferred *Phacidiaceae* to *Helotiales*. The morphological characteristics and biogeography of the 14 genera and 40 species of *Rhytismataceae* from the Indian subcontinent were examined and described by Cannon & Minter (1986). In this monograph, *Hypodermataceae* was treated as a synonym of *Rhytismataceae*. *Cryptomycetaceae* was treated as a synonym of *Rhytismataceae* in the 9th edition of Ainsworth & Bisby's Dictionary of the Fungi (Kirk et al. 2001).

Lantz et al. (2011) used nuclear LSU and mtSSU rDNA sequences for phylogenetic analyses to define a core clade of *Rhytismatales sensu stricto*, and suggested to treat *Ascodichaenaceae* as a synonym of *Rhytismataceae*. In the Outline of *Ascomycota*: 2017, two other families are accepted in the order *Rhytismatales*, namely *Marthamycetaceae* and *Cudoniaceae* (Wijayawardene et al. 2018). Johnston et al. (2019b) proposed *Marthamycetales* to accommodate *Marthamycetaceae* because this family is phylogenetically isolated within *Leotiomycetes*. Karakehian et al. (2019) placed *Triblidiaceae* in *Rhytismatales* as a result of a multi-locus phylogenetic analysis. Ekanayaka et al. (2019a) synonymized *Cudoniaceae* under *Rhytismataceae* based on rather sketchy evidence, so this conclusion is not widely accepted. Wang et al. (2023b) studied rhytisma-like species including many details, and the family *Rhytismataceae sensu stricto* is proposed with eight genera accepted in a narrow family concept. Additionally, evidence complemented by diversification time estimates indicates that the order *Rhytismatales* contains *Cudoniaceae*, *Triblidiaceae* and *Rhytismataceae sensu stricto* (Wang et al. 2023b). Recently, the species diversity, taxonomy and phylogeny of species of *Rhytismatales* on twigs of *Rhododendron* spp. have been comprehensive investigation worldwide, a total of 56 species recognized, among them, eight new genera, 33 new species and three new combinations were proposed (Guo et al. 2024).

General description

Diverse morphological characteristics are used to define taxa of *Rhytismatales*. The shape of ascomata was considered to be very important for the identification of taxa by Darker (1967). It may be circular, angular, elliptical, oblong, irregular, or sometimes conspicuously elongated (Cannon & Minter 1986, Lin 2012) (Fig. 170). The opening of ascomata can be roughly divided into two types, one with a longitudinal split and the other one with several irregular splits. The two largest genera of *Rhytismataceae*, *Coccomyces* (several irregular splits) and *Lophodermium* (one longitudinal split) were distinguished according to the opening of their ascomata. The size of ascomata of *Rhytismatales* also varies, with the smallest such as in some species of *Lophodermium* being less than 0.5 mm and the largest such as in species of *Rhytisma* with up to 4 mm length (Lin 2012, Wang et al. 2023b). Ascomata of *Rhytisma* spp. typically develop in groups below a common, large covering stroma, while there is a single ascoma below one covering stroma in species of other genera. The color of ascomata is usually black, brown or grey, sometimes shiny, or concolorous with the surface of the substrate (Wang et al. 2023b). The depth of embedding of ascomata in host tissue is diverse, including subcuticular, intraepidermal, subepidermal, intrahypodermal, subhypodermal, intracortical or subcortical positions. This feature is considered to be important at the species level (Cannon & Minter 1986) (Figs. 170, 171).

The ascomata of *Rhytismatales* mostly develop in stromata, and the covering stroma (also called clypeus) often surrounds the ascomata at an early stage. The cellular organization of covering stroma is diverse, and can present various types of fungal cells. The most common cell types are angular cells, global cells, and hyphae (Cannon & Minter 1986, Lantz et al. 2011, Lin 2012). Some species

of *Rhytismatales* have lips along the splits of their ascomata. Lip cells are thin-walled, hyaline to pigmented, aseptate to septate, round to cylindrical, and often embedded in hyaline gel. The potential function of lips may be to open ascomata in an appropriate humid environment (Minter 1981, Cannon & Minter 1986, Lin 2012).

A few species of *Rhytismataceae* have periphysoids, which are hyaline, filiform, or cylindrical, straight or curved, sometimes embedded in hyaline gel (Sherwood 1980, Cannon & Minter 1986). Paraphyses are present in almost all species of *Rhytismatales*. The paraphyses of different species can be simple or branched, aseptate or septate, and swollen or unswollen at the tips (Cannon & Minter 1986). Members of *Rhytismatales* have thin-walled, unitunicate asci, ripening sequentially or simultaneously, cylindrical to clavate, 4- or 8-spored (Cannon & Minter 1986, Hou 2004). Features of asci provide some of the most important diagnostic characteristics of the *Rhytismatales*. The shape and details of ascospores are extremely diverse. Ascospores can be elliptical, bifusiform, filiform, fusiform, cylindrical, clavate, or muriform, aseptate or septate, hyaline to pigmented, eguttulate or pluriguttulate, with gelatinous sheaths or not, the sheath is variable in thickness, appendages are present or absent, and cell wall reactions in iodine-based reagents are present or absent (Fig. 171). Further morphological features that can be important for species identification of *Rhytismatales* are details of the basal stroma, an internal matrix of the stroma, subhymenium, hymenium, excipulum and epithecium.

Most species of the *Rhytismatales* are teleomorphs with associated anamorphs (Minter 1981, Cannon & Minter 1986). The absence or presence and morphological features of conidiomata, conidiogenous cells and conidia are useful aspects at the species level (Hou 2004). Many species of *Rhytismatales* develop frequent or infrequent, brown or black lines, which surround ascomata. These zone lines may help to conserve water supplies in colonized host tissue essential for the development of the fungus (Jones 1935). Brouard et al. (1979) showed that the humid environment is favorable for the formation of zone lines.

Members of *Cudoniaceae* differ morphologically from species of *Rhytismatales* by forming smaller fruiting bodies that have a flattened to club-shaped apex, known as ascigerous area (Ge et al. 2014). The form of the ascigerous areas is used to separate the two genera of *Cudoniaceae*, *Cudonia* from *Spathularia* (Wang et al. 2002). The micromorphology of these two genera is similar: both genera have curved paraphyses, club-shaped asci, and long, thin, hyaline ascospores that are surrounded by gelatinous sheaths. These characteristics are also shared by many species of *Rhytismataceae* (Kirk et al. 2001, Wang et al. 2002). In addition to the ascigerous areas, a stromatic membrane and ascoconidia are unique characteristics of *Cudoniaceae* (Wang et al. 2002).

Sexual morph: *Ascomata* variable in shape and color, stalked to sessile, often covered individually or in groups by a black covering stroma, opening by a longitudinal split or irregular splits. *Depth of embedding* various. *Lips* present or absent, aseptate to septate, hyaline to pigmented. *Hymenium* variable in color. *Covering stroma* variable in composition. *Periphysoids* present or absent. *Excipulum* present or absent. *Basal stroma* present or absent, variable in composition. *Internal matrix of stroma* present or absent, variable in composition. *Subhymenium* variable in composition. *Paraphyses* branched or unbranched, aseptate or septate, swollen or unswollen at the tips. *Asci* ripening sequentially or simultaneously, cylindrical to clavate, 4- or 8-spored. *Ascospores* variable in shape, aseptate to septate, hyaline to pigmented, nonguttulate or pluriguttulate, gelatinous sheaths present or absent, variable in thickness, appendages present or absent. *Epithecium* present or absent. *Ascigerous areas* if present, capitate to pileate. *Stromatic membrane* present or absent. *Ascoconidia* sometimes present. Asexual morph: *Conidiomata* small, usually round to elliptical or slightly irregular, dark brown, usually opening by an ostiole to liberate the conidia. *Conidiogenous cells* usually cylindrical but tapering towards the apex, hyaline. *Conidia* usually cylindrical, small, hyaline. Zone lines frequent or infrequent, brown or black lines (adapted from Lin 2012) (Figs. 170, 171).

Families included in *Rhytismatales*

Cudoniaceae P.F. Cannon

Rhytismataceae Chevall.
Triblidiaceae Rehm

Evolution

Many studies found that individual species of *Rhytismatales* are restricted to specific plant genera or even species (Sherwood 1980, Ortiz-García 2003, Hou 2004, Hou & Piepenbring 2005, Lantz et al. 2011, Lin 2012). Recent phylogenetic multigene analysis, show rhytisma-like species are monophyletic (except *Neorhytisma panamense*), and they divided into eight subclades with high support, each of them with strong host-preference and unique ascoma morphology (Wang et al. 2023b). Wang et al. (2023b) further pointed out that rhytisma-like species started to radiate on species of *Ericaceae* by host jumping and subsequent speciation on species of *Arbutoideae*, *Rhododendroideae* and *Vaccinioideae*. Apparently, this process is not limited to rhytisma-like species. Host jumps between more or less distantly related host taxa most probably shaped the diversity of genera of *Rhytismatales*. Species apparently also diversified by host shifts by coevolution.

Justification of order and problems

The complicated relationship of *Cudoniaceae* and *Rhytismatales* has been considered by many studies (Gernandt et al. 2001, Wang et al. 2002, 2006b, Lantz et al. 2011, Ge et al. 2014). The club-shaped fruiting bodies formed on soil or humus by species of *Cudoniaceae* are similar to fruiting bodies of macrofungi and strongly deviate from the small apothecia covered by black stroma formed in plant tissue by most other species of *Rhytismatales* (Lantz et al. 2011). Ge et al. (2014) found that *Cudoniaceae* are nested within the *Rhytismataceae*, based on the phylogenies of the combined data from ITS, LSU, RPB2 and TEF-1a sequences, and suggested treating it as a synonym of *Rhytismataceae*. Similarly, *Triblidiaceae* and *Rhytismataceae sensu stricto* are also nested within the *Rhytismataceae sensu lato* (Karakehian et al. 2019, Wang et al. 2023b). By following the proposal of a new concept of *Rhytismataceae sensu stricto* proposed by Wang et al. (2023b), more families will be needed. These should be described when more data on species and corresponding molecular sequence data are available.

Rhytismataceae are a paraphyletic group, and the majority of the genera in this family are polyphyletic. This is due to the previous morphological classification by Darker (1967), in which the shapes of ascospores and ascomata, as well as the depth to which ascomata are embedded in host tissue, are emphasized (Cannon & Minter 1986, Johnston 1990). With an increasing number of molecular sequence data being available, many studies show that the classification in Darker (1967) is artificial and unnatural for many groups (Powell 1974, Sherwood 1980, Cannon & Minter 1986, Lin et al. 2004). The polyphyly of key genera such as *Lophodermium*, *Hypoderma* and *Coccomyces* especially needs to be addressed, and *sensu stricto* concepts for these genera need to be defined. Unfortunately, molecular sequence data are available only for approximately 25% of ~800 known species of *Rhytismatales* and many species remain to be described for science. The latter fact is evident by the observation, that *Rhytismatales* have not been searched for in many countries all over the world, especially in the tropics (e.g., Piepenbring et al. 2020 for West Africa) and unpublished result of own fieldwork. Therefore, broad sampling, morphological analyses, type studies and laboratory work to obtain molecular sequence data are important for clarifying the concepts of genera. The traditionally used characteristics of ascospores and ascomata should be combined with other morphological characters, host preferences, geographical distribution data, and molecular sequence data, in order to establish a natural taxonomic system for *Rhytismatales*.

Significance

Ecological and economic roles

Many species of *Rhytismatales* have been repeatedly isolated from apparently healthy plant tissues (Carroll & Carroll 1978, Minter 1981, Lin 1987, Oono et al. 2014, Salas-Lizana & Oono 2018,



Figure 170 – Morphology of ascomata of *Rhytismatales*. a *Hypoderma minter*. b *Lophodermium johnstonii*. c *Coccomyces strobi*. d *Coccomyces mucronatus*. e *Coccomyces quercicola*. f *Colpoma quercinum*. g *Tryblidiopsis sichuanensis*. h *Xyloma shennongjiaense*. i *Triblidium hubeiense*. j *Tryblidiopsis sinensis*. k *Nematococcomyces oberwinkleri*. l *Fanglania parasitica*. m *Lirula exigua*. n *Coccomyces anhuiensis*. o *Terriera houjiazhuangensis*. p *Fanglania huneiensis*. q *Coccomyces shennongjiaensis*. r *Coccomyces delta*. s *Xyloma muelleri*. t *Spathularia flavida* (from L. Fan). Scale bars: a, b, d, f, g, i, m, o, p, r = 500 µm, c, n, q = 300 µm, e, h, j, k, l, s = 1000 µm, t = 5000 µm.

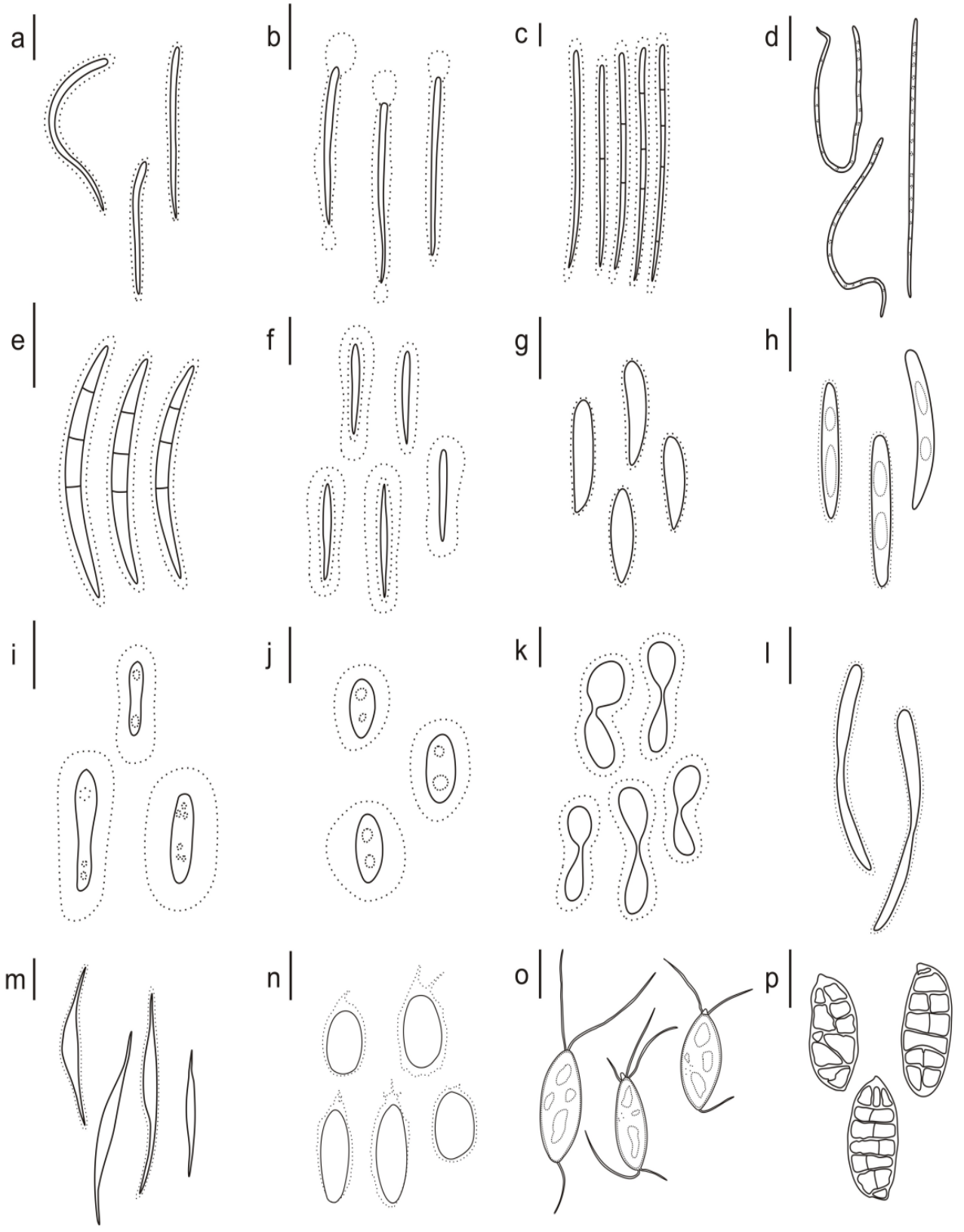


Figure 171 – Morphology of ascospores of *Rhytismatales*. a *Colpoma sinense*. b *Lirula yunnanensis*. c *Lophodermium autumnale*. d *Terriera rotundata*. e *Colpoma intermedium*. f *Ploioderma pini-armandii*. g *Hypoderma rubi*. h *Hypoderma linderae*. i *Soleella pinicola*. j *Hypoderma cuspidatum*. k *Soleella junipericola*. l *Neococcomyces yunnanensis*. m *Therrya abieticola*. n *Hypoderma urniforme*. o *Nematococcomyces rhododendri*. p *Triblidium rostriforme*. Scale bars: a–e, g, h, j, l–n = 10 μm, f, i, p = 20 μm, k, o = 5 μm.

McMullin et al. 2019). These endophytic fungi coevolved with their host plants. Some species produce metabolites that reduce the population density of some pests of woody plants and have potential biocontrol capability (Carroll & Carroll 1978). Some species of *Rhytismatales* have the habit of developing secondarily infections by certain nervisequious species, such as *Lophodermium autumnale* commonly found on needles first attacked by *Isthmiella faullii* in Eastern America, by *Virgella robusta* (in western America and by *Lirula nervisequa* in China. *L. autumnale* sometimes is present in such abundance that it serves to check the spread of the nervisequious species (Darker 1932, Lin et al 1995, Lin 2012).

In agroforestry ecosystems, members of the order *Rhytismatales* play an important role as decomposers. These fungi decompose coriaceous dead leaves, branches, and roots, promote the recycling of carbon, nitrogen, and sulfur, and help plants to establish their own fertilization system (Shao et al. 1948). Certain species of *Rhytismatales* on woody plants can be used as indicator organisms of atmospheric pollution, because these fungi are very sensitive to sulfide, nitrogen oxides, or chlorides (Bevan & Greenhalgh 1976, Cannon & Minter 1986, Kirk et al. 2001). *Rhytisma acerinum* for example, is susceptible to high levels of sulphur dioxide in the atmosphere and has been recommended in Europe as a biological indicator of pollution (Bevan & Greenhalgh 1976). *Rhytisma acerinum* is a common parasite on leaves of *Acer* spp. (*Sapindaceae*). By its large, black covering stromata it is easy to find and to distinguish, making it a good textbook species to explain a life cycle of a species of *Rhytismatales* (Piepenbring 2015).

Chemical diversity

Species of *Rhytismatales* produce diverse metabolites, which have been studied by many researchers. *Coccomyces strobi* for example, was isolated from white pine as an endophytic fungus. Extracts of culture filtrates of *C. strobi* demonstrated moderate antifungal activity and were shown to contain two new phthalides, (±)-strobides A-B (McMullin et al. 2019). Another endophyte within the family *Rhytismataceae* produces two new dihydropyrones as major metabolites together with phthalides, isocoumarins, and tyrosol (McMullin et al. 2017). The effects of these metabolites include but are not limited to antifungal (Tabuchi et al. 1994), antibacterial (McMullin et al. 2017), and toxic to spruce budworm larvae (Sumarah et al. 2008). Metabolites of the phenolic bisabolane-type, sesquiterpenoids, and macrolides obtained from extract of culture filtrate of *Lophodermium nitens* are antifungal to biotrophic pathogens and yeast (McMullin et al. 2015). Anti-mycobacterial activity of *Lophodermium culmigenum* which is a plant decay fungus isolated from Trounson Kauri, has been demonstrated by Grey et al. (2021).

Other relevant data and future recommendations

In order to understand the diversity patterns, host spectra, and evolution of *Rhytismatales*, it is important to collect and to analyse these fungi in many understudied areas worldwide and to recollect already described species to obtain sequence data from them for molecular phylogenetic analyses. These data are important for the assessment of the phytopathological impact that may be caused by species of *Rhytismatales* on cultivated plants.

By the end of spring and during summer, green leaves are infected and the fungus produces groups of small black stromata covering cavities full of tiny mitospores. These cells probably correspond to spermatia, because it is not possible to use them to infect other host plants (Healy et al. 2013). They probably fuse with receptive cells somewhere to establish the dikaryotic nuclear state. When the leaves wilt and are shed in autumn, the small black stromata of each group are fused forming large black spots due to covering stromata composed of thick-walled pigmented fungal cells. These black stromata resist against decomposition and contain living fungal cells that survive during winter. On the covering stroma, curved lines become evident that correspond to elongated ascomata that develop within the stroma. Only after a period with low temperature (winter, vernalization) and with higher temperature as well as moisture in spring, the asci in the hymenia develop. Finally, the covering stroma on top of the hymenia breaks open to expose the light colored hymenia. Filiform

ascospores are actively discharged in flushes and carried away by wind. By gelatinous sheaths, ascospores stick to moist surfaces that might correspond to new leaves of *Acer* sp.

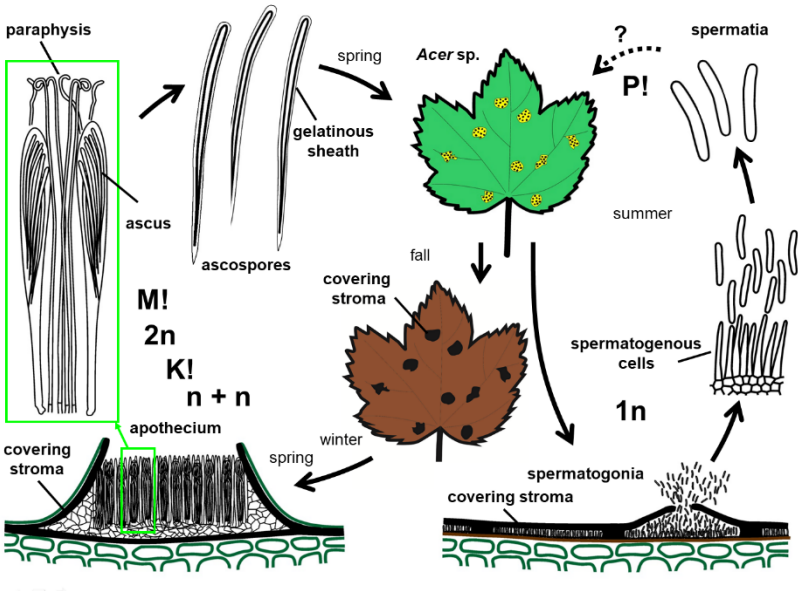


Figure 172 – Life cycle of *Rhytisma acerinum* (*Rhytismatales*) on leaves of *Acer* sp. (*Sapindaceae*). 1n = haploid, n+n = dikaryotic, 2n = diploid, K! = karyogamy, M! = meiosis, P! = plasmogamy.

Thelebolales **E. Haeckel, Systematische Phylogenie der Protisten und Pflanzen. Entwurf eines natürlichen Systems der Organismen auf Grund ihrer Stammesgeschichte. [T. 1] Systematische Phylogenie der Protisten und Pflanzen 1: 316 (1894)**

Subphylum : *Pezizomycotina*
Class : *Leotiomycetes*
Subclass : *Leotiomycetidae*

Introduction

Thelebolales, an order in the class *Leotiomycetes*, consists of three families, *Holwayaceae*, *Pseudeurotiaceae* and *Thelebolaceae* in which some genera (e.g., *Caccobius*, *Coprobolus*, and *Leptokalpion*) are erected based only on their sexual morphs (Wijayawardene et al. 2017a, Quijada et al. 2022). The members of *Thelebolaceae* produce antifreeze proteins, ice-binding proteins, and some secondary metabolites which have potential application values that offer valuable resources for biotechnological exploitation (Batista et al. 2020). *Thelebolaceae* was introduced by Eckblad (1968) and typified by *Thelebolus* with *Thelebolus stercoreus* as the type species. Members of this family are characterized by apothecial, or cleistothecial ascomata (Van Brummelen 1985, Stchigel et al. 2001, De Menezes et al. 2017, Ekanayaka et al. 2019a). Quijada et al. (2022) showed that *Thelebolaceae* is monophyletic whereas *Pseudeurotiaceae* is polyphyletic (Ekanayaka et al. (2019a). *Thelebolales* recovered as well-resolved order in the phylogenetic analyses reconstructed by Zhang et al. (2023f). Based on the recent studies conducted by Quijada et al. (2022) and Zhang et al. (2023f), three families, namely *Holwayaceae*, *Pseudeurotiaceae* and *Thelebolaceae* have been accepted with 23 genera with 260 species and the familial position of several genera or taxa needs further studies that are remains in *incertae sedis*.

History

Haeckel (1894) introduced the order *Thelebolales*; however, the taxonomy of this order has long been contentious. De Hoog et al. (2005) accepted a single family, whereas others suggested that at least two families were involved (Ekanayaka et al. 2019a, Johnston et al. 2019b, Batista et al. 2020). *Thelebolales* originally included a single family *Thelebolaceae* (Wijayawardene et al. 2017a). Some studies have proposed that the *Thelebolales* consists of *Pseudeurotiaceae* and *Thelebolaceae*

based on phylogenomic approach (Johnston et al. 2019b, Batista et al. 2020). *Thelebolaceae*, represented by *Thelebolus* and *Antarctomyces*, share a common ancestor with the family *Pseudeurotiaceae* (Johnston et al. 2019b, Batista et al. 2020). However, *Pseudeurotiaceae* nested within *Thelebolaceae* in the phylogenetic analysis and the family was treated under *Thelebolaceae* (Ekanayaka et al. 2019a). The same authors discovered that several genera, previously classified as *Leotiaceae* and *Leotiomycetes* genera *incertae sedis*, clustered within *Thelebolales* as a sister clade to *Thelebolaceae* and defined them as the *Alatospora– Miniancora* clade (Ekanayaka et al. 2019a). Therefore, there are three families (*Holwayaceae*, *Pseudeurotiaceae* and *Thelebolaceae*) in *Thelebolales*. *Pseudogeomyces, Solomyces* and *Zongqia* were newly established in recent years, and their differences in morphological characteristics from the other genera were as follows.

Pseudogeomyces differs from *Geomyces* and *Pseudogymnoascus* in the presence of two to three irregular branches at the tip of the conidiophores (Kuehn 1958, Van Oorschot 1980). However, the characteristics of *Geomyces* and *Pseudogymnoascus* are similar and they can be distinguished in the phylogeny. The genus *Pseudogymnoascus* was established by Raillo (1929). However, no type strain was formally specified during the establishment of the genus. Several years later, Samson (1972) designated *Pseudogymnoascus roseus* the neotype of *Pseudogymnoascus*, as CBS 395.65 could be cultivated. At present, the genus *Pseudogymnoascus* comprises 18 valid species (Zhang et al. 2020c, 2021b, 2023f, Villanueva et al. 2021) belonging to 13 clades (Minnis & Lindner 2013). The genus *Pseudogymnoascus* comprises a diverse group of fungi that are widely distributed and are highly ecologically diverse.

The genera *Ascophanus*, *Ascozonus*, *Caccobius*, *Coprobolus*, *Leptokalpion*, *Neelakesa* and *Pseudascozonus* are only found in the sexual stage and have no ITS and LSU sequence data (Wijayawardene et al. 2017a, Ekanayaka et al. 2019a). The genus *Solomyces* was established with *Solomyces sinensis* as the type species based on the multi-gene phylogeny (Zhang et al. 2020c), and the species are reported only in asexual morph. *Thelebolus* is an exceptional case of ascomatal evolution within the order. Its species are the most diverse in functional traits, encompassing species with closed ascomata and evanescent asci, and species with open ascomata, active ascospore discharge, and paraphyses. Open ascomata were previously suggested as the ancestral state in the genus and these ascomata depend on mammals and birds as dispersal agents (Quijada et al. 2022).

General description

Sexual morph: *Ascomata* open or closed, membranous, usually globose. Peridium pseudoparenchymatous. *Asci* irregularly disposed, evanescent, unitunicate, usually 8-spored, filiform, globose, broadly ellipsoidal or even broadly clavate. Ascospores conglobate, ellipsoidal, ovoidal, hyaline to pale yellow, thin-walled. Asexual morph: Colonies fluffy. Hyphae thin-walled, hyaline, branched. *Conidiophores* limited or sometimes degenerated. *Conidia* globose, ellipsoidal or obovate, one-celled, solitary or in short chains, smooth or rough (Figs. 173, 174).

Families included in *Thelebolales*

Holwayaceae Quijada, Matočec & I. Kušan
Pseudeurotiaceae Malloch & Cain
Thelebolaceae Engl.

Thelebolales genera *incertae sedis*
Bettsia Skou
Zongqia Zhi Y. Zhang & Y.F. Han

Evolution

Quijada et al. (2022) described the evolution of *Thelebolales*. The study revealed that the ancestral state of the group is apothecial-paraphysate with forcible spore discharge, as seen in the monophyletic family *Holwayaceae*. The closed, aparaphysate ascoma of *Thelebolaceae* and *Pseudeurotiaceae*, with the passive release of spores, is a derived condition. *Holwaya*, *Patinella*, and *Ramgea* share several traits such as open ascoma, outer layer of the excipulum with globose/angular

cells, capitate paraphyses with intra- or extracellular pigments, and asci with forcible spore discharge augmented by an OLR-type apical apparatus. They showed that nutritional switches and habitat preferences in *Holwayaceae* are accompanied by several phenotypic modifications. In *Holwayaceae*, fruitbody size is variable. Larger ascomata occur in the woody saprobes (*Holwaya*, *Patinella*) compared to the dung saprobes (*Ramgea* spp.). Dung saprobes, such as *Ramgea*, must develop more rapidly to maturity due to the transient nature of their substrate and the spatial competition for limited resources (Halbwachs & Bässler 2020). *Patinella hyalophaea* produces apothecia that are intermediate in size (up to 1.2 mm in diameter) (Baral & Carter, 2013). The production of relatively large, energy-demanding ascomata in *Holwaya* and *Patinella* is probably permitted by their ability to colonize wood, a substrate that is nutritionally, temporally, and spatially less restrictive compared to the ephemeral animal dung where the constrained colonies produced by *Ramgea* can develop only small fruiting bodies (Halbwachs & Bässler 2020). The ancestor of *Holwayaceae* was reconstructed with active discharge asci (OLR) and hyaline ellipsoid-ovoid-fusoid ascospores (Quijada et al. (2022). Species of *Holwayaceae* possess a subapical wall reinforcement, like a ring (OLR) (Brummelen. 1998). Its function is to limit tearing below the ring level, allowing opening above an irregular tear. *Ramgea* is the only genus in the family with ornamented ascospores. *Holwaya* is the most divergent lineage inside the family and has developed several apomorphies in adaptation to its ecology. The OLR is positioned closer to the apex, producing a narrower opening. This correlates with the ascospores shape (narrow-long) that has evolved to be less sensitive to desiccation (high surface/volume relationship), travel further in calm air, deposit above the ground by impaction (Magyar et al. 2016), and resist wash-out by precipitation (Calhim et al. 2018). *Ramgea* and *Patinella* have ellipsoid, smaller ascospores that presumably can disperse further than *Holwaya* (Norros et al. 2014). However, *Holwaya* has a unique apomorphy: each cell of the ascospore produces up to several secondary spores, very small conidia and are specialized to penetrate deeper into the host substrate (e.g., bark furrows), to enable a further increase in propagule productivity per fruiting body and secure better long-distance dispersal (Kellogg & Griffin 2006), or to serve as spermatia. Changes in pigmentation are also observed in *Holwayaceae*. Dark pigments might have evolved to protect against UV radiation, temperature fluctuation, desiccation, digestion by hydrolytic enzymes, or to absorb heat and warm ascomata quickly during a brief winter thaw (Baral et al. 2020). *Holwayaceae*, the basal family of the order, retained all phenotypic traits of the ancestor of *Thelebolales,* including apothecioid, paraphysate ascomata with actively discharging asci. Phenotypic variation in ascoma size, cell pigmentation, ascus, ascospore shape and biometry are correlated with nutritional strategies in this family (Quijada et al. (2022).

Due to the similarities of morphology and ecology between *Holwayaceae* and *Thelebolaceae*, in the past, the genera of *Holwayaceae* were placed together within the same family (*Thelebolaceae*). However, this convergent evolution is likely a response to similar lifestyles (Torruella et al. 2015), habitat (cold environments), substrate (dung), ecology (saprobes), and a similar mechanism for dispersal. The ascospores of these dung inhabitors need to actively escape their habitat, “sinking islands”, an ephemeral source of nutrients, and reach a distance to avoid the zone of repugnance and be ingested/transported by animals (De Hoog et al. 2005). Due to OLR asci and the presence of adhering ascospores (Hyde et al. 2017b), ascospores are ejected as a single projectile, which helps increase shooting distance, a common phenomenon in coprophilous fungi (Baral et al. 2020). In this case, the thick wall of the ascospores protects against hazards of gut passage (pH, digestive enzymes) (De Hoog et al. 2005).

The ancestor of *Thelebolaceae*/*Pseudeurotiaceae* was found as closed ascoma, without paraphyses, with evanescent asci that contain ellipsoid-fusoid ascospores. The *Thelebolaceae* clade achieved adaptive radiation in all traits analyzed compared with all other lineages, where a smaller number of changes through their evolution were found. Only the shape and color of ascospores were constant in *Thelebolaceae*. Species in the family evolved different types of ascomata (open, closed, or naked), asci (active or passive discharge), the presence or absence of paraphyses, and changes in ascospore number and ornamentation. The genus *Cleistothelebolus* retains all the ancestral traits of the order *Thelebolales,* similar to *Pseudeurotium*. Species of both genera *Cleistothelebolus* and

Pseudeurotium have closed ascomata that are considered cleistothecia, with a membranaceous peridium composed of polygonal cells, and the ascogenous system spread irregularly throughout the ascomatal interior (Malloch & Cain 1971b). In other closed ascomatal lineages, such as *Bettsia*, *Gymnostellatospora*, *Leuconeurospora*, and *Pseudogym noascus* (*Pseudeurotiaceae sensu lato*), the peridium evolved differently, although they also have a similar ascogenous arrangement (Wynns 2015). Conversely, species with closed ascoma in *Thelebolus* have an ascogenous system that are regularly arranged in a hymenial layer (De Hoog et al. 2005). The loss of active ascospore discharge in *Cleistothelebolus* and *Pseudeurotium* can be more effective protection during ascosporogenesis, opening only after the ascospores are completely mature and capable of withstanding environmental stresses (Malloch & Cain 1971b). *Cleistothelebolus* is sister to *Thelebolus*, and both genera have similar ecologies (mostly isolated from dung), and its morphology is similar to those species of *Thelebolus* with closed ascoma (De Hoog et al. 2005). However, *Cleistothelebolus* has a narrow optimum temperature for fruiting of around 25 °C and evolved in adaptation to warmer environments compared to the more psychrotolerant/psychrophilic *Thelebolus* (Malloch & Cain 1971b, De Hoog et al. 2005). Although they are not closely related in phylogenetic analysis, *Cleistothelebolus* and *Pseudeurotium* share all traits except ascospore color (hyaline vs. dark) and the composition of the cover layer of the ascoma (i.e. arrangement of cells), which is one layer in *Cleistothelebolus* and several in *Pseudeurotium*.

Quijada et al. (2022) showed another homoplastic trait, ornamented ascospores, which were evolved multiple times in different lineages, including *Holwayaceae* (*Ramgea*), *Pseudeurotiaceae* (*Gymnostel latospora*, *Leuconeurospora*, *Pseudogymnoascus*), and *Thelebolaceae* (*Antarctomyces*). Ornaments of spores are generally hydrophobic and tend to facilitate the attachment to substrates (Jennings & Lysek 1999), which are present in many diverse, animal-associated fungi with enclosed or partially enclosed ascomata in some lineages of *Pseudeurotiaceae*. *Leuconeurospora* has closed ascomata with a peridial cover modified into groups of radiating cells with well-defined lines of dehiscence. This special peridial covering is called cephalothecoid and has been correlated with arthropod dispersal (Greif et al. 2004). *Pseudogymnoascus* and *Gymnostellatospora* have cage- or mesh-like closed ascomata that are very similar to the reticuloperidial gymnothecia in *Myxotrichaceae*. These highly reduced ascomata have also evolved to be dispersed by insects (Greif & Currah 2003). *Pseudeurotium* species have evolved in adaptation to harsh habitats (heat, cold, osmotic pressures), where whole ascomata and ascospores are likely dispersed by wind/water. De Hoog et al. (2005) suggested water dispersal for species of *Thelebolus* with similar traits. Species of *Pseudeurotium* have two interesting apomorphies: small globose ascospores that are dark-walled. These spore traits are found in species that evolved long-distance dispersal. Vanderwolf et al. (2016) found that arthropods contribute to the dispersal of *Pseudogymnoascus* and *Leuconeurospora*; species of both genera have also been isolated from the fur and skin of hibernating bats (Malloch et al. 2016). In the future, more sequence data and taxon sampling from those genera currently without sequences in *Thelebolales* are needed to determine the real affinities of these genera inside the order (Quijada et al. (2022).

Justification of order and problems

The genera of *Thelebolales* were previously classified by morphology, however, multi-gene phylogeny provides better understanding of morphologically similar species to define their classification and evolution. However, several genera such as *Ascophanus*, *Ascozonus*, *Caccobius*, *Coprobolus*, *Leptokalpion*, *Neelakesa* and *Pseudascozonus* lack molecular data. The recently established genus *Pseudogeomyces* was assigned in *incertae sedis* (Zhang et al. 2023f). However, the results showed that it clustered as a separate subclade in *Pseudeurotiaceae* in the phylogenetic tree and sister to *Pseudogymnoascus*. So far, it had been confirmed to belong in *Pseudeurotiaceae*.

Several generic names have been reported in the *Thelebolaceae* and have been invalid or illegitimate, so they have been cancelled or synonym of valid genus name. The current name of *Streptotheca* is *Ascozonus*; *Lasiothelebolus*, *Pezizula*, *Ryparobius*, and *Telebolus* are all as the synonym of *Thelebolus*. *Neelakesa* has been reported in *Pseudeurotiaceae*, which is invalid.

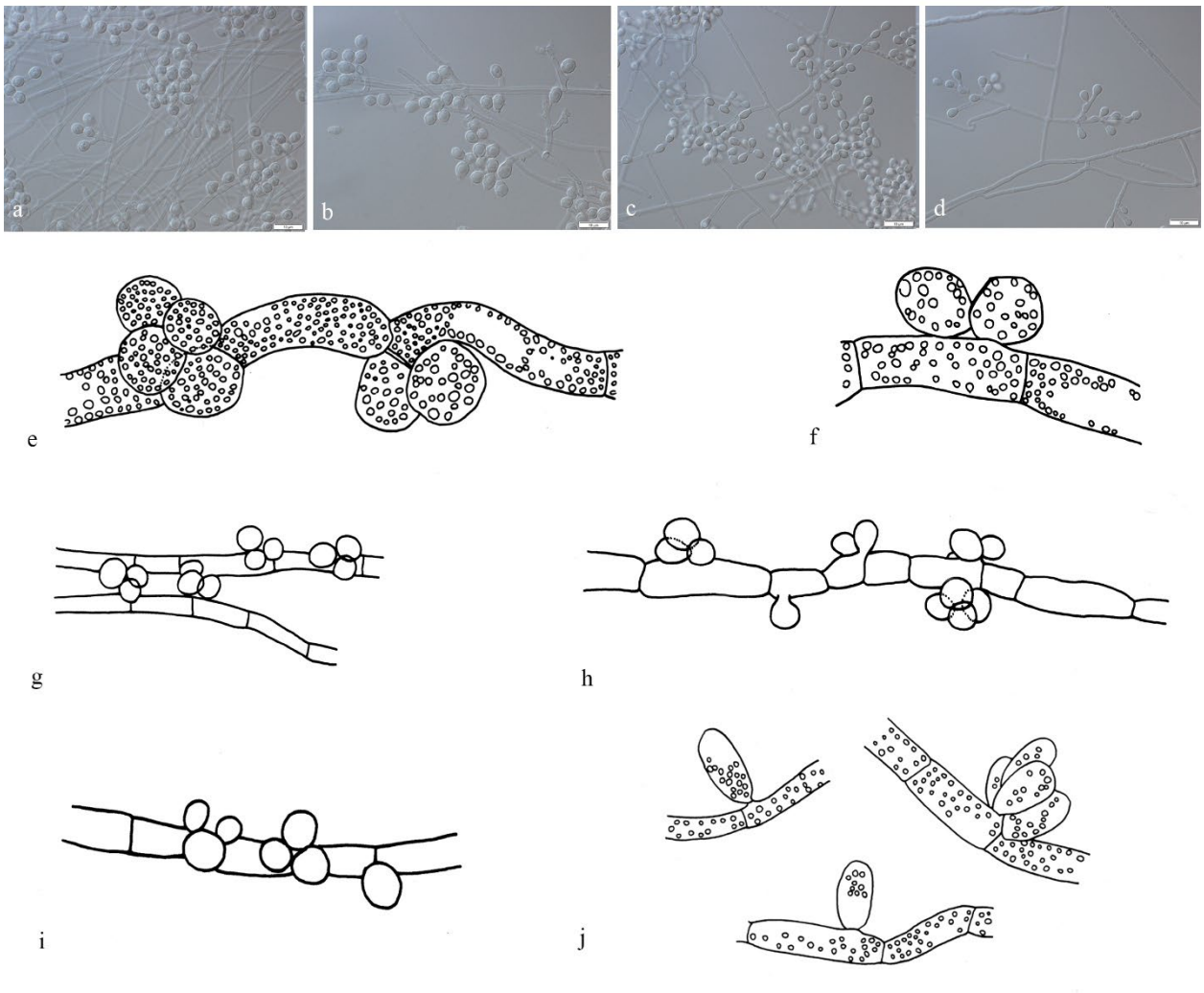


Figure 173 – Sexual morph of *Thelebolales*. a, c Initials of ascomata (a *Thelebolus ellipsoideus*, c *T. globosus*). b, d Ascoma seen from outside (b *T. globosus*, d *T.* ellipsoideus). e Ascomata in optical section (*T. globosus*). f Ascocarp (f *Leuconeurospora pulcherrima*). g Ascomata (*T. microsporus*). h Ascomata in optical section (*T. ellipsoideus*). i Emptied asci (*T. microsporus*). j Asci and capitate paraphyses (*Ascobolus* microspores). k Asci (*Leuconeurospora pulcherrima*). l, m Ascospores (l *Thelebolus microsporus*, m *Leuconeurospora pulcherrima*) (redrawn from Malloch & Cain 1970b, De Hoog et al. 2005). Scale bars: a, d, h = × 1250, b, c, e = × 3200, i, j, l = × 1600, f = × 130, g = × 630, k, m = × 1500.

Significance

Ecological and economic roles

The members of *Thelebolales* are ubiquitous in the environment. Several taxa belonging to this order have been isolated from tropical to arctic regions. They are often coprophilous and frequently isolated from freshwater and saline lakes (De Hoog et al. 2005). They have also been recorded from soil and epiphytic soil in tree holes (Chen et al. 2017a), mine sediments (Crous et al. 2019e), and sponges (Bovio et al. 2018). *Thelebolales* have been recorded as saprobic on dead plant material, rarely as plant-parasitic, and also as animal pathogens, e.g., the well-known white-nose disease of bats caused by *Geomyces destructans* (Lorch et al. 2011). In addition, several members of *Thelebolales* are keratinophilic; i.e. they can invade and degrade keratin material (Saxena et al. 2005).

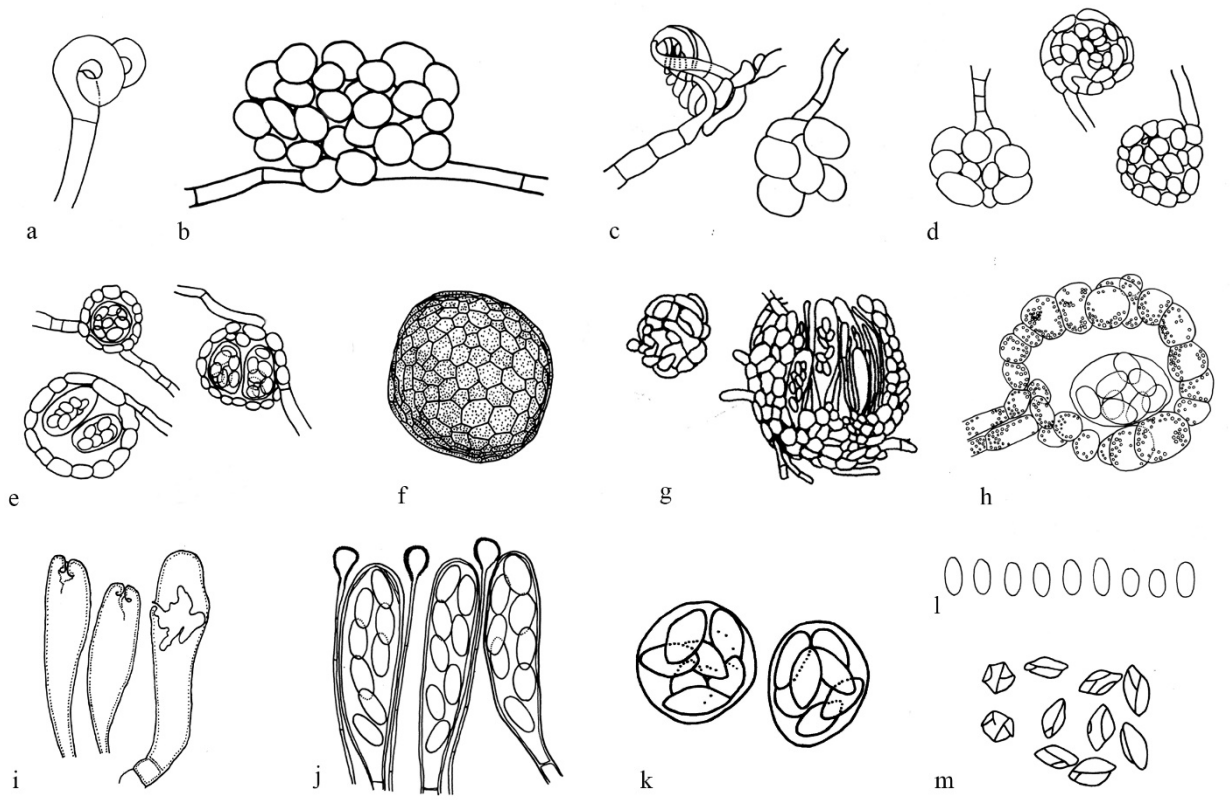


Figure 174 – Asexual morph of *Thelebolales*. Conidia arising on hyphae (a, b *Pseudogeomyces lindneri*. c, d *Pseudogymnoascus campensis*. e–i *Thelebolus globosus*. j *Thelebolus ellipsoideus*). (redrawn from Malloch & Cain 1970b, De Hoog et al. 2005). Scale bars: e, f, j = × 3200, g–i = × 1250.

Holwayaceae is so far comprised of saprobes on wood or dung (Hyde et al. 2017b). *Holwaya mucida* is well known in the northern hemisphere (Palearctic, Nearctic), with most reports of it on fallen trunks of *Tilia*. The species is found in boreal forests or taiga and temperate broadleaf and mixed forests (Korf & Abawi 1971). This species prefers old-growth forests, high atmospheric humidity (Aronsson 1991). *Holwaya byssogena* is found in tropical and subtropical dry or moist broadleaf forests (Neotropic realm) on unidentified wood, *Bactris*, and *Psidium*. Both species of *Holwaya* are considered saprobes on wood, but little is known in detail about the ecology (Quijada et al. 2022). The discovery of *Patinella hyalophaea* in New Brunswick, Canada possibly represented its second collection since the original description of it from Italy. *Patinella hyalophaea* was isolated from historic wood in Deception Island and from buried wooden artifacts in Western Greenland and lacustrine sediment cores from a lake in King George Island, Antarctica (Held & Blanchette 2017, Ogaki et al. 2020). *Ramgea annulispora* was described from pheasant dung in the Netherlands (Van Brummelen 1992), and *R. ozimecii* was described from bat droppings in Croatia (Hyde et al. 2017b). The species in *Thelebolaceae* also dwell in different habitats. *Cleistothelebolus* has been only recorded a few times from carnivore dung (op. cit.), but *Pseudeurotium* is a cosmopolitan genus that has been reported as an endophyte in algae, isolated from grass, wood, freshwater, marine sponges, soil (including permafrost), diesel fuel, dung, and sea-bottom sediments (Da Silva et al. 2020). Despite these many reports, the ecology of *Pseudeurotium*, as well as its dispersal mechanism, remains unclear.

Chemical diversity

Taxa in *Thelebolales* can produce many potential substances. In an extremely low-temperature environment requires many adaptations are usually achieved by producing antifreeze proteins and

ice-binding proteins. The endemic Antarctic fungus *Antarctomyces pellizariae* (UFMGCB 12416) was sequenced with nuclear and mitochondrial genomes. The results annotated the nuclear and mitochondrial genomes and mined secondary metabolite gene clusters, and identified a putative ice-binding proteins of 236 amino acids that shared sequence similarities with two ice-binding proteins isoforms from *A*. *psychrotrophicus*, making these the only two species of ascomycetous fungi with confirmed ability to produce antifreeze proteins, which will deepen the understanding of microbial ice-binding proteins and the genomic aspects of psychrophilic fungi (Batista et al. 2020).

Other relevant data and future recommendations

Thelebolales species are limited, so the diversity needs to be investigated in different habitats, which is primary task to find out the *Thelebolales* spp.The application of *Thelebolales* species is also needed to be further explored, which is expected to find more active compounds.

***Umbellidiales* G.G. Barreto & Gusmão, Mycological Progress 22(7, no. 48): 3 (2023)**

Subphylum : *Pezizomycotina*
Class : *Leotiomycetes*

Introduction

Umbellidiales was recently established to accommodate a monotypic family and a genus with its type *Umbellidion radulans* (Barreto et al. 2023).

History

Umbellidion radulans was reported on fallen leaves of *Eucalyptus grandis* from Brazil. However, the phylogenetic placement of the genus was unknown due to a lack of molecular data and was accepted under *Ascomycota* genera *incertae sedis* (Wijayawardene et al. 2017a, 2022a). During a survey of "Microfungi from Brazil", several *U. radulans* collections were obtained and investigated based on morphological and phylogenetic analyses. The species formed a distinct basal clade to the extant orders of *Leotiomycetes* with strong bootstrap support in the multigene phylogenetic analyses based on ITS, LSU, SSU, TEF1, and RPB2 sequences data. Another anamorphic order *Lauriomyces* also formed a basal lineage within *Leotiomycetes* but differs from *Umbellidiales* in having branched conidiophore, blastic conidiogenous cells, acropetal chains of conidia with ramoconidia whereas *Umbellidiales* has unbranched or branched conidiophores, polyblastic conidiogenous cells that are sympodially extending and arranged in whorl of umbels with aseptate conidia (Hernández-Restrepo et al. 2017, Barreto et al. 2023). Consequently, a new order, *Umbellidiales* and a family *Umbellidiaceae* were established to accommodate *Umbellidion radulans* (Barreto et al. 2023).

General description

The order is only reported from the hypomycetous asexual morph. Barreto et al. (2023) provided a detailed morphological comparison of *Umbellidiales* with anamorphic members of *Leotiomycetes*.

Sexual morph: Not observed. Asexual morph: *Conidiophores* macronematous, mononema tous, unbranched or branched, swollen base, septate, brown to pale brown. *Conidiogenous cells* polyblastic, sympodially extending, arranged in whorl of umbells, hyaline. *Conidia* aseptate, solitary, dry, hyaline (adapted from Barreto et al. 2023) (Fig. 175).

Families included in *Umbellidiales*

Umbellidiaceae G.G. Barreto & Gusmão

Justification of order and problems

The hyphomycetous order *Umbellidiales* was established based on morpho-molecular analysis. However, the links between sexual and asexual collections have not been explored for many *Leotiomycetes* which need further studies.

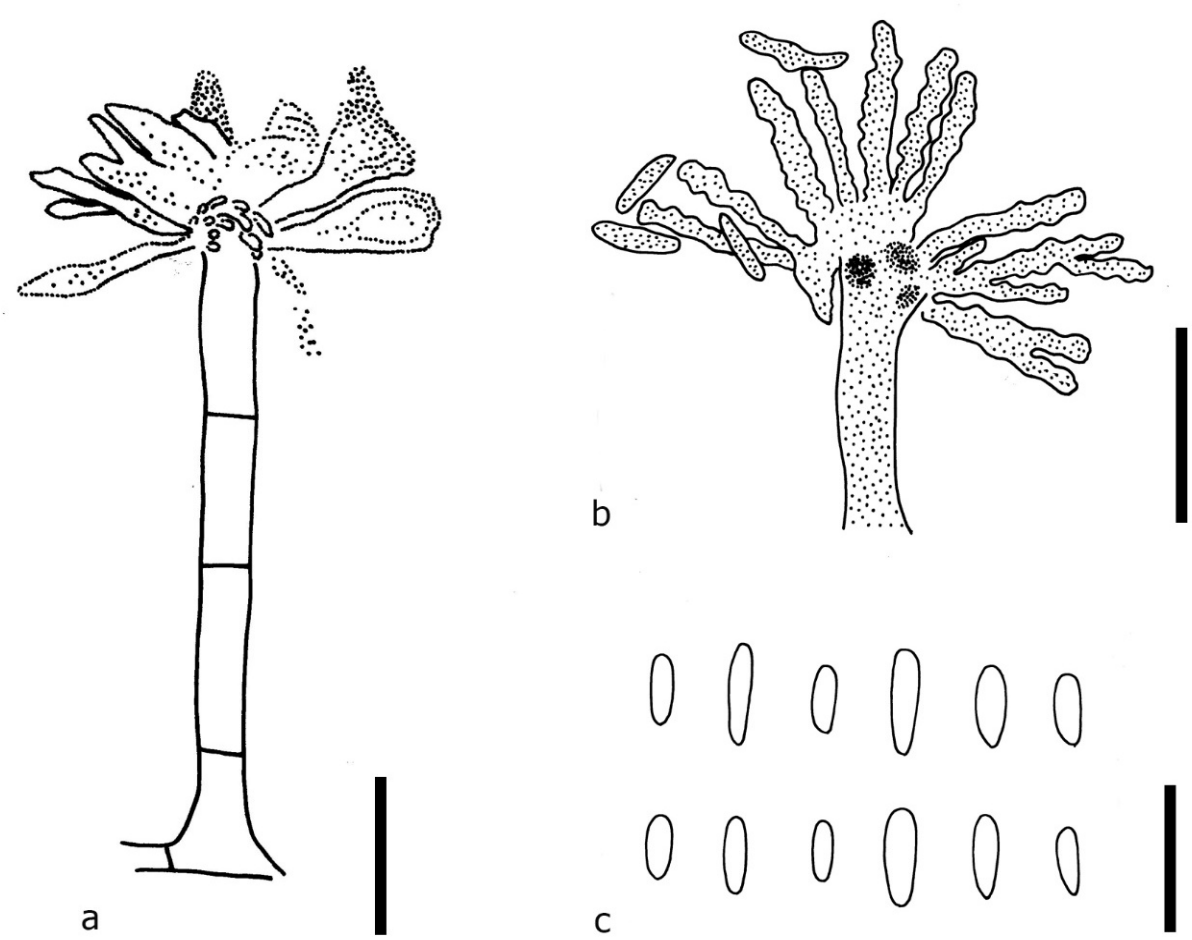


Figure 175 – Asexual morph of *Umbellidiales* (*Umbellidion radulans*). a Conidiophores, conidiogenous cells, and conidia. b, c Conidiogenous cells and conidia (drawn from Barreto et al. 2023). Scale bars: a–b = 10 μm.

Significance

Ecological and economic roles

Umbellidion radulans commonly reported in Brazil on dead leaves of *Alchornea triplinervia*, *Bucida palustris*, *Calliandra hygrophila*, *Chamaecrista belemii*, *Clusia melchiorii*, *Clusia nemorosa*, *Eucalyptus grandis*, *Eucalyptus paniculata* and *Humiria balsamifera* var. *parvifolia* (Barbosa et al. 2009, Barreto et al. 2023) and also reported from Caribbean region (Minter et al. 2001) as saprobe. Barreto et al. (2023) highlighted that the report of *Umbellidion* on *Eucalyptus* could be due to host jumping.

Chemical diversity

No relevant studies are available regarding the chemical diversity of the members of *Umbellidiales.*

***Lichinomycetes* V. Reeb, Lutzoni & Cl. Roux, Molecular Phylogenetics and Evolution 32(3): 1055 (2004)**

***Lichinales* Henssen & Büdel, Systema Ascomycetum 5(1): 138 (1986)**

Subphylum : *Pezizomycotina*
Class : *Lichinomycetes*
Subclass : *Lichinomycetidae*

Introduction

Lichinales is a medium sized order in *Ascomycota* which comprises ca. 400 species assigned to ca. 64 genera (Lücking et al. 2017, Wijayawardene et al. 2020, Prieto et al. 2024). They are lichen forming fungi obligatorily associating with cyanobacterial photobionts. Most of the species are small, inconspicuous blackish jelly lichens with homoiomerous thalli (Henssen 1963a, Schultz & Büdel 2002; Fig. 176 – XY). However, they are unrelated to other groups of gelatinous lichens such as *Collemataceae* (*Peltigerales*), *Physma* (*Pannariaceae*, *Peltigerales*), *Gabura* (*Arctomiaceae*, *Baeomycetales*). Evidently, the jelly lichen type of life form has evolved independently several times within the *Ascomycota*. Species of *Gloeoheppia*, *Heppia*, *Peltula* and *Pseudopeltula* have a subgelatinous thallus consistency approaching that of *Epiphloea* (*Collemataceae*, *Peltigerales*) and even pannariaceous lichens (*Pannariaceae*, *Peltigerales*) though always lacking a distinct dark hypothallus. Most of the *Lichinales* are characterized by thin-walled, prototunicate asci with passive ascospore discharge (Henssen & Jahns 1974, Büdel 1987a, b, Schultz & Büdel 2002, 2003, Prieto et al. 2024; Fig. 176 – XY m, o), whereas unitunicate rostrate asci with active discharge occur only in *Peltula* (Büdel 1987a, b; Fig. 176 – XY l), *Pyrenopsis* (Henssen et al. 1987) as well as *Allopyrenis* and *Pleopyrenis* (Prieto et al. 2024). The ascospores are simple and hyaline (Fig. 176 – XY l, m). Septate spores are very rarely observed. Molecular studies have shown that the *Coniocybales* (*Coniocybomycetes*) are closely related to the *Lichinomycetes* (Prieto et al. 2013).

Species of *Lichinales* are distributed worldwide mostly occurring on rock, but also in soil crust communities. A few species are short lived pioneers colonizing disturbed, meager soils. Only five species are epiphytes. Most species prefer open situations, occurring for example in rain tracks on inclined rock faces. A number of species live in (semi)aquatic conditions on lake shores and rocky river banks. Three species grow in the intertidal and splash zones along cool temperate coasts in both hemispheres. Diversity seems higher in (sub)tropical regions with hotspots e.g., in the Sonoran Desert and Arabian Peninsula indicating that diversification may have benefitted from successful adaptation to arid conditions. *Lichinales* are among the last lichens to occur in hyper arid deserts (Schultz 1998, Brown et al. 2002). However, they occur in the wet tropics as well (Büdel et al. 1997a, Schultz et al. 2000, Schultz & Aptroot 2008). Diversity is low in temperate, lowland regions (e.g., in Central Europe), but increases towards higher latitudes and cool-moist conditions. As pioneer species they are able to grow in a variety of open habitats as long as microclimatic conditions are suitable. Thus, several species that are widely distributed in the Mediterranean occur with isolated, azonal outposts in suitable thermophilic sites in Central and northern Europe. Examples are *Lichinella stipatula* and *Peltula euploca* lichens that are rare north of the Alps and redlisted e.g., in Germany and Sweden (Thor 1998, Wirth et al. 2011). Several (semi)aquatic species occupying narrow ecological niches and requiring clear water have declined considerably in the past due to water pollution and eutrophication as well as habitat loss caused e.g., by reforestation and are thus listed as endangered in Germany (Wirth et al. 2011).

There are no fossils known. Interestingly, the zygomycetous *Winfenatia reticulata* described from Rhynie Chert in the Lower Devonian (Taylor et al. 1997) has a thallus composition partly resembling that found in modern *Lichinales* (e.g., *Paulia*).

History

Lichina, on which order *Lichinales* is based, was erected by Agardh (1817) as a genus of algae in section *Fucoideae*. The corresponding species, *Lichina pygmaea* was described in 1777 as a species of sea weeds, *Fucus pygmaeus*. Interestingly, the other marine species of *Lichina*, *L. confinis*, was described in 1782 as a lichen, *Lichen confinis*. Nylander (1854) established for genus *Lichina* the family *Lichinaceae* in tribe *Lichineae*, and placed *Ephebe* and *Gonionema* in tribe *Ephebeae* of the same family. Other genera today classified in *Lichinales* were placed by Nylander (1854) in families *Collemaceae* (*Synalissa*, *Omphalaria*, *Phylliscum*) and *Lichenaceae*, tribe *Lecanoreae* (*Pyrenopsis*) along with many unrelated lichens. The anatomically simple jelly lichens took a basal position in Nylander's system linked with algae (Nylander 1854). In general, early classifications from late 18th until mid of the 20th century remained strongly artificial regarding the placement of

gelatinous lichens, and members of the *Lichinales* were no exception. A fundamental step forward was achieved by Henssen (1963a) who revised the families *Ephebaceae* and *Lichinaceae* and included the former in the latter, thus uniting species in just one family that had been kept apart for a long time and by various authors basically because of their different external appearance and type of cyanobionts. Instead, Henssen's new family and genus concept was largely based on similarities in ascoma ontogeny and mycobiont hyphal systems. Henssen & Jahns (1974) included in suborder *Lichinineae* (*Lecanorales*) the bulk of the genera classified in family *Lichinaceae*, while *Peltula* and *Heppia* remained in *Heppiaceae* suborder *Lecanorineae*. However, *Lichinaceae sensu* Henssen & Jahns already included *Lempholemma*, a genus of species with *Nostoc* photobionts that starting with Bernhardi's Lichenes gelatinosi (1799) had been treated for 175 years together with other cyanolichens, mostly of the *Collemataceae*. Finally, Henssen (1980) included all *Pyrenopsidaceae* into *Lichinaceae*. The order *Lichinales* was established by Henssen & Büdel (1986) for *Lichinaceae* and the family *Peltulaceae* was erected within this order by Büdel (1986, 1987a). After Hafellner (1984) described the new family *Harpidiaceae* for *Euopsis* and *Harpidium*, Henssen et al. (1987) moved these two genera to *Lichinaceae*. The *Heppiaceae sensu* Henssen (1994) remained monotypic and were thought to take an isolated position with affinities to *Coccocarpiaceae*, *Collemataceae* and *Placynthiaceae* (all today in *Peltigerales*). Finally, *Gloeoheppiaceae* have been established by Henssen (1995) for *Gloeoheppia*, *Gudelia* and *Pseudopeltula* and placed in *Lichinales*. Besides the reshaping of family classification, A. Henssen monographed several genera of the *Lichinaceae*, described many new genera and species, providing valuable and lasting contributions to our understanding of the *Lichinales*. New insight was gained with molecular data becoming available. Lutzoni et al. (2001) reconstructed genera *Peltula* and *Lempholemma* of *Lichinales* at a basal position in *Ascomycota* with affinities to *Sordariomycetes* and *Dothideomycetes*, though with low support. Schultz et al. (2001) found *Lichinales* to be monophyletic based on species from eight genera covering *Heppiaceae*, *Peltulaceae* and *Lichinaceae* but basal relationships remained unresolved. Schultz & Büdel (2003) found *Heppia* and *Heppiacea* to be nested within *Lichinaceae*. Reeb et al. (2004) formally described the class *Lichinomycetes*, however basal relationships of this clade remained poorly supported. Subsequent phylogenies found *Lichinales*/*Lichinomycetes* in varying basal positions and affinities to different other major fungal groups (Peršoh et al. 2004, James et al. 2006, Lücking et al. 2008, Schoch et al. 2009a). Prieto et al. (2013) reconstructed a phylogeny with *Lichinomycetes* in a highly supported sister relationship with the new class *Coniocybomycetes*. Prieto et al. (2019) excluded *Lichinodium* from *Lichinomycetes* because it was shown to fall into *Leotiomycetes* representing the only currently known lichen-forming lineage in this class.

Recently, Diaz-Escandón et al. (2022) proposed to include six different fungal classes (*Coniocybomycetes*, *Geoglossomycetes*, *Xylonomycetes*, *Candelariomycetes* and *Sareomycetes*) in *Lichinomycetes* arguing similarities on genome content and gene repertoires. This decision is not well supported as it is based on a low number of representatives, which also showed genomic similarities with other classes. Thus, and although these classes are shown to have a common ancestor there is no further support for grouping all together in the same class as it is confusing to encompass a disparate range of morphologies and vital forms. Based on a comprehensive sampling across the order and a robust three gene phylogeny Prieto et al. (2024) showed that the current family classification into families *Gloeoheppiaceae*, *Heppiaceae*, *Lichinaceae* and *Peltulaceae* is highly artificial and that most of the large crustose genera are polyphyletic (*Lempholemma*, *Psorotichia*, *Pterygiopsis*, *Pyrenopsis*). The improved understanding of evolutionary character change has been translated into a novel family classification with an emended circumscription of family *Lichinaceae* (incl. *Gloeoheppiaceae*), reestablishment of *Porocyphaceae* (incl. *Ephebaceae* p.p., *Heppiaceae*, *Pyrenopsidaceae* p.p.) and *Phylliscaceae* (incl. *Lichinaceae* p.p., *Peltulaceae*, *Pyrenopsidaceae* p.p.) and description of the new family *Lichinellaceae* (*Lichinaceae* p.p.). At genus level, many genera have been reshaped to form monophyletic taxa which required resurrection of genera from synonymy (*Cladopsis*, *Collemopsis*, *Forssellia*, *Pleopyrenis*, *Synalissina*), the description of many new genera (*Allopyrenis*, *Gonotichia*, *Lapismalleus*, *Lingolemma*, *Paludolemma*, *Paracyphus*, *Peltolemma*,

Pseudocarpon, *Pseudotichia*, *Pycnolemma*, *Tichocyphus*) and the synonymization of *Cryptothele* under *Phylliscum* and *Gonohymenia*, *Rechingeria* and *Thallinocarpon* under *Lichinella*.

General description

Lichen-forming Ascomycetes with cyanobacterial photobionts from *Chroococcales* (*Gloeocapsa*), *Chroococcidiopsidales* (*Aliterella*, *Chroococcidiopsis*, *Pseudocyanosarcina*), *Nostocales* (*Nostoc*, *Rivularia*, *Scytonema*), *Pleurocapsales* (*Myxosarcina*) and *Stigonematales* (*Stigonema*) (Büdel 1982, 1992, Jung et al. 2021). Mostly jelly lichens characterized by small, inconspicuous thalli of blackish or dark olivaceous color, usually homoiomerous and distinctly swelling when wet or stratified and subgelatinous.

Sexual morph: *Thallus* crustose, squamulose, foliose, dwarf fruticose or filamentous (Fig. 176 – a–i), superficial or immersed in the substrate. *Thallus* color black, dark olive, rarely greyish from pruinose or whitish, soralia, isidia, superficial outgrowths or accessory lobules present. *Apothecia* roundish, adnate to immersed, sometimes shortly stalked (Fig. 176 – b, d–i) or gall like, discs blackish, dark reddish or brownish, open or remaining very narrow (perithecioid) or covered by sterile thalline plectenchyma (thallinocarps; Fig. 176 – o). *Excipulum* zeorine, lecanorine or biatorine, excipulum thallinum a continuation of the vegetative thallus, excipulum proprium of parallel or interwoven hyphae, pale or brownish or blue green. *Hypothecium* pale, roundish, inversely cone-shaped or shortly stalked. *Asci* clavate to cylindrical or irregular (Fig. 176 – l, m, o), thin-walled and prototunicate opening by apical ruptures and releasing ascospores passively (Fig. 176 – m) or apically thickened and unitunicate-rostrate discharging ascospores actively (Fig. 176 – l), 8-spored or polysporous, formed from ascogenous hyphae with croziers, ascoma development with different pathways, either ascogones and trichogynes directly formed from thallus hyphae or in spheroid or cone-shaped tangles of generative hyphae or below pycnidia (pycnoascocarps; Fig. 176 – n). *Ascospores* simple, ellipsoid, or spherical, pale, smooth (Büdel 1987a, Henssen 1963a, 1994, 1995b, Schultz & Büdel 2002; Fig. 176 – l, m). Asexual morph: Anamorphs growing independently from the lichen thallus in nature are unknown so far and attempts to establish axenic cultures from mitotic as well as meiotic spores remained unsuccessful to date. *Pycnidia* formed in the vegetative lichen thallus are immersed or sessile, pyriform to globose, wall hyaline, simple, sometimes involute, thin, of interwoven hyphae, pycnospores small bacilliform, ellipsoid or globose, or large and filiform, terminally produced on simple or apically branched conidiophores (adapted from Büdel 1987a, Henssen 1963a, 1994, 1995, Schultz & Büdel 2002) (Fig. 176).

Families included in *Lichinales*

Lichinaceae Nyl.
Lichinellaceae M. Prieto & M. Schultz
Phylliscaceae Th. Fr.
Porocyphaceae Körb.

Evolution

With the exclusion of *Lichinodium* from the *Lichinaceae* and *Epiphloea* from the *Heppiaceae*, *Lichinales* is a monophyletic group forming its own class *Lichinomycetes* (Schultz et al. 2015, Prieto et al. 2019, 2024) and with *Coniocybomycetes* as closest relatives (Prieto et al. 2013). Yet, there is considerable variability in characters of both, the vegetative thallus (including the type of cyanobiont) and reproductive structures. Major types of growth forms such as crustose, foliose, dwarf fruticose are present in several genera and evolved independently several times as the ancestor for the *Lichinomycetes* and for the different families is reconstructed as crustose (Prieto et al. 2024). Because *Lichinales* often grow together under similar ecological conditions, the parallel presence of various growth forms between different genera or even within one genus likely reflects successful solutions in adaption to similar site conditions. This is true for example in the species rich genus *Peltula* (Kauff et al. 2018), but also *Lichinella* and *Peccania* (Prieto et al. 2024).



Figure 176 – *Lichinales* growth form, thallus and ascoma anatomy. a *Lichina confinis*, thallus dwarf-fruticose (Schultz 13122). b *Synalissa ramulosa*, clavate branches with terminal apothecia (Schultz 08929). c *Ephebe lanata*, thallus filamentous (Schultz 03544). d *Cladopsis schaereri*, thallus crustose with adnate apothecia (Schultz 03437). e *Pyrenopsis subareolata*, thallus areolate, apothecia immersed (Halda 17346). f *Peltula obscurans* var. *deserticola*, thallus small squamulose with adnate apothecia (Schultz 19132). g *Peltula coriacea*, thallus squamulose-lobate with immersed apothecia (Schultz 19168). h *Heppia adglutinata*, thallus squamules adpressed to substrate, apothecia widely open (Schultz (03481). i *Gloeoheppia turgida*, inflated squamules with immersed apothecia (Schultz 18035f). j *Anema decipiens*, homoiomerous, gelatinous thallus anatomy (Schultz 03424a). k *Peltula farinosa*, thallus heteromerous, subgelatinous (Schultz 19115). l *Peltula euploca*, polysporous, unitunicate-rostrate ascus (Marques 1247). m *Lempholemma polyanthes*, 8-spored, prototunicate ascus with simple ascospores (Schultz 08654). n *Lempholemma minutulum*, early stage of ascoma development with abortive pycnidium and coiled ascogones in tangle of generative hyphae below, in LPCB (Schultz 03644). o *Lichinella myriospora* s.l. thallinocarp with polysporous asci and sparse paraphyses covered by sterile thallus tissue (Schultz 17157). Scale bars: a–i = 1 mm, j–o = 25 µm.

Genera not accepted or excluded here: *Corynecystis* Brusse (= *Peltula*, based on *P. capensis*), *Finkia* Vain. (to *Thelenella*, unpubl.), *Mawsonia* Dodge (nom. conf, unpubl.), *Phylliscidiopsis* Sambo (to *Peltula*, unpubl.), *Placoheppia* (Zahlbr.) Oxner (=*Peltula*, based on *P. placodizans*), *Pseudarctomia* Gyeln. (uncertain), *Solorinaria* (Vain.) Gyeln. (likely to *Peltula*, unpubl.).

A peculiar feature shared by roughly half of the species of *Lichinales* is the formation of pycnoascocarps. This type of ontogeny is predominantly found in *Porocyphaceae*, but also occurs in a few genera in *Lichinaceae* and *Phylliscaceae*, whereas it is absent in *Lichinellaceae*. The successive transformation of pycnidia with ascogones and trichogynes below into common apothecia is a slow, complex process and several subtypes have been described (Henssen 1963a). Furthermore, such pycnoascocarps are also found in *Harpidium*, a lichen genus included in *Lichinales* together with *Euopsis* (Henssen et al. 1987). However, molecular data indicate that both genera fall outside *Lichinales* and are currently placed in *Harpidiaceae*, a family of uncertain position within the *Pezizomycetes*. Another peculiar type of fruiting bodies in the *Lichinales* are the so called thallinocarps. This type of ascoma is characterized by a strong reduction of excipular and hamathecial structures. It is restricted to *Lichinella*, in family *Lichinellaceae,* but thallinocarpous fruit bodies have also been described from the enigmatic genus *Edwardiella* (Henssen 1986). Approximately half of the *Lichinales* produce common apothecia as ascocarps. This type of ontogeny is predominantly found in *Lichinaceae*, but also occurs in a few genera of *Lichinellaceae* (*Synalissina*), *Phylliscaceae* (*Peccania*, *Peltula*) and *Porocyphaceae* (e.g., *Heppia*), The ascomata develop from free coiled ascogones or within a tangle of generative hyphae. Again, conidiospores produced from pycnidia likely serve as spermatia just like in pycnoascocarps, and occasionally small conidia sticking to the tips of trichogynes protruding from ascoma primordials can be observed. Nothing, however, is known about the fertilization genetics. Prieto et al. (2024) have shown that *Lichinomycetes* and all families ancestors are reconstructed as having pycnoascocarps except the *Lichinellaceae* which is reconstructed as having thallinocarps.

Several ascus types are present in the *Lichinales*. Unitunicate-rostrate asci with a markedly thickened apex, strong amyloid staining in KOH/Lugol and active ascospore discharge occur in *Peltula* and *Allopyrenis* (*Phylliscaceae*), but also in *Pleopyrenis* and *Pyrenopsis* (*Porocyphaceae*). This type of ascus thus evolved at least twice in the order. The majority of the *Lichinales*, however, possess prototunicate asci. The latter are uniformly thin walled, but may the surrounded by a strongly or weakly amyloid coat (hymenial gelatin) and open by ruptures in the apical wall or by disintegration of the entire wall, thus releasing ascospores passively. There is no obvious correlation between dispersal mode and number of ascospores. While *Peltula* invariably produces polysporous asci, there are octosporous as well as polysporous asci in species of *Allopyrenis* and *Pleopyrenis* with unitunicate-rostrate asci. And among those species of *Lichinales* with prototunicate asci, there are also species with constant eight or 16–24 ascospores. Prieto et al. (2024) have shown that type of asci is not reconstructed with confidence in most families except *Lichinaceae* which is reconstructed as *Lichina* type asci. Multisporic asci have evolved at least nine times within the order. Main results from divergence time estimate analyses (Prieto et al. 2024) show that the *Lichinomycetes* diversified between 114–209 MYA and families *Lichinaceae, Porocyphaceae* and *Phylliscaceae* diversified in similar dates in the lower Cretaceous, *Lichinellaceae* being the youngest family (upper Cretaceous).

Justification of order and problems

Phylogenetic studies showed *Lichinales* as an independent lineage in *Ascomycota***,** closely related with *Coniocybales* (Prieto et al. 2013, Beimforde et al. 2014, Voglmayr et al. 2019a). This result is partially supported by genomic data (Díaz-Escandón et al. 2022). However, in this latter study the authors proposed to subsume other classes of *Ascomycota* (including *Coniocybomycetes, Candelariomycetes, Geoglossomycetes, Sareomycetes and Xylonomycetes*) under *Lichinomycetes*. In our opinion this decision is not well supported as it includes a wide variety of morphologies, ecology and trophic modes and it is only justified by the presence of small genomes with reduced metabolic arsenals and it is based on a low number of representatives. Moreover, the phylogenetic analyses

from this review do not support the latter decision. Thus, *Coniocybomycetes, Candelariomycetes, Geoglossomycetes, Lichinomycetes, Sareomycetes and Xylonomycetes* should be considered as different classes.

Significance

Ecological and economic roles

Lichinales are jelly lichens and these require liquid water for activation of photosynthesis after desiccation (Büdel & Lange 1991, Lange et al. 1993). Therefore, they colonize steep rocky walls moistened by seeping water after rain fall or that get seasonally wetted from melting snow. In such habitats they are always accompanied by free living cyanobacteria (*Chroococcidiopsis*, *Gloeocapsa*, *Scytonema* and others). Either free living or in lichenized stage, these cyanobacteria are able to fix atmospheric nitrogen (Crittenden et al. 2007). Thus, *Lichinales* is an ecologically important group of lichens (Dojani et al. 2007, Lumbsch & Lücking 2016, Weber et al. 2016), especially in arid soil crust communities where species of *Lichinales* often occur (*Gloeoheppia*, *Heppia*, *Lichinella*, *Peccania*, *Peltula*). The accumulation of fixed nitrogen in raw soils is a crucial element for the establishment of vascular plant communities (Nash 2008, Weber et al. 2016).

Lichinales growing in sites fully exposed to the sun show different adaptations to minimize negative effects from excess radiation. Examples include the dark coloration of the lichen thallus caused by pigments of the cyanobacterial photobionts in ecorticate, homoiomerous *Lichinales* (Büdel et al. 1997b), epinecral layers and a thickened upper cortex resulting in total reflection of striking light causing an unusual pale coloration ranging from yellow olive or grey to even white in certain species of *Pseudopeltula*, *Peltula* and *Heppia* (Büdel 1992, Henssen 1994), deposition of mineral pruina on the thallus (*Thyrea confusa*) and inverse thallus anatomy in *Peltula inversa* growing on quartz pebbles in desert habitats (Büdel & Schultz 2003).

Potential economic applications lie in biological properties of cyanobacterial pigments in UV absorption as reported e.g., by Büdel et al. (1997b) for different cyanolichens including *Lichinales*. Recent advances are directed to search biosynthetic enzymes and natural products from symbiotic cyanobacteria (D'Agostino 2023).

Chemical diversity

Complex chemical compounds typical for so many groups of lichens (lichen acids) are unknown in the *Lichinales*. However, myeloconone B1 and 2 have been reported from *Peltula langei* (Büdel & Elix 1997). Ascomatal and pycnidial fruiting structures contain various fungal pigments of yellowish, reddish, brownish or emerald coloration. The reddish-brown epithecial pigment in *Peltula obscurans* var. *obscurans* turns purple in KOH. The emerald green pigment in the upper exciple, hymenial umbo and ostiole of the pycnidium turns blue in nitric acid. The blackish coloration of the thallus, however, is caused by cyanobacterial pigments deposited by the cyanobionts in their thick gelatinous sheaths. The resulting coloration is strongest in sun exposed thallus parts indicating that the pigmentation is connected with avoidance of excess radiation and photo respiration. Examples are scytonemin, an aromatic indole alkaloid, and gloeocapsin, a pigment of indetermined nature showing a characteristic change of color from red under low, acidic pH conditions to purple at high, alcaline pH values.

Other relevant data and future recommendations

The taxonomy of many genera and species is insufficiently known. Molecular studies in one of the most speciose genera of the order, *Peltula*, revealed considerable problems in matching traditionally circumscribed morphospecies with their reconstructed phylogenetic relationships (Kauff et al. 2018). Problems emerge from the overall simple general organization of the lichen thallus with few characters to observe, a very uniform ascoma anatomy, the parallel gain of certain growth forms in evolutionary adaptation to similar habitat conditions and an obviously high infraspecific phenotypic plasticity of supposedly very widespread and variable species. Such morphospecies should be carefully scrutinized for (sub)cryptic speciation using molecular data retrieved from broad sampling. Yang et al. (2022b) described new species of *Peltula* superficially resembling known taxa

but clearly deviating in their phylogenetic placement. Chrismas et al. (2023) reported that the marine lichen *Lichina pygmaea* not only contains the well-known *Rivularia* cyanobionts, but also a pleurocapsalean cyanobiont that is believed to contribute substantially to the lichens' metabolism. However, photographic evidence provided in that paper to illustrate presence of different cyanobionts in *Lichina pygmaea* remains ambiguous and occurrence of free living *Pleurocapsa* in the studied type of habitat is well known (B. Büdel, pers. comm.). Aptroot & Schumm (2010) reported chimeras in *Peltula corticola* containing cyanobacterial and green algal photobionts and compared these with photosymbiodemes in unrelated cyanolichens such as *Lobaria* and *Sticta* (*Peltigerales*). Garrido-Benavent et al. (2023) showed that long distance dispersal across oceans played a major role in speciation events in marine lichen genus *Lichina*.

***Orbiliomycetes* O.E. Erikss. & Baral, Myconet 9: 96 (2003)**
***Orbiliales* Baral, O.E. Erikss., G. Marson & E. Weber, Myconet 9: 96 (2003)**

Subphylum : *Pezizomycotina*
Class : *Orbiliomycetes*
Subclass : *Orbiliomycetidae*

Introduction

Orbiliales is an early-branching lineage within the subphylum *Pezizomycotina* of the *Ascomycota* (Pfister 1997). However, its recognition as a formal taxonomic entity at the order level came relatively later. Initially, *Orbiliaceae* was considered as a minor family within *Helotiales* (an order later recognized within the class *Leotiomycetes*) (Kimbrough 1970). Throughout the 19th and 20th centuries, *Orbiliaceae* was often confused with *Helotiales*, *Phacidiales*, *Pezizales*, and even some groups within the *Basidiomycota* (Baral et al. 2020). Only recently, through the use of vital taxonomy based on microscopic morphological features, *Orbiliaceae* was clearly distinguished from its confusing counterparts (Baral et al. 2020). Additionally, molecular data demonstrated the monophyletic nature of *Orbiliaceae*. Consequently, this group was eventually elevated to the independent class *Orbiliomycetes*, encompassing the order *Orbiliales.* The order *Orbiliales* comprises one family, *Orbiliaceae*, which includes seven accepted sexually-typified genera (*Amphosoma*, *Bryorbilia*, *Liladisca*, *Lilapila*, *Pseudorbilia*, *Hyalorbilia*, *Orbilia*) and three asexually-typified genera (*Lecophagus*, *Mycoceros*, *Retiarius*). While, *Mycoceros* and *Retiarius* lack known sexual forms (Baral et al. 2020).

Orbilia, the largest genus within *Orbiliales*, encompasses nearly 90% of the species within the entire order (Baral et al. 2018a). The difficulty in studying this large genus is due to few morphological characteristics, from tiny ascomata and the lack of molecular data for many old specimens. The asexual forms were studied independently from *Orbilia* for a long time, and their narrower criteria were applied to separate asexual genera (Baral et al. 2018a, 2020). In the past two decades, many connections between sexual and asexual forms have been established (Pfister 1994, Mo et al. 2005, Liu et al. 2005, Qiao et al. 2012), leading to several asexual-defined genera within *Orbilia* based on conidial morphological features. One fungus one name working group of *Orbiliales* proposed a practice solution within the broader context of the genus *Orbilia* to address this incongruity, and three subgenera, eight sections, and 30 series were introduced to guide their usage in different scenarios (Baral et al. 2018a).

Orbiliaceous fungi are mainly saprobic, and some groups obtain nutrition through carnivorism and parasitism. The carnivorous can develop various specialized trap devices to capture small invertebrates such as nematodes, thereby securing additional nitrogen sources (Hyde et al. 2014). This unique feature holds promise for developing biological control agents targeting agricultural and pastoral nematode pests (Jiang et al. 2017c). Most *Orbiliales* fungi are ubiquitous in global habitats, including extreme environments, due to their versatile substrate preference and lack of strict host-specificity (Jiang et al. 2017c, Baral et al. 2020). However, sexual forms are more often encountered in natural habitats than in disturbed habitats like crop fields.

History

The study of fungi belonging to the order *Orbiliales* spans over 220 years (Persoon 1801, Albertini & Schweinitz 1805, Fries 1815). Initially, macroscopic features such as the shape, color, transparency of the apothecia, and the presence or absence of a stalk served as the primary classification criteria for this group (Persoon 1801, Fries 1815). However, these macroscopic features closely resembled those of *Helotiales*, leading to a situation where orbiliaceous fungi were not initially recognized as a distinct natural lineage. Instead, they were often confused with various distantly related genera. During the 19th and 20th centuries, as many as 30 genera now recognized as belonging to *Helotiales*, *Phacidiales*, *Pezizales*, or even *Basidiomycota* were placed within *Orbiliaceae* (Baral et al. 2020). Only when the significance of microscopic features became evident did the study of *Orbiliales* fungi enter a new phase. Based on the morphological characteristics and molecular data, the *Orbiliaceae* was formally elevated to class *Orbiliomycetes* in 2003 (Eriksson et al. 2003a).

Baral et al. (2020) published a comprehensive monograph presenting a systematic research framework for the class *Orbiliomycetes*, marking the most comprehensive study of *Orbiliales*. Their work reported 331 new sexually reproducing species, proposed 38 new combinations, two new names, and designated 33 epitypes, 39 lectotypes, three neotypes, and four reference specimens. Baral et al. (2020) highlighted several microscopic features as critical criteria for the classification of *Orbiliales*, including the structure of the ascus apex, the ascogenous system (croziers versus simple septa), the presence and shape of spore bodies (SBs) within living ascospores, the type of ectal excipulum, and the gel among and exudate over the paraphyses.

Orbiliaceous fungi exhibit a pleomorphic life cycle consisting of two markedly different states: apothecial (sexual) and conidial (asexual). Numerous asexual-typified species, notably in the *Orbilia* section *Arthrobotrys*, are known to belong to the latter state (Hyde et al. 2014, Baral et al. 2020). These nematode-trapping fungi were previously categorized into various genera based on the morphology of their conidia and conidiophores, such as *Arthrobotrys*, *Dactylellina*, *Drechslerella*, *Dactylella*, *Gamsylella* and *Monacrosporium* (Yu et al. 2014). Phylogenetic studies utilizing rDNA sequence data confirmed that the presence of trapping devices is a key morphological criterion for defining natural phylogenetic groups within this section. Subsequent molecular analyses by various researchers led to the redefinition of anamorphs in *Orbiliaceae*, and the section *Arthrobotrys* was subdivided into genera based on specific trapping mechanisms. Scholler et al. (1999) classified them into *Dactylellina*, characterized by stalked adhesive knobs and non-constricting rings; *Gamsylella*, characterized by stalkless adhesive knobs and adhesive branches; *Arthrobotrys*, characterized by adhesive networks; and *Drechslerella*, characterized by constricting rings. Non-carnivorous species were assigned to *Dactylella*. However, further molecular phylogenetic analysis led to different conclusions. Li et al. (2005) and Yang & Liu (2006) did not maintain *Gamsylella* as a separate genus but included its members in *Dactylellina*. In their recent monograph, Baral et al. (2020) retained *Gamsylella* as a valid genus, considering it a sister group to *Dactylellina*. However, we recommend to reject *Gamsylella* and *Dactylellina* characterized by two-dimensional traps including adhesive branches, knobs and non-constricting rings, *Arthrobotrys* by adhesive three-dimensional adhesive networks, and *Drechslerella* by mechanical constricting rings (Fan et al. 2021, Zhao et al. 2022b, Zhang et al. 2024b).

General description

Sexual morph: *Apothecia* round to undulating, cupulate to flat or convex, sessile or sometimes distinctly stalked, with a gymnohymenial, sometimes cleistohymenial development, superficial to erumpent, not or sometimes medium gelatinous, hyaline to bright, rarely dark-colored, exterior smooth or with short to long prolongations being frequently agglutinated as teeth, rarely with protruding teeth-like excipular tissue. *Asci* ± cylindrical in the region of the pars sporifera, apex of dead asci either hemispherical to subconical (irrespective of the viewing direction), or ± saddle-shaped (± truncate or hemispherical depending on the viewing direction), thin- or thick-walled, never with a ring structure in the apical wall, 8–128-spored, usually some of the spores inversely oriented

(if spores heteropolar), at maturity spores generally glued together to form a compact body being ejected as a single entity, arising from croziers or simple septa (then base often furcate). *Ascospores* hyaline at all development stages, almost always aseptate when mature but sometimes septate prior to germination, thin-walled, smooth or rarely warted by minute cell wall protrusions, never with sheaths or appendages, sporoplasm at maturity generally containing one or several variously-shaped refractive spore bodies (SBs, visible only in living state) and a few small lipid bodies (LBs), rarely also glycogen bodies. *Paraphyses* septate, apically inflated or not, with anastomoses at the base, branched below or also above. *The excipulum* is sharply or indistinctly divided into a compact rectal tissue of angular to prismatic cells and a dense or loose medullary tissue, usually a mixture of slender hyphae and inflated cells. *Cortical cells* at the margin and flanks sometimes terminated in short to very long, solid prolongations (glassy processes) or septate hairs. *Cells of paraphyses* and ectal excipulum often contain globose or elongated vacuolar bodies (VBs), globose or crystalloid cytoplasmic bodies (SCBs), or globose lipid bodies (LBs), the former two visible only in living state, the latter often containing carotenoids; exterior of apothecium usually covered by a granular to cloddy, hyaline to yellowish (rarely dark-colored) exudate.

Asexual morph: *Mycelium* hyaline, septate, smooth. *Conidiophores* are hyaline, thin-walled, smooth, unbranched or branched, mononematous or reduced, rarely synnematous, with holoblastic conidiogenesis, never included in a peridium. *Conidia* hyaline, smooth, thin-walled, either unbranched (amero-, didymo-, phragmo- or scolecosporous), straight or curved (falcate to canoe-shaped, rarely helicoid), sometimes with protuberances or variously branched (staurosporous), with straight or curved arms, 2- or 3-dimensional, lipid content low to sometimes high. Trapping devices known in some groups: adhesive pegs capturing rotifers in *Lecophagus*, peg-like knobs capturing rhizopods in *Hyalorbilia*, or various, mainly nematode-trapping devices (adhesive knobs, columns or networks, constricting and non-constricting rings) in *Orbilia* section *Arthrobotrys* (Figs. 177, 178).

Families included in *Orbiliales*

Orbiliaceae Nannf.

Evolution

Orbiliomycetes and *Pezizomyces* represent the oldest lineages within the *Ascomycota*, constituting two of the most basal or early diverging branches of *Pezizomycotina*. They form a monophyletic clade, which is the first segregate within *Pezizomycotina* (Pfister 1997, Eriksson et al. 2003a). Segregation of *Orbiliomycetes* must have occurred much earlier than in the Cretaceous era, which dates 145–66 million years. According to phylogenetic analyses, calibrated mainly by pyrenocarpous, lichenized, and calicioid (mazaediate) ascomycetous fossils from amber and chert pyrenocarpous, lichenized, and calicioid (mazaediate) ascomycetous fossils from amber and chert dating between around 460 and 15 MYA, the earliest diversification of *Pezizomycotina*, which resulted in the *Orbiliomycetes* and *Pezizomycetes*, took place about 550–350 MYA (Gueidan et al. 2011, Beimforde et al. 2014, Ekanayaka et al. 2017a, Baral et al. 2020).

The origin of carnivorous behaviour in fungi within the order *Orbiliales* is one of the most intriguing scientific inquiries. The earliest fossil evidence of fungi possessing predatory structures is represented by *Palaeoanellus dimorphus*, discovered in amber (Schmidt et al. 2007, 2008). This fungal fossil features a ring-shaped trapping structure and dates back approximately 100 million years. Based on fossil evidence, Yang et al. (2007, 2012) conducted a multi-gene analysis of the ITS sequences and five protein-coding genes of nematode-trapping fungi within *Orbilia* to estimate the time of origin of this carnivorous trait. Their analysis indicates that the origin of nematode-trapping fungi predates approximately 419 MYA, around 550-600 million years after the appearance of nematodes. During the third mass extinction event from the Permian to Triassic periods, around 246 MYA, the mechanically active predatory organ (constricting ring) evolved. Subsequently, during the fourth mass extinction event from the Triassic to Cretaceous periods, around 208–198 MYA, adhesive trapping organs emerged and further diversified into various types.

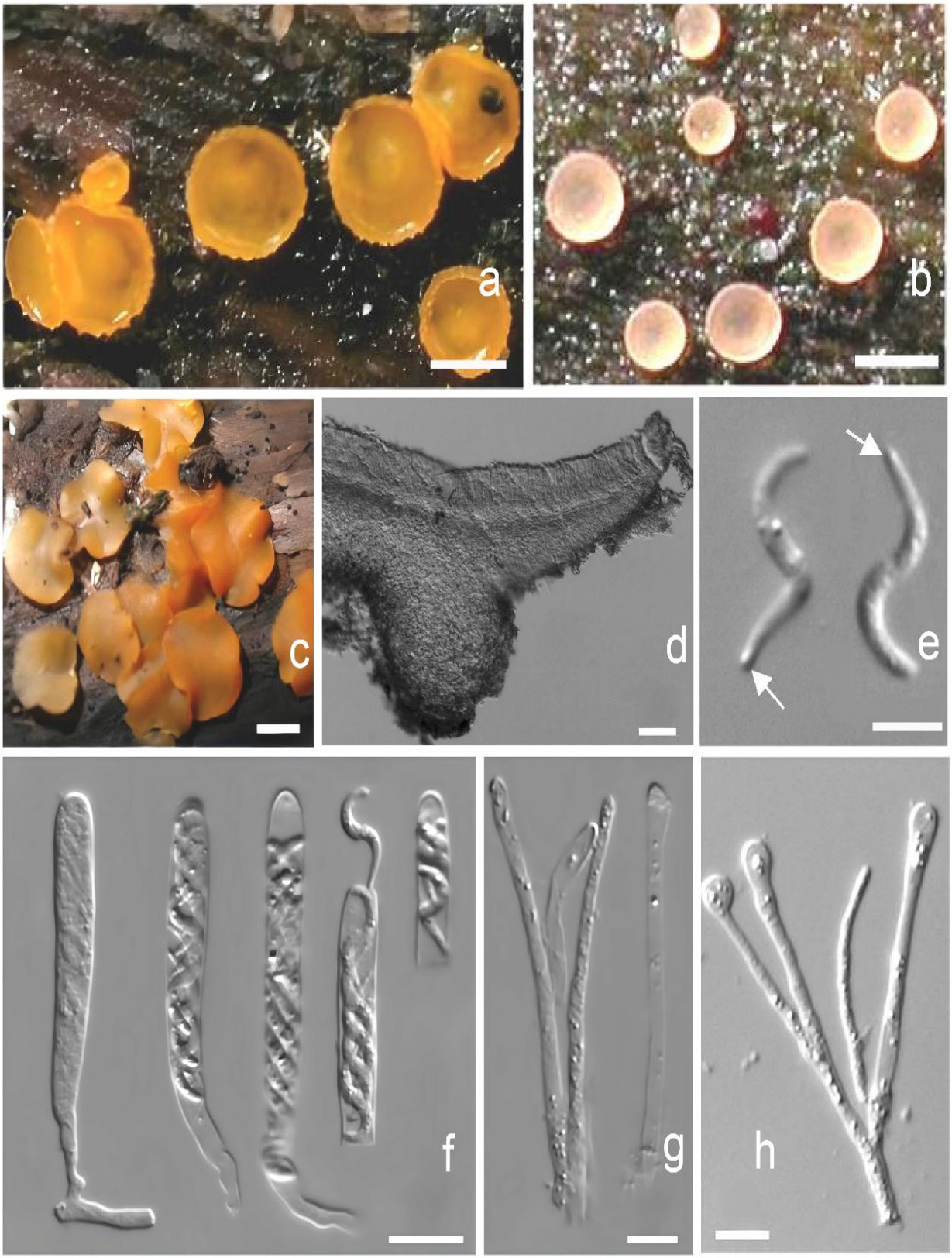


Figure 177 – Sexual morphs of *Orbiliales*. a–d Apothecia. e Ascospores with spore bodies (SB). f A asci. g, h Paraphyses. a, d, e, f, g *Orbilia bomiensis* (from Liu rt al. 2006). b *Orbilia sarraziniana* (from Liu et al. 2006). c *Orbilia delicatula* (from Liu 2006). h *Orbilia coccinella* (from Liu et al. 2006). Scale bars: a, b, c = 1 mm, d = 50 µm, e = 5 µm f = 10 µm, g = 5 µm, h = 5 µm.

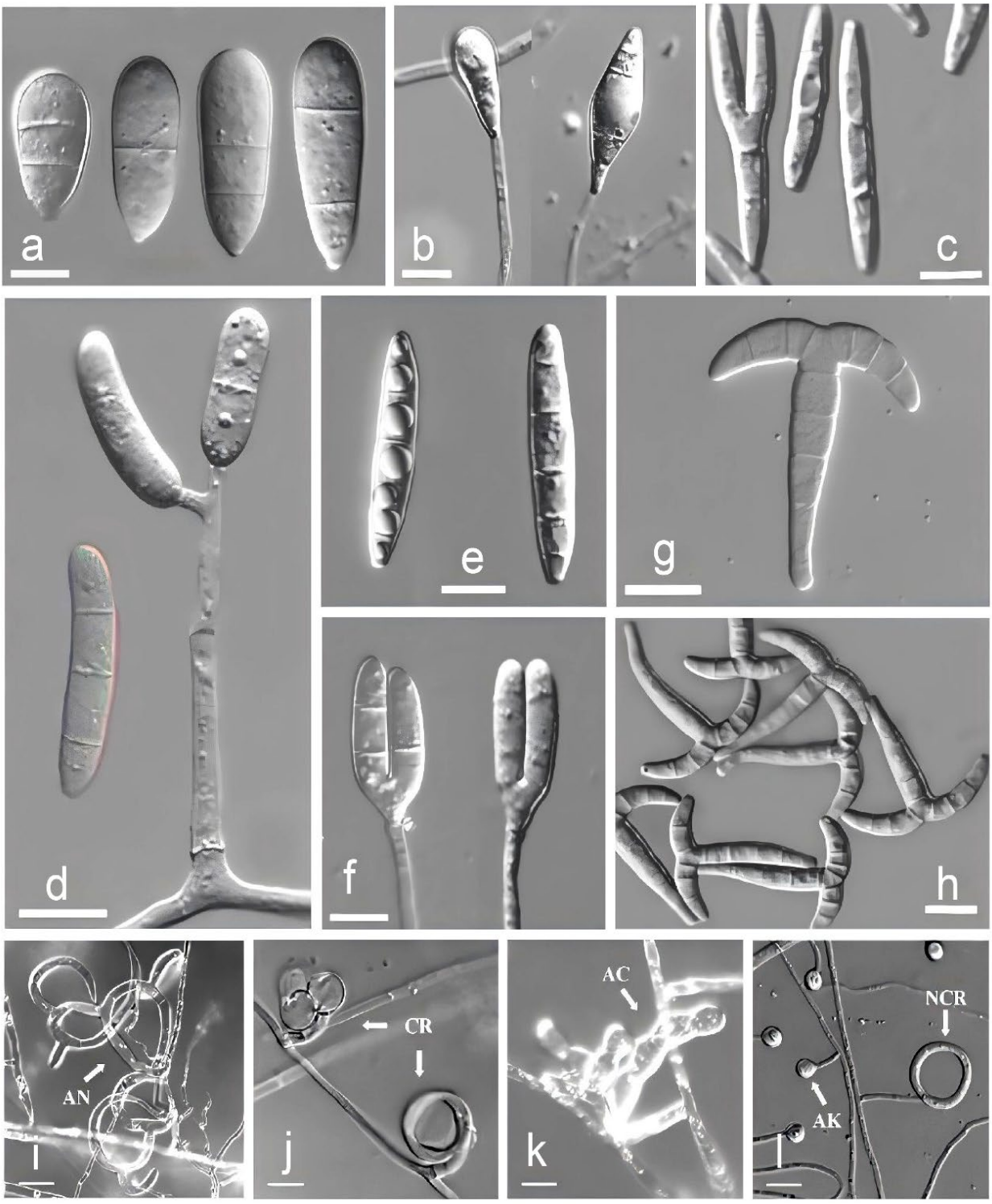


Figure 178 – Asexual morphs of *Orbiliales*. a–h: conidia and conidiophores; i-l: Trapping organs in series *Arthrobotrys* (from Yang et al. 2007). a *Arthrobotrys vermicola* (from Qiao et al. 2012). b *Dactylellina lysipaga* (from Liu 2006). c *Dicranidion tenue* (from Liu 2006; fit the asexual morphs of *O. leucostigma* and *O. xanthostigma*). d *Drechslerella brochopaga* (from Liu 2006). e, f *Dicranidion fragile* (from Liu 2006; fit the asexual morphs of *Orbilia eucalypti*). g, h *Trinacrium incurvum* (from Liu 2006; *Orbilia* subgenus *Hemiorbilia*). i Adhesive network. j Constricting rings. k Adhesive columns. l Non-constricting rings and adhesive knobs. Sclae bars: a, d, g, h, i, j, k, l = 10 µm, b = 20 µm, c, e, f = 5 µm.

Phylogenomic analyses on a whole-genome scale indicate that during the radiation evolution described above, NTF experienced extensive incomplete lineage sorting (ILS—a phenomenon where

ancestral genes are randomly retained during rapid radiation), localized introgression within lineages, and some events of horizontal gene transfer (Zhang et al. 2024b). Genes under significant positive selection among the ILS genes are associated with the morphological development of predatory organs (Zhang et al. 2024b).

This sequence of events could be attributed to the accumulation of substantial amounts of organic matter resulting from mass extinctions, leading to severe nitrogen deficiency in the environmental context and heightened competition among species. To adapt to these drastic environmental changes, fungi within the order *Orbiliales* evolved predatory structures to capture and obtain nitrogen sources, thus enhancing their competitive advantage. In a recent comparative genomics analysis based on whole-genome data from 18 nematode-trapping fungi in our research group, there is a significant genome trait for adaptation of high carbon/lower nitrogen niche and carnivorous lifestyle (Fan et al. 2024).

Justification of order and problems

The current species diversity within *Orbiliales* remains underexplored, with many described species lacking molecular data. Numerous genera are currently defined based on asexual morphologies due to the absence of observations of their sexual stages. As future research enriches the aforementioned data, many of the current classifications are expected to undergo changes, particularly in the genus *Orbilia*, which includes numerous subgenera and sections. Additionally, the recent genome-based study has revealed that the genomes of three strains of *Dactylellina cionopaga* within the *Arthrobotrys* section of the genus *Orbilia* exhibit interspecies-level differences, suggesting that *D. cionopaga* may represent a species complex (Zhang et al. 2024b). Currently, a single asexual morph corresponds to multiple sexual morphs, indicating the existence of more complex species. It is likely that similar species complexes within *Orbiliales* will require further investigation and revision in the future.

Significance

Ecological and economic roles

Orbiliales exhibit a broad ecological range from subtropical to polar regions and from deserts to humid evergreen forests (Baral et al. 2020). Some species even demonstrate extreme tolerance to drought and high temperatures, with certain anamorphs being found in thermal springs (Liu et al. 2014b). The substrates for saprobic fungi are remarkably diverse, ranging from decaying herbaceous and woody materials to fungal fruiting bodies, faeces, and even synthetic materials like textiles and ropes (Baral et al. 2020). Teleomorph forms of these fungi have not been reported to produce apothecia in soil, although soil serves as a habitat for their anamorphic forms. Orbiliaceous taxa do not exhibit strict substrate preferences or specialize for their prey hosts (Baral et al. 2020). Recent studies in phylogenetic biogeography have revealed that the spatial distribution of the long-believed globally distributed *Arthrobotrys oligospora* (= *Orbilia oligospora*) is not random or uniform but rather influenced by watersheds that shape its geographical distribution (Deng et al. 2023a, b). This phylogenetic distribution can even reflect the geological history of local watershed changes, providing valuable information for geography (Fornacca et al. 2024).

Economically, the main focus of exploiting those fungi lies within the carnivorous *Orbilia*. In agricultural settings, parasitic nematodes affecting crops and livestock can lead to significant economic losses (Poveda et al. 2020). The predatory abilities of *Orbilia* provide promising potential for developing biocontrol agents targeting these nematode pests. Currently, efforts are being made to enhance the virulence of *Orbilia* species against nematode pests, and biological nematicides containing nematode-trapping fungi have been either commercialized or are under development (Dong & Zhang 2006, Singh et al. 2012, Li et al. 2015).

Chemical diversity

The chemical diversity of orbiliaceous fungi has been primarily studied in nematode-trapping species, with a particular focus on metabolic compounds that are toxic to nematodes. Anderson et al. (1995) reported that three new oligosporon derivatives from *Arthrobotrys oligospora* were reported

to exhibit toxicity against intestinal parasitic nematodes. Additionally, various aliphatic and heterocyclic compounds, including linoleic acid, have been detected in several *Arthrobotrys* species (e.g., *A. brochopaga*, *A. conoides*), showing significant toxicity against *Caenorhabditis elegans* and *Meloidogyne incognita* (Anke et al. 1996, Wei et al. 2011).

A unique group of sesquiterpenyl epoxy-cyclohexenoids (SECs), including oligosporons, arthrobotrisins, and arthrosporols, has been isolated from *A. oligospora* (Stadler et al. 1993, Wei et al. 2011, He et al. 2019). These metabolites share a characteristic structure composed of a terpenoid-derived (TP) sesquiterpenyl unit linked to a polyketide-derived (PK) epoxy nucleus (He et al. 2019). Studies have shown that oligosporon and its dihydro derivatives exhibit selective toxicity against *Haemonchus contortus*, while among the three types of arthrobotrisins (A–C), only type A is effective against *Panagrellus redivivus* (Wei et al. 2011). Arthrobotrisin C has also demonstrated antimicrobial activity against *Bacillus subtilis* (Wei et al. 2011). Notably, these compounds play a regulatory role in the formation of trapping structures in nematode-trapping fungi (NTF), suggesting their involvement in trap morphogenesis (Wu et al. 2013, Yu et al. 2021).

Recent investigations have further highlighted the role of metabolites in the trapping process. *A. flagrans* produces 6-methyl salicylic acid (6-MSA) and arthrosporols, which inhibit premature trap formation (Yu et al. 2021). The mechanism involves 6-MSA secretion at the fungal hyphal tip, attracting nematodes into the colony. Upon nematode entry, ascarosides secreted by the nematodes trigger a fungal response that suppresses 6-MSA and arthrosporol production (Yu et al. 2021), ultimately enhancing trap formation within the hyphae for nematode capture. Additionally, several volatile compounds from *A. oligospora*, such as 2-methyl-1-butanol, 2,4-dithiapentane, methyl 3-methyl-2-butenoate, and S-methyl thioacetate, have been identified as nematode attractants (Hsueh et al. 2017).

Genomics and metabolomics approaches have been applied to explore the chemical diversity of *Orbiliales* fungi. While the gene clusters for secondary metabolites have undergone contraction in NTF, comparative genomic analysis has revealed key gene family expansions related to nematode capture, including adhesion proteins, CAP superfamily members, and aspartic proteases (Fan et al. 2024). Moreover, novel secondary metabolites, such as 2-furoic acid from *Dactylellina haptotyla*, have been shown to increase during nematode infection, effectively reducing damage caused by root-knot nematodes in tomatoes (Lei et al. 2023).

Despite these advancements, research on the chemical diversity of *Orbiliales* has remained largely focused on NTF, particularly a few model species like *A. oligospora* and *A. flagrans*, leading to an imbalance given the high species diversity within this fungal order. A deeper investigation into the ecological function of key metabolites in NTF, such as SEC compounds (oligosporons, arthrobotrisins, arthrosporols), as well as the broader chemical diversity of orbiliaceous fungi beyond NTF, is necessary. Future studies should integrate advanced techniques such as single-cell metabolomics, gene editing technologies, and *in situ* metabolome analysis to systematically uncover the multidimensional role of chemical diversity in the evolution and ecological functions of *Orbiliales* fungi.

Other relevant data and future recommendations

As a ubiquitous group of fungi and many associated with nematode pests, research in many regions and ecological settings, especially in specialized environments, needs to be conducted. Baral et al. (2020) noted that the canopy layer of forests could potentially host numerous xerophilic *Orbiliales* fungi. Nevertheless, our current exploration of such habitats remains a gap in our knowledge. Zhang et al. (2023a) discovered extant species in Yunnan, China's Three Parallel Rivers region (Nujiang River, N 27°43′14.60″, E 98°41′30.20″), resembling the earliest known nematode-trapping fungal fossil, *Palaeoanellus dimorphus*. This suggests that the area shaped by the uplift of the Qinghai-Tibet Plateau, which aided numerous species through the Quaternary glaciation, holds significance for the origin and evolution of *Orbiliales* species. Otherwise, recent findings have indicated that wildfires can alter the vertical ecological distribution of carnivorous *Orbilia* species in soil, making rare species more detectable (She et al. 2023). Researchers such as Zhang et al. (2022a,

in press) discovered numerous new species of nematode-trapping fungi within the family *Orbiliaceae* in such specialized habitats. These studies underscore the need to explore the biodiversity and ecological function of those promising fungi.

Furthermore, the genomic analysis has provided an excellent approach, especially for carnivorous orbiliaceous fungi. In addition to the biodiversity and ecological functions, several exciting issues like the origination and evolutionary history of carnivorous traits and behaviour (Zhang et al. 2024b), how fungi attract nematodes and nematodes trigger trapping device formation (Li et al. 2005, Fan et al. 2024, Hu et al. 2024, Kuo et al. 2024), and the instant inflation mechanism of constricting ring cells (Chen et al. 2023a).

***Pezizomycetes* O.E. Erikss. & Winka, Myconet 1(1): 8 (1997)**
***Pezizales* J. Schröt., Die Natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten 1 (1): 173 (1894)**

Subphylum : *Pezizomycotina*
Class : *Pezizomycetes*
Subclass : *Pezizomycetidae*

Introduction

Pezizales represents the sole order within the class *Pezizomycetes* (Ekanayaka et al. 2018). The taxa are mainly identified by operculate asci (Ekanayaka et al. 2018). *Pezizales* have a dehiscence mechanism that involves an apical circumscissile rupture of the ascus wall to produce a lid also known as operculum. However, operculate asci have been lost or reduced in several taxa (Trappe 1979) or ascus ruptures by a slit (Harrington et al. 1999). The order comprises more than 22 families that are accommodated in approximately 200 genera while several genera are placed in *incertae sedis* in the order (Pfister & Healy 2021) and this classification is also accepted in the recent outline (Hyde et al. 2024b).

History

The generic type *Peziza* was established by Dillenius (1719) who proposed the first formal classification of *Discomycetes*. The genus was later accepted by Linnaeus (1753) in Species Plantarum. Persoon (1801) treated eight discomycete genera in the order *Hymenothecii* in the class *Gymnocarpi*. Karsten (1871) treated *Discomycetes* as an order and accepted three families and 53 genera based on texture and shape of apothecia and ascospores. Saccardo (1884) used ascospore characters, including size, shape, color and septation for novel discomycetes classification and introduced two divisions, *viz*., those with a receptacle (the structure to support the hymenium), and those without and accepted eight families within the class *Discomycetes*.

Boudier's classification in 1885, primarily relied on the presence or absence of an operculum at the ascus apex. The classification of discomycetous fungi was continued based on microscopic measurements and microchemical reactions (Rehm 1887–1896, Höhnel 1917a, b, Seaver 1928b, 1951). Nannfeldt (1932) proposed three main groups of higher ascomycetes: *Plectoascales*, *Ascoloculares*, and *Ascohymeniales* and introduced nine orders within *Ascohymeniales* including four discomycetous orders; *Pezizales*, *Ostropales*, *Helotiales*, and *Lecanorales*. However, the phylogenetic analyses revealed that paraphyletic assemblages of discomycetes. Le Gal (1946) recognized two families in *Pezizales*, *viz*. *Sarcoscyphaceae* and *Pezizaceae* and both families are now being considered as families of *Pezizales*. Later, *Pezizales* and *Helotiales* were identified as distantly related based on the phylogenetic analyses conducted based on SSU sequence data (Landvik & Eriksson 1994). However, *Pezizales*, has been considered as a monophyletic group despite the clade was not strongly supported (Gargas & Taylor 1995). Consequently, a new class *Pezizomycetes* was established for *Pezizales* (Eriksson & Winka 1997) and which included both operculate discomycetes and *Tuberales*. The classification of *Tuberales* has been debated over the years and is being considered as synonymy of *Pezizales.* Ekanayaka et al. (2018) provided a detailed study of *Pezizomycetes* and accepted 21 families under *Pezizales*. Wijayawardene et al. (2022a) accepted 20

families with 17 genera were treated in *incertae sedis*. However, Pfister & Healy (2021) accepted 22 families and provided a recent overview of the order.

General description

Key characters used for the identification of *Pezizales* include the apical apparatus, operculum and its position, and reactions of ascus wall layers to various staining agents. Variation in ascus shape and spore number is observed, with coprophilous species typically having numerous spores, while truffle-like species often exhibit reduced spore numbers. Spore guttulation can be used at the generic and species level identification. However, oil droplets may fuse into a single large inclusion under dried conditions (Pfister & Healy 2021). Asexual morphs are reported in many families, though they are not known in *Glaziellaceae*, *Helvellaceae*, *Karstenellaceae*, *Otideaceae* or *Pseudombrophilaceae* (Pfister 2015, Pfister & Healy 2021) and occur in hyphomycetous states in several genera. The conidia are formed blastically and no phialidic states are reported. Conidia failed to germinate in many species. Thus, suggested to be a spermatia (Hansen & Pfister 2006, Pfister 2015, Pfister & Healy 2021). The mitotic spores germinate to produce hyphae and are considered true conidia (Paden 1967, Sánchez et al. 2014, Pfister & Healy 2021).

Sexual morph: *Ascomata* apothecial, several millimeters to about 20 centimeters, sessile, stalked, stipitate-pilate, often highly pigmented, particularly the hymenium. *Paraphyses* septate, branched or unbranched. *Asci* cylindrical, 8-spored, operculate but absent in some species. *Ascospores* aseptate, globose to naviculate, surface smooth or ornamented, mostly hyaline also purple, brown or yellowish ascospores, sometimes oil guttule. Asexual morph: hyphomycetous cushions or mats. *Conidia* holoblastic in development (Fig. 179).

Families included in *Pezizales*

Ascobolaceae Boud. ex Sacc.
Ascodesmidaceae J. Schröt.
Caloscyphaceae Harmaja
Chorioactidaceae Pfister
Coprotaceae U. Lindem. & Van Vooren
Discinaceae Benedix
Glaziellaceae J.L. Gibson
Helvellaceae Fr.
Kallistoskyphaceae Ekanayaka, K.D. Hyde, Q. Zhao & E.B.G. Jones
Karstenellaceae Harmaja
Morchellaceae H.G.L. Reichenbach
Pezizaceae Dumort. (= *Carbomycetaceae* Trappe)
Pseudombrophilaceae Ekanayaka, K.D. Hyde, Q. Zhao & E.B.G. Jones
Pulvinulaceae Ekanayaka, K.D. Hyde, Q. Zhao & E.B.G. Jones
Pyronemataceae Corda (= *Otideaceae* Eckblad)
Pyropyxidaceae M. Zeng, Q. Zhao & K.D. Hyde
Rhizinaceae Bonord.
Sarcoscyphaceae LeGal ex Eckblad
Sarcosomataceae Kobayasi
Strobiloscyphaceae Ekanayaka, K.D. Hyde, Q. Zhao & E.B.G. Jones
Tarzettaceae Ekanayaka, K.D. Hyde, Q. Zhao & E.B.G. Jones
Tuberaceae Dumort.

Pezizales genera *incertae sedis*
Aparaphysaria Speg.
Ascocalathium Eidam ex J. Schröt.
Boudierella Sacc.

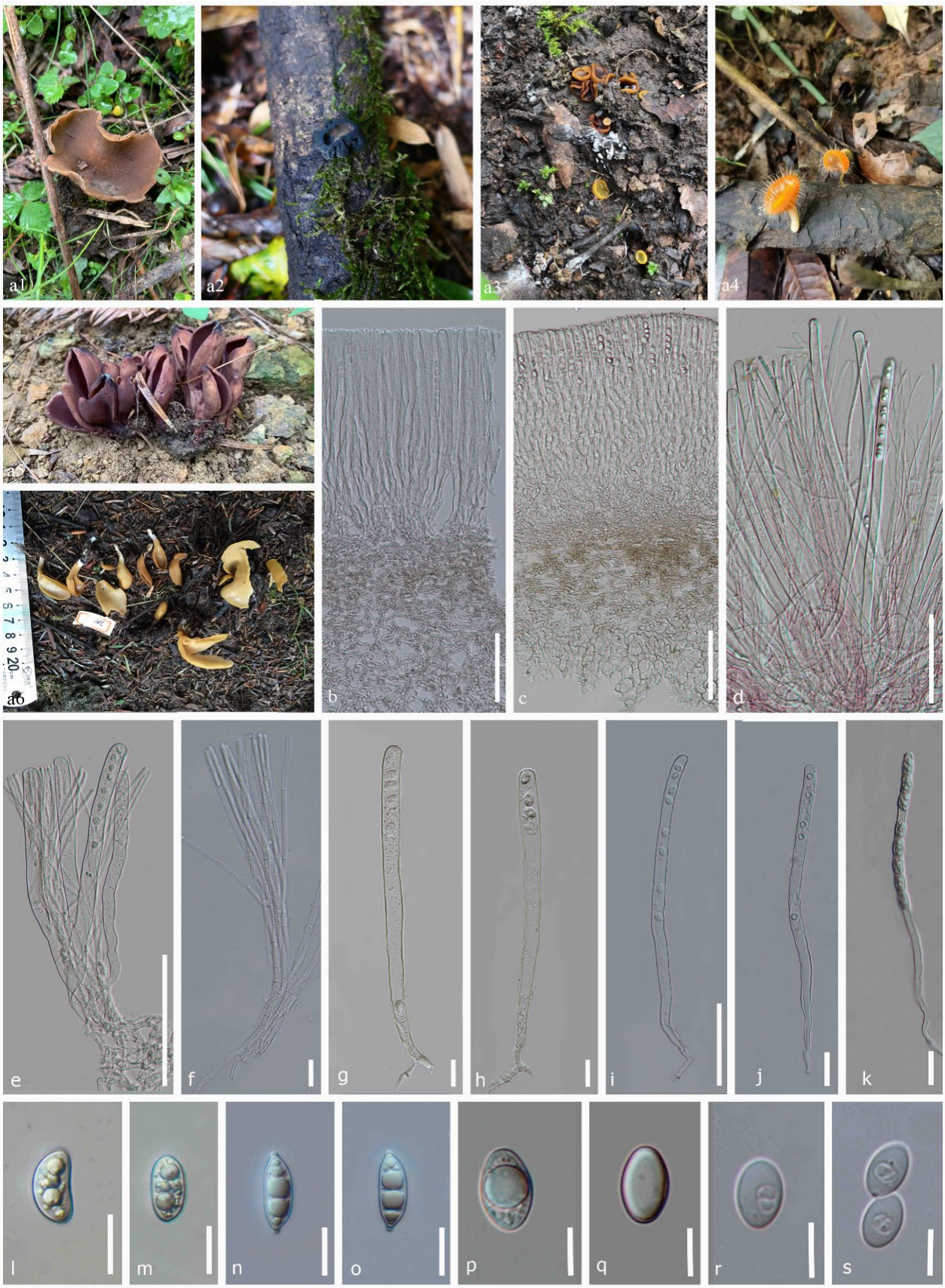


Figure 179 – Morphology of *Pezizales*. a1–a7 Thallus morphology in natural substrate (*Pezizales* sp). b, c Hamathecium, asci and paraphyses morphology of *Pezizales*. (b *Tarzetta urceolata*, *c T. tibetensis*). d–f Asci and Paraphyses (d *Pezizales* sp., e *T. tibetensis*, f *T. urceolata*), g–k Asci (g, h *T. tibetensis*, i, j *T. urceolata,* k *Pezizales* sp.). l–s Ascospores (l–o *Pezizales* sp., p, q *T. tibetensis,* r, s *T. urceolata*). Scale bars: c, d, e, i, k = 100 µm, g, h, f, j, l–o = 20 µm, p–s = 10 µm.

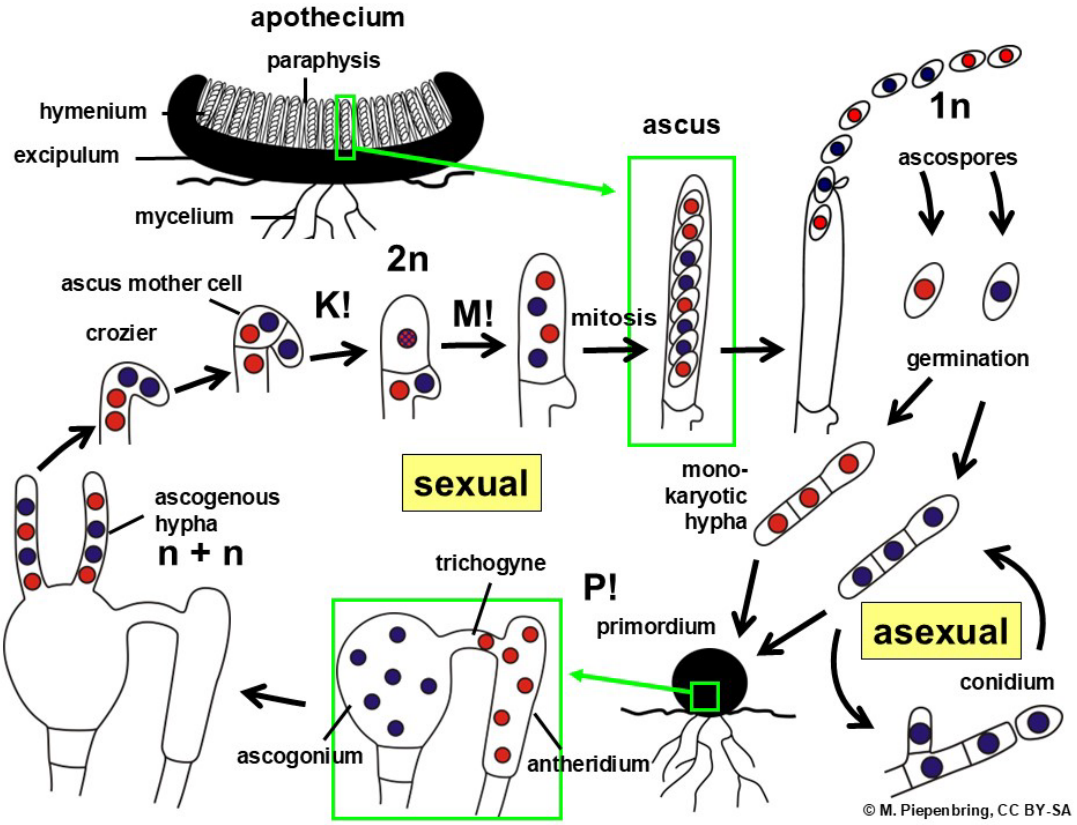


Figure 180 – Sexual and asexual life cycles of *Pezizales* (From Mycological teaching diagrams by Meike Piepenbring (2023)). Abbreviations: 1n = haploid, 2n = diploid, P! = plasmogamy, K! = karyogamy, M! = meiosis. Black and white circles represent haploid nuclei of different mating types, circles of both colors represent diploid nuclei.

Cidaris Fr.
Dennisiopsis Subram. & Chandras.
Filicupula Y.J. Yao & Spooner
Microeurotium Ghatak
Mycoarctium K.P. Jain & Cain
Mycogalopsis Gjurašin
Orcadia G.K. Sutherl.
Sphaerosoma Klotzsch

Evolution

The order was one of the early diverging lineages of *Pezizomycotina*. However, the whole genomic sequencing availability is limited (Shen et al. 2020b). The estimated divergence of *Tuber* from other genera occurred during the early Cretaceous Period was 156 MYA. The truffles are in important group of studying the evolution of *Pezizales* (Payen et al. 2014).

Justification of order and problems

Many species lack sequence data especially TEF and RPB2 in *Pezizales*. Genera that are included in *incertae sedis* also lack molecular data. The type specimens of many genera are not in good condition. Thus, recollections of fresh specimens and sufficient molecular data along with a detailed study of the generic delineation are important to circumscribe this order (Ekanayaka et al. 2018, Zeng et al. 2022a). *Tuber* is one of the most diverse groups but the diversity has yet to be described (Payen et al. 2014).

Significance

Ecological and economic roles

The taxa are distributed worldwide and occur as bacterial farmers, or mutualistic with certain bacteria, endophytes, mycorrhizae, parasites on bryophytes or vascular plants and the majority are saprobic (Hansen & Pfister 2006,Tedersoo et al. 2006, Arnold 2007). The saprobic species occur on decaying wood, dung, leaf litter and twigs (Pfister 2015). However, the distribution of the taxa is uneven. The soil-inhabiting taxa show high diversity in temperate regions (Tedersoo et al. 2014). Many *Pezizales* species are reported as pyrophilous fungi that occur on burned soil, and they are known as fire-responsive fungal colonizers on burned soil (Bruns et al. 2020). However, pyrophilous fungi that later appear dominate the earlier colonizers (Wicklow & Hirschfield 1979). Some species are edible and for example *Morchella* species have become important in mushroom cultivation (Yu et al. 2024a). Truffles are hypogeous ascomycetes fungi and is distributed in *Discinaceae*, *Morchellaceae*, *Glaziellaceae*, *Helvellaceae*, *Pezizaceae*, *Pyronemataceae* and *Tuberaceae*. The truffles belonging to *Tuber* (*Tuberaceae*) have high economic value due to their food consumption with high nutritional profile and is also reported to show mycorrhizal symbioses (Üstün et al. 2018).

Chemical diversity

Bills et al. (2013) reported the antifungal activity of *Ascobolaceae*, *Ascodesmidaceae*, *Pyronemataceae* and *Thelebolaceae*. Therapeutic compounds with anti-inflammatory, antioxidant, antiviral, antimicrobial, anti-mutagenic, anti-carcinogenic and hepatoprotective bioactivities and volatile organic compounds (VOCs) are reported in Truffles.

Sareomycetes **Beimforde, A.R. Schmidt, Rikkinen & J.K. Mitch., Fungal Systematics and Evolution 6: 33 (2020)**

Sareales **Beimforde, A.R. Schmidt, Rikkinen & J.K. Mitch., Fungal Systematics and Evolution 6: 33 (2020)**

Subphylum : *Pezizomycotina*
Class : *Sareomycetes*

Introduction

Sareales was recently described in the newly established class *Sareomycetes*. The order originally included a single family *Sareaceae* and the generic type *Sarea* (Beimforde et al. 2020). However, the subsequent studies of this order have led to the expansion and the reduction of generic concepts and raised questions about the taxonomic placement of this order (Beimforde et al. 2020, Hashimoto et al. 2021, Mitchel et al. 2021).

History

Sarea accommodates three species namely *Sarea coeloplata*, *S. resinae*, and the type species *S. difformis* (Species Fungorum 2025). The taxonomy of *Sarea* was problematic and was placed in *Lecanoromycetes*, *Leotiomycetes*, and *Pezizomycetes* over time. *Sarea resinae* is one of the oldest fungi that was reported on resin and was introduced by Elias Fries in 1815. The species was originally reported as *Sphaeria resinae* and *Lecidea resinae* in their asexual and sexual morph, respectively, and later combined into a single species *Sarea resinae*. *Sarea difformis* was originally introduced as *Peziza difformis*. Nannfeldt (1932) transferred the genus under *Tromera* within *Lecanorales* due to their thick ascus walls and the presence of an epithecium and amyloid reaction in the hymenium. Hawksworth & Sherwood (1981) also assigned *Sarea* to *Lecanoromycetes* because it resembles *Agyrium rufum* (*Agyriaceae*) in ascus structure, pigmentation and excipular structure. In the nineteenth century, the taxa were mostly placed with fleshy discomycetes *Dermateaceae* (Karsten 1885, Saccardo 1889a), *Patellariaceae* (Fuckel 1871), *Lecideaceae* (Tuckerman 1872, Stein 1879). Lumbsch & Huhndorf (2010) and Hodkinson & Lendemer (2011) transferred *Sarea* to *Trapeliales*. However, later molecular studies showed a close phylogenetic relationship to *Leotiomycetes* (Reeb et al. 2004, Wang et al. 2006b, 2009, LoBuglio & Pfister 2010, Miadlikowska et al. 2014). *Sarea* was

recovered within *Lecanoromycetes* without statistical support in the single gene phylogenetic analysis conducted by Giraldo et al. (2014a). However, the genus showed a distance relationship to *Trapeliales* or any other order in the *Lecanoromycetes* and the placement within *Leotiomycetes* was also not supported. Thus, Beimforde et al. (2020) established a new family, order, and class (*Sareaceae*, *Sareales*, *Sareomycetes*) to accommodate *Sarea* based on seven genes (ITS, SSU, mtSSU, LSU, RPB1, RPB2, MCM7) phylogenetic analysis along with ecological and morphological data. *Sareomycetes* formed a distinct clade between *Xylonomycetes* and *Candelariomycetes* in their analyses. Mitchel et al. (2021) restudied this group with broad taxon sampling by including many fresh specimens with phylogenetic analyses and broadened the generic concept of the order. Based on their analyses, *Sarea difformis sensu lato* and *Sarea resinae sensu lato* were established in two distinct genera, namely *Sarea* and *Zythia,* respectively. *Sarea* accommodates three phylospecies including *Sarea difformis sensu stricto* and two morphologically indistinct species which were combined under *Sarea coeloplata*. The monotypic genus *Zythia* accommodates Z. *resinae*. In addition, Mitchel et al. (2021) also erected a new genus *Atrozythia* and resurrected the family name *Zythiaceae* as an earlier name for *Sareaceae*. However, Hashimoto et al. (2021) restudied *Sarea* and synonymized *Sareomycetes* under *Xylonomycetes*, *Sareales* under *Xylonales* and *Sareaceae* under *Xylonaceae* based on morpho-molecular analyses. Hashimoto et al. (2021) also resurrected *Tromera* to accommodate *S. resinae*. Further, *Tromera* and *Sarea* formed a close phylogenetic clade to *Xylona* and *Trinosporium* within *Xylonomycetes* in the SSU, LSU, RPB1, RPB2 and mtSSU genes phylogenetic analysis. Hyde et al. (2024b) accepted *Atrozythia*, *Sarea* and *Zythia* within *Sareaceae* (*Sareales*) following Mitchel et al. (2021).

General description

Apothecial ascomata are reported in the sexual morph. Pycnidial asexual morph is observed in *Sarea* species. *Atrozythia lignicola* was originally introduced as *Arthrographis lignicola* which produces arthroconidia in the culture (Sigler & Carmichael 1983).

Sexual morph: *Apothecia* discoid to cupulate. *Pruina* black, orange, white to light blue grey. *Paraphyses* unbranched or branched and anastomosing, sometimes lipid guttules present. *Excipulum* sometimes pigmented. *Asci* cylindric-clavate, multi-spored. *Ascospores* are globose to subglobose, hyaline, inamyloid, and aseptate (refer to Mitchell et al. 2021 for detailed morphological description). Asexual morph: *Conidiomata* pycnidia, ostiolate or lacking. *Conidiophore* hyaline, branched. *Conidiogenous cells* phialidic and/or annellidic. *Conidia* subglobose, heart-shaped, pale brown to brown with or without catenate or arthroconidia (adapted from Hawksworth & Sherwood 1981, Sigler and Carmichael 1983) (Fig. 181).

Families included in *Sareales*

Sareaceae Beimforde, A.R. Schmidt, Rikkinen & J.K. Mitch.

Evolution

Mitchel et al. (2021) noted that the group emerged during the late Jurassic or Cretaceous period, with subsequent diversification roughly coinciding with the diversification of *Cupressaceae* and *Pinaceae*. Different strains or species within *Sordariomycetes* demonstrate selective growth preferences based on the presence or absence of certain components in resin. However, Tappert et al. (2011) noted that the production of specific resin components does not necessarily reflect evolutionary relationships.

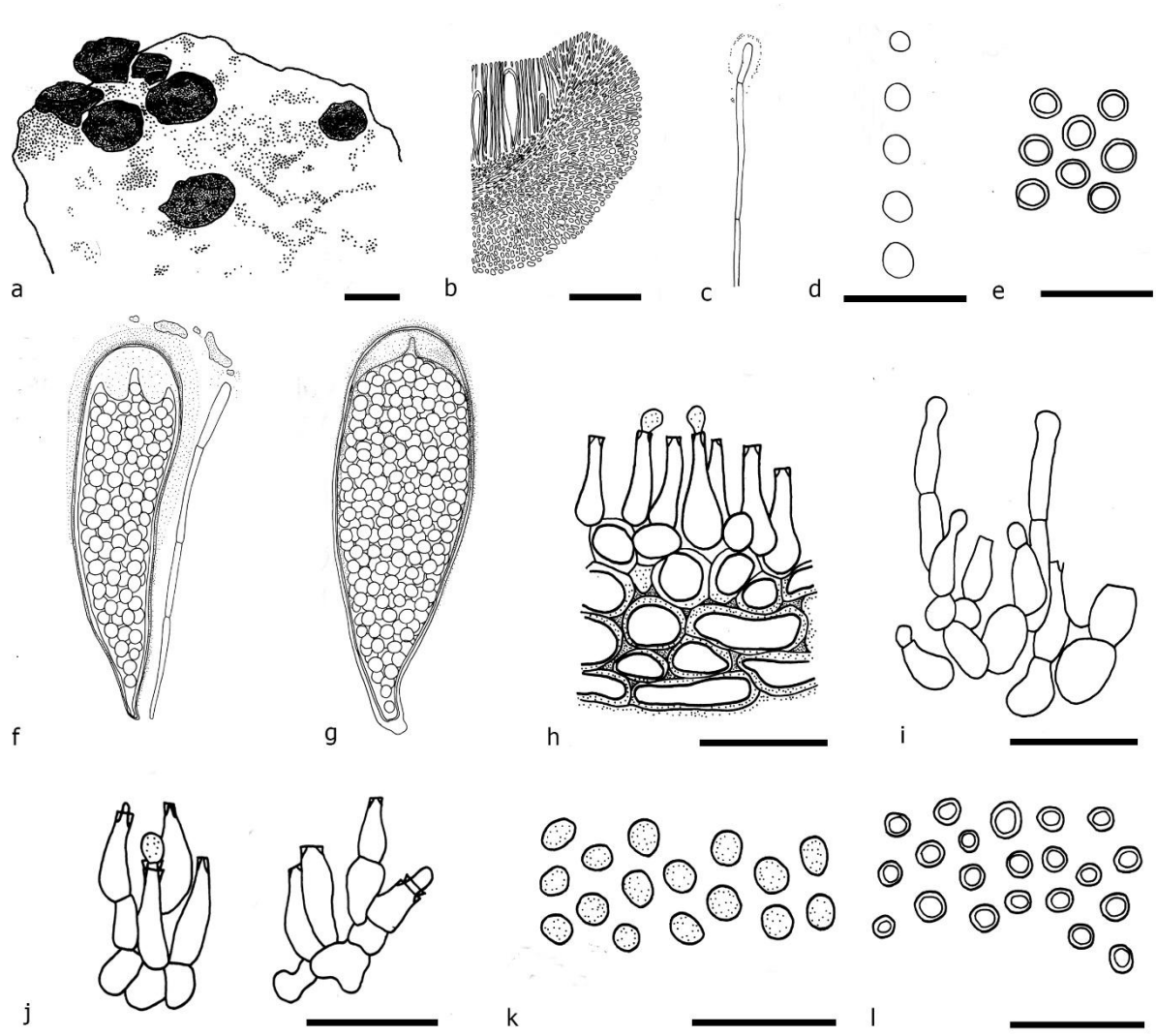


Figure 181 – Sexual and asexual morph of *Sareales*. a Ascomata of *Sarea difformis*. b Vertical section of apothecium (*Sarea resinae*). c Paraphysis with epithecial granules. d, e Ascospores (d *Atrozythia klamathica*, e *Sarea resinae*). f, g Ascus (f *Sarea difformis*, g *Sarea resinae*). h–l Conidia, conidiogenous cells, and vertical section of a portion of the pycnidial wall in *Sarea* species (redrawn from Hawksworth & Sherwood 1981, Beimforde et al. 2020). Scale bars: a = 500 µm, b = 50 µm, d–l = 10 µm.

Justification of order and problems

Numerous studies have been conducted on the taxonomy of *Sarea* over time. A significant study by Beimforde et al. (2020) resolved the confusion and uncertainty of the members and the establishment of their own family, order, and class. However, recent studies conducted by Hashimoto et al. (2021) and Mitchel et al. (2021) again raised a need for reinvestigation of the group which is explained in detail in the last section of this entry.

Significance

Ecological and economic roles

Sareales species are reported on a wide range of hosts and geographies. Members of *Sarea* often co-occur in the same substrate on resins and are distributed in northern latitudes and reported in a broad host range including *Abies*, *Cedrus*, *Chamaecyparis*, *Cryptomeria*, *Cupressus*, *Juniperus*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga* and *Tsuga* (Ayers 1941, Baranyay 1966, Malençon 1979, Hawksworth & Sherwood 1981, Petrini & Carrol 1981, Garrido-Benavent 2015). Both *Sarea difformis* and *S. resinae* (= *Zythia resinae*) are commonly reported resinicolous fungi.

These species were also treated as lichen symbionts, endophytes, mild to serious parasites and saprobes. The taxa are also reported as endophytes in conifers in *Pinaceae* and *Cupressaceae*, grasses, and reported on thalli of foliose and fruticose lichens and marine algae (Mitchel et al. 2021). *Atrozythia* species are reported on dead and living conifers and *Atrozythia klamathics* showed potential resinicolous habit (Mitchel et al. 2021).

Chemical diversity

No relevant studies are available for the chemistry of the order.

Other relevant data and future recommendations

Mitchel et al. (2021) recommended additional research on the family, including a detailed investigation of the type species of several taxa. The type species, *Atrozythia klamathica*, exhibits a resinicolous habit, but further information is required to fully understand the ecology of this species. The ecology of these fungi remains unresolved, especially regarding their pathogenicity (Mitchel et al. 2021). The pycnidial asexual morph was reported in *S. difformis* and *S. resinae* but a recent investigation of the fresh collection of these species didn't show any asexual morph. The important recent studies for *Sareales* including Hashimoto et al. (2021) and Mitchel et al. (2021) were overlooked in each study which could also be acceptable as they were done in the same year. Díaz-Escandón et al. (2022) suggested combining *Sareomycetes* under *Lichinomycetes* based on molecular analysis. *Sarea* formed a close clade to *Xylona* and *Symbiotaphrina* formed a sister clade to both *Sarea* and *Xylona* (Díaz-Escandón et al. 2022). The study of Mitchel et al. (2021) involved numerous new collections of *Sarea* strains and other accepted genera of *Sareales* but lacked detailed investigation above order level classification.

On the other hand, the study of Hashimoto et al. (2021) deals with a limited number of strains of *Sarea difformis* and *Sarea resinae* (= *Tromera resinae*) unlike the former study but investigates the ordinal relationship among classes of *Ascomycota*. Both *Sareomycetes* and *Xylonomycetes* have been recovered as sister clades in the multigene phylogenetic analysis conducted by Beimforde et al. (2020). However, reinvestigation of *Sarea* and associated genera with further fresh collections and ordinal-level relationships is needed to resolve the taxonomic confusion of the order. In addition, the reinvestigation of the type material of *Sarea* could provide a better resolution for the taxonomy of this group.

***Sordariomycetes* O.E. Erikss. & Winka, Myconet 1(1): 10 (1997)**
***Amphisphaeriales* D. Hawksw. & O.E. Erikss., Systema Ascomycetum 5(1): 177 (1986)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Xylariomycetidae*

Introduction

Eriksson & Hawksworth (1986c) introduced *Amphisphaeriales* based on *Amphisphaeriaceae*. Over the years, studies have focused on refining the taxonomy of this group based on morphological traits and molecular data. Based on the morphology and sequence analysis of ITS and LSU regions, *Xylariomycetidae* was proposed to include two orders, *Amphisphaeriales* and *Xylariales* (Smith et al. 2003, Tang et al. 2009). Senanayake et al. (2015) considered *Xylariales* and *Amphisphaeriales* to be morphologically distinct and treated them as distinct orders. However, their phylogenetic analysis of combined LSU and ITS sequences did not well-resolve the separation between the two orders. Jaklitsch et al. (2016b) and Maharachchikumbura et al. (2016) regarded *Amphisphaeriales* as a synonym of *Xylariales* as they were not statistically supported in their phylogenies. However, consecutive studies (Samarakoon et al. 2016, Perera et al. 2017, Hongsanan et al. 2017a, Crous et al. 2018a, Hyde et al. 2020d) provided phylogenetic and divergence time estimations for the subclass *Xylariomycetidae* and accepted *Amphisphaeriales* and *Xylariales* as distinct orders. This was followed in Hyde et al. (2020d, 2024b).

History

Amphisphaeriaceae was initially introduced as *Amphisphaerieae* by Winter (1885) and later established as *Amphisphaeriaceae* based on *Amphisphaeria* as the type. *Amphisphaeriales* was introduced based on *Amphisphaeriaceae* (Eriksson & Hawksworth 1986c), and this was the first formal recognition of *Amphisphaeriales* as a separate taxonomic group. *Amphisphaeriales* and *Xylariales* were treated as closely related orders or even as synonyms by Smith et al. (2003) and Tang et al. (2009). Smith et al. (2003) revealed that these two orders were part of the same clade within the subclass *Xylariomycetidae* based on the evidence of molecular data. Furthermore, *Amphisphaeriales* has been considered synonymous with *Xylariales* by Jaklitsch et al. 2016b and Maharachchikumbura et al. (2016). However, Senanayake et al. (2015) resurrected the order *Amphisphaeriales* and later Samarakoon et al. (2016) and Hongsanan et al. (2017a) revealed *Amphisphaeriales* diverged from *Xylariales* around 152–187 MYA in their analyses of divergence time estimations. Hyde et al. (2020d) excluded *Cainiaceae*, which was placed in *Amphisphaeriales* by Hongsanan et al. (2017a) and placed in *Xylariales*. *Cylindriaceae* and *Pseudotruncatellaceae* were placed in *Amphisphaeriales* by Crous et al. (2018a).

Based on previous studies, Wijayawardene et al. (2022a) accepted 15 families in *Amphisphaeriales*, i.e. *Amphisphaeriaceae*, *Apiosporaceae*, *Beltraniaceae*, *Castanediellaceae*, *Clypeophysalosporaceae*, *Hyponectriaceae*, *Iodosphaeriaceae*, *Melogrammataceae*, *Oxydothidaceae*, *Phlogicylindriaceae*, *Pseudomassariaceae*, *Pseudosporidesmiaceae*, *Pseudotruncatellaceae*, *Sporocadaceae* and *Vialaeaceae*. Currently, *Xylariomycetidae* comprises three orders namely, *Amphisphaeriales*, *Delonicicolales* and *Xylariales*, as discussed by Hyde et al. (2020d) based on the analysis of combined LSU, SSU, ITS and RPB2 loci. Currently, there are 16 families and two *incertae sedis* genera in *Amphisphaeriales* (Hyde et al. 2024b).

General description

The sexual morph of *Amphisphaeriales* is characterized by solitary, globose to subglobose, coriaceous ascomata immersed to erumpent in stromatic tissues. However, stromatic tissues can be present or absent. Asci are cylindrical or clavate, with J+ or J- apical ring and bearing ellipsoid, apiosporous, fusiform or oval, unicellular to trans-septate, variously-colored ascospores. Ascospores can be smooth or ornamented walled and with or without appendages or mucilaginous sheaths (Senanayake et al. 2015). The asexual morph is characterized by acervular or pycnidial conidiomata with holoblastic, annellidic, ampulliform, or lageniform, conidiogenous cells and aseptate to transeuseptate, variously-colored conidia that often bear appendages (Senanayake et al. 2015).

Sexual morph: *Pseudostromata or stromata* present or absent. *Ascomata* immersed to erumpent, solitary, rarely aggregated, scattered, globose to subglobose, coriaceous, brown to black. Ostioles periphysate. *Peridium* of one or few layers, mostly comprises an outer layer of brown, thick-walled cells and inner layer of hyaline, thick or thin-walled cells. *Hamathecium* comprises hyaline, septate paraphyses. *Asci* 8-spored, unitunicate, cylindrical, clavate or narrowly globose, having a short pedicel and a J+ or J- apical ring. *Ascospores* uniseriate or multi-seriate, apiosporous, ellipsoid, fusiform or oval, aseptate to 4-septate, hyaline, light brown to dark brown, smooth-walled or ornamented, sometimes bearing hyaline, slender, unbranched appendages or a gelatinous sheath. Asexual morph: Coelomycetous. *Conidiomata* stromatic, immersed to erumpent, solitary to cellular, gregarious, acervular or pycnidial to irregular, unilocular or irregularly plurilocular, dark brown to black. Peridium comprises brown cells forming textura angularis. Conidiophores indistinct or if distinct, arising from the inner layer cells of basal stroma, sometimes reduced to conidiogenous cells, long, cylindrical, hyaline, septate and sometimes branched. Conidiogenous cells discrete, holoblastic, annelledic, integrated, indeterminate, cylindrical to ampulliform or lageniform, hyaline and becoming pale brown with age, smooth-walled. Conidia cylindrical, clavate, ellipsoid or fusiform, aseptate to 4-euseptate, hyaline to subhyaline, pale olivaceous or brown, bearing cellular,filiform or attenuated, sometimes having only apical appendages or both apical and basal appendages (Fig. 182).

Families included in *Amphisphaeriales*

Amphisphaeriaceae G. Winter
Appendicosporaceae Samarak. & K.D. Hyde
Apiosporaceae K.D. Hyde, J. Fröhl., Joanne E. Taylor & M.E. Barr
Beltraniaceae Nann.
Castanediellaceae Hern.-Restr., Guarro & Crous
Clypeophysalosporaceae Giraldo & Crous
Hyponectriaceae Petr.
Iodosphaeriaceae O. Hilber
Melogrammataceae G. Winter
Oxydothidaceae Konta & K.D. Hyde
Phlogicylindriaceae Senan. & K.D. Hyde
Pseudomassariaceae Senan. & K.D. Hyde
Pseudosporidesmiaceae Crous
Pseudotruncatellaceae Crous
Sporocadaceae Corda
Vialaeaceae P.F. Cannon

Amphisphaeriales genera *incertae sedis*
Chitonospora E. Bommer, M. Rousseau & Sacc.
Neoarthrinium Ning Jiang

Justification of order and problems

There have been many taxonomic confusions regarding the existence of this order. Current molecular phylogenetic and evolutionary analyses have given an understanding of the *Amphisphaeriales* and recognized it as a distinct order in the subclass (Samarakoon et al. 2016, Perera et al. 2017, Hongsanan et al. 2017a, Crous et al. 2018a, Hyde et al. 2020d). Furthermore, the high morphological similarity among species of pestalotioid taxa in *Amphisphaeriales* can lead to misidentifications, especially when molecular data is lacking. Continuous efforts in comprehensive sampling, morphological assessments, and molecular analyses are essential to refine the taxonomy of pestalotioid fungi.

Evolution

Molecular-based evolutionary studies on the order *Amphisphaeriales* have been extensively conducted over the past decade (Samarakoon et al. 2016, 2022, Hongsanan et al. 2017a, Hyde et al. 2020d). Hyde et al. (2017a) estimated that *Amphisphaeriales* and *Xylariales* diverged approximately 152 MYA. A recent study by Samarakoon et al. (2022) refined this divergence to around 154 (117–190) MYA with a crown age of 127 (92–165) MYA and 147 (111–184) MYA respectively. Similar divergence ranges were also reported in the studies of Hongsanan et al. (2017a) and Hyde et al. (2020d). Samarakoon et al. (2022) also conducted an in-depth study on the evolution of several traits among species within *Amphisphaeriales* using ancestral character reconstruction. Song et al. (2023) suggested that *Ciliochorella* originated from the Eurasian continent during the Paleogene period, approximately 38 MYA, based on ancestral character state analysis.

Significance

Ecological and economic roles

Species of the order are mainly saprobes, pathogens or endophytes on plants (Senanayake et al. 2015). *Arthrinium* species are known to cause scabs and spots on leaves or culms of crops, or even cause damping-off (Liu et al. 2023b, Ai et al. 2024). Some *Arthrinium* species, such as *A. phaeospermum* were reported as human pathogens causing cutaneous mycosis (Rai 1989). Bonthond et al. (2018) revealed that *Seiridium* includes plant pathogenic taxa (*Seiridium cardinale*, *S. cupressi* and *S. unicorne*) known as causal organisms of cankers on *Cupressaceae*. *Physalospora* species were also reported as lichenicolous (Hoffmann & Hafellner 2000).



Figure 182 – Morphology of *Amphisphaeriales*. a–e Ascomata of host substrate (a *Amphisphaeria ailaoshanensis*, b *Neoamphisphaeria shangrilaensis*, c *Iodosphaeria sichuanensis*, d *Amphisphaeria kunmingensis*, e *Broomella vitalbae*). f–i Vertical section through ascoma (f *Neoamphisphaeria shangrilaensis*, g *Iodosphaeria sichuanensis*, h *Amphisphaeria ailaoshanensis*, i *Amphisphaeria kunmingensis*). j–p Asci (j *Neoamphisphaeria shangrilaensis*, k *Amphisphaeria ailaoshanensis*, l *Amphisphaeria kunmingensis*, m *Discosia neofraxinea*, n *Broomella vitalbae*, o *Iodosphaeria sichuanensis*, p *Hyalotiella rubi*). q–v Ascospores (q *Amphisphaeria kunmingensis*, r *Neoamphisphaeria shangrilaensis*, s *Iodosphaeria sichuanensis*, t *Amphisphaeria ailaoshanensis*, u

Broomella vitalbae, v *Discosia neofraxinea*). w–z Conidiomata on host substrate (w *Broomella meilishanguensis*, x *Apiospora pseudoparenchymatica*, y *Apiospora koreana*, z *Pestalotiopsis chamaeropis*). a1 Verical section through conidioma (a1 *Broomella meilishanguensis*). a2–a7 Developing conidia attached to conidiogenous cells (a1 *Broomella meilishanguensis*, a2 *Pestalotiopsis chamaeropis*, a3 *Apiospora koreana*, a4 *Apiospora pseudoparenchymatica*, a5 *Broomella meilishanguensis*, a6 *Beltraniella fertilis*, a7 *Hyalotiella spartii*). a8–a14 Conidia (a8 *Seimatosporium rhombisporum*, a9 *Apiospora pseudoparenchymatica*, a10 *Beltraniella fertilis*, a11 *Broomella meilishanguensis*, a12 *Pestalotiopsis chamaeropis*, a13 *Apiospora koreana*, a14 *Hyalotiella spartii*). Scale bars: a–u, w–z, a1–a5, a7, a9–a14 = 10 μm, v = 5 μm, a6 = 20 μm, a8 = 15 μm.

Pestalotioid genera such as *Pestalotiopsis*, *Neopestalotiopsis*, and *Pseudopestalotiopsis*, are known to cause a variety of plant diseases, primarily manifesting as leaf spots, blights, and diebacks (Cui et al. 2024, Koodalugodaarachchi et al. 2024). *Truncatella angustata* has been identified as the causative agent of fruit rot in olives (*Olea europaea*) (Arzanlou et al. 2012). *Amphisphaeriaceae* taxa have a significant role as saprobes on dead plant material in terrestrial, aquatic and marine habitats (Wang et al. 2004b, Liu et al. 2015a, Senanayake et al. 2015). *Oxydothis* species have been identified as endophytes in various plants, including palms (Konta et al. 2016). Konta et al. (2016) isolated *Oxydothis obducens* from palm leaves and rachides without causing obvious harm to the host.

Chemical diversity

Arthrinium species associated with marine environments have been recognized as a source of bioactive natural products by Heo et al. (2018). They revealed antioxidant, antifungal, tyrosinase inhibition and quorum sensing inhibition activities in *Arthrinium* species (Heo et al. 2018). Species of *Amphisphaeriales* such as *Arthrinium arundinis* have been applied in the pharmaceutical industry as antifungal agents (Zhang et al. 2018d). *Seiridium* species are known to produce seiridins, specifically seiridin and iso-seiridin, which have been studied for their phytotoxic properties and potential antimicrobial activities (Sparapano & Evidente 1995). Some *Pestalotiopsis* species contain bioactive compounds with promising applications in medicine and agriculture. Pestalotiopsolide B, a metabolite isolated from *Pestalotiopsis* species, has been reported to exhibit cytotoxic activity (Wu et al. 2022). Pestalopyrone is another secondary metabolite with potential bioactivity, is produced by *Pestalotiopsis* species. However, further research is needed to elucidate its biological effects (Wu et al. 2022, Jiang et al. 2023).

Amplistromatales **M.J. D'souza, Maharachch. & K.D. Hyde, Fungal Diversity 72: 212 (2015)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Incertae sedis*

Introduction

Amplistromatales comprises a single family *Amplistromataceae* with four genera including *Acidothrix*, *Amplistroma*, *Neoacrodontium* and *Wallrothiella* (Wijayawardene et al. 2022a, Hyde et al. 2024b).

Introduction

Amplistromatales comprises a single family *Amplistromataceae* with four genera including *Acidothrix*, *Amplistroma*, *Neoacrodontium* and *Wallrothiella* (Wijayawardene et al. 2022a, Hyde et al. 2024b).

History

Amplistromatales was introduced by Maharachchikumbura et al. (2015) to accommodate two families namely, *Amplistromataceae* and *Catabotrydaceae* within *Sordariomycete*s order *incertae sedis*. *Amplistromataceae* comprised two genera *Amplistroma*, and *Wallrothiella* while

Catabotrydaceae comprised a monotypic genus *Catabotrys*. This classification was further accepted by Daranagama et al. (2017). Hongsanan et al. (2017a) accepted *Amplistromatales* in *Sordariomycetes incertae sedis* with a stem age of 165 MYA. Nonetheless, Hyde et al. (2017a) accepted *Amplistromatales* under *Diaporthomycetidae* and proposed to keep *Catabotrydaceae* in a different order due to stem age (165 MYA) as it falls in the order range. Later, *Catabotrydaceae* was transferred to its own order *Catabotryales* by Hyde et al. (2020d) and only *Amplistromataceae* is retained under *Amplistromatales*. *Amplistromataceae* was established to accommodate *Amplistroma* and *Wallrothiella* based on morpho-molecular analyses. *Amplistroma* differs from *Wallrothiella* in the presence of stromatic structure. The family formed a sister clade to *Chaetosphaeriales* without stable statistical support based on LSU sequence data and was treated under *Sordariomycetidae incertae sedis* (Huhndorf et al. 2009). The generic concept of the order has been expanded over time, which lead to the inclusion of four genera (Hyde et al. 2024b).

General description

Both sexual and asexual morphs are reported for these taxa. The asexual morph shows mostly acrodontium-like morphology (Hujslová et al. 2014)

Sexual morph: *Stromata* superficial, turbinate, obovoid to irregularly pulvinate, texture soft or firm with polystichous or monostichous ascomata, or stromata absent and ascomata single to clustered, with or without a hyphal subiculum. *Ascomata* globose or subglobose, with a cylindrical or rostrate neck. *Paraphyses* abundant, tapering, of broad cells. *Asci* 8-spored, unitunicate, cylindrical to clavate, pedicellate, apical ring, J-. *Ascospores* uniseriate, unicellular, tiny, globose, hyaline. Asexual morph: Hyphomycetous. acrodontium-like. *Conidiophores* semi-macronematous or macronematous. *Conidiogenous cells* lageniform to ampulliform, elongating sympodially forming a rachis; conidiogenesis holoblastic- denticulate. *Conidia* single, globose, subglobose or ellipsoidal to lacrimose, hyaline to pale brown (adapted from Maharachchikumbura et al. 2016, Crous et al. 2022b) (Fig. 183).

Families included in *Amplistromatales*

Amplistromataceae Huhndorf, A.N. Mill. Greif & Samuels

Evolution

Hyde et al. (2017a) accepted *Amplistromatales* in *Sordariomycetes incertae sedis* with a stem age of 165 MYA. Hyde et al. (2020d) found that the stem age of *Amplistromatales* is 172 MYA and accepted under *Diaporthomycetidae*. Consequently, Hyde et al. (2021a) found the stem age as 204 MYA in the same subclass.

Justification of order and problems

The order includes four genera, one of which is the recently established genus *Neoacrodontium*. This genus consists of two species: *Neoacrodontium gallicum* (the type species) and *Neoacrodontium hydnicola*. Phylogenetic analyses based on LSU or ITS sequences show that *Neoacrodontium gallicum* clusters with an unidentified strain, CBS 349.55, which was subsequently identified as *Neoacrodontium hydnicola*. Additionally, *Amplistromatales* has been placed under *Sordariomycetidae*, and the order shows a close phylogenetic relationship with *Pleurotheciales* based on limited taxon sampling in the LSU sequence analysis (Crous et al. 2022b). However, Hyde et al. (2024b) classified the order under *Sordariomycetes* orders *incertae sedis,* which is in contradiction to the previous studies in which the order was accepted under *Diaporthomycetidae* (Hyde et al. 2020d, Hyde et al. 2021a). Therefore, broad taxon sampling, incorporating all genera of this order, is crucial for a more accurate taxonomic placement within *Sordariomycetes*.

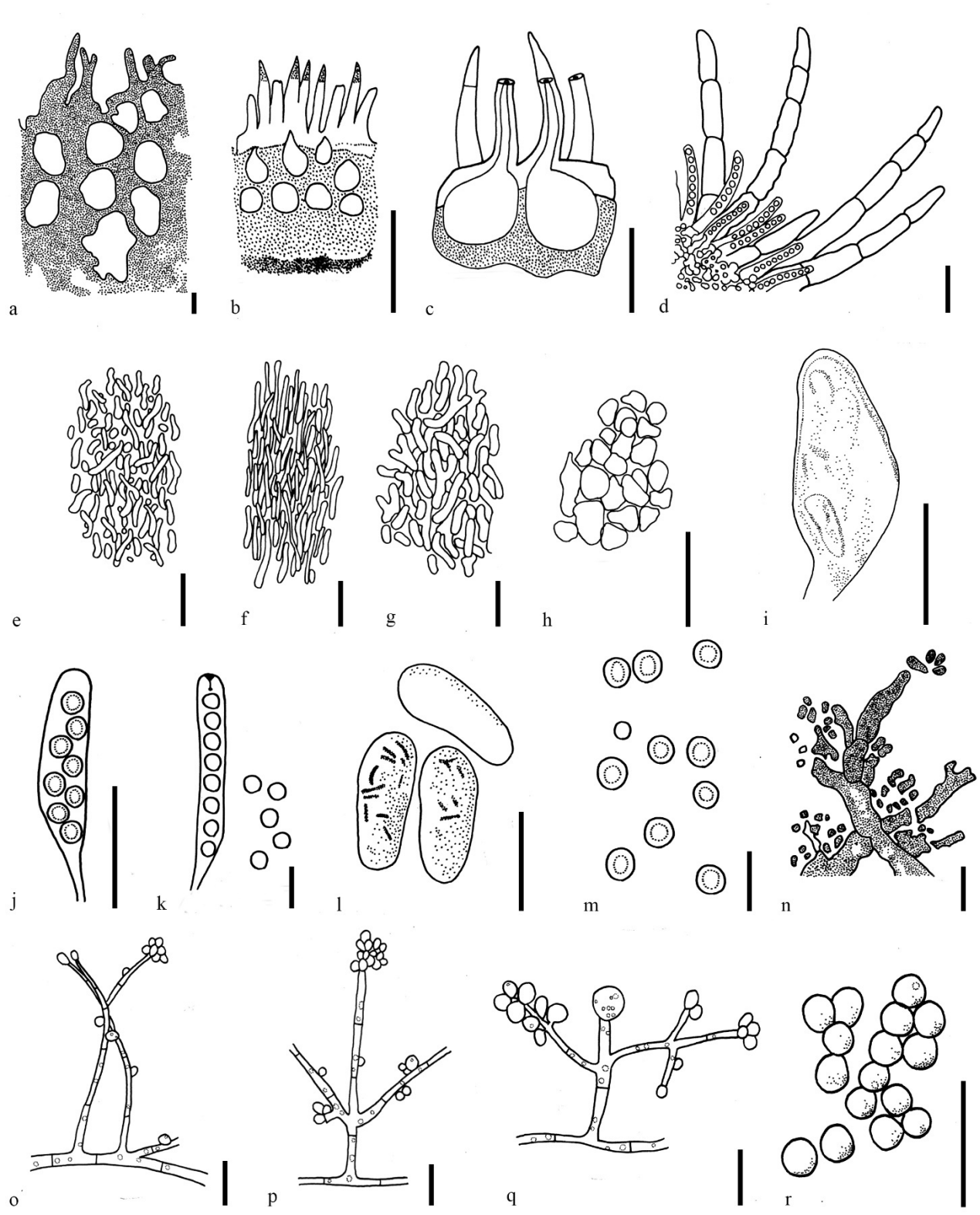


Figure 183 – Sexual and Asexual morph of *Amplistromatales*. a Polystichous perithecia in the stromata (*Amplistroma longicolli*). b Longitudinal section of the stroma (*Amplistroma erinaceum*). c Perithecia (*Amplistroma erinaceum*). d Paraphyses and asci (*Amplistroma* erinaceum). e Hyphae from the stroma among perithecia. f Hyphae from perithecial neck. g Detail of the hyphae of *textura intricata* from the stroma. h Perithecial walls with pseudoparenchymatic cells (*Amplistroma erinaceum*). i, j Ascus (i *Wallrothiella bromelia*, j *Amplistroma carolinianum*). k Ascus and

ascospores (*Amplistroma erinaceum*). l, m Ascospores (l *Wallrothiella bromelia*, m *Amplistroma carolinianum*). n Conidiophores and conidia *in vitro* (*Amplistroma longicollis*). o Conidia proliferating by hyphae and bearing other conidia (*Acidothrix acidophila*). p, q Conidiophores and conidia (*Acidothrix acidophila*). r Conidia (*Acidothrix acidophila*) (redrawn from Checa et al. 2012, 2014, Hujslová et al. 2014). Scale bars: a = 200 µm, b, c = 1000 µm, d, e–h, 0–r, k, l = 10 µm, i, j = 20 µm, m = 5 µm, n = 25 µm.

Significance

Ecological and economic roles

The taxa are mainly reported as saprobes on bark or wood or in highly acidic soil (Huhndorf et al. 2009, Hujslová et al. 2014) and are reported from Costa Rica, Ecuador, Europe, France, French Guiana, Puerto Rico, Singapore, and United States (Huhndorf et al. 2009, Crous et al. 2022b). Crous et al. (2022c) reported *Neoacrodontium gallicum* from France that was present on the bore-insect *Xestobium rufovillosum*, which was feeding on *Quercus* wood.

Chemical diversity

There is no chemical diversity reported in this group.

Annulatascales **M.J. D'souza, Maharachch. & K.D. Hyde, Fungal Diversity 72: 212 (2015)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Annulatascales was established by Maharachchikumbura et al. (2015) with *Annulatascaceae* as the type family. The monotypic order *Annulatascales* is distinguished by its preference for freshwater habitats, with the majority of its members being collected from submerged woody materials. *Annulatascales* is characterized by cylindrical asci with a massive, J-, refractive, apical ring, and fusiform, hyaline ascospores which are often equipped with appendages or sheaths (Maharachchikumbura et al. 2015). The asexual morph is rarely reported, and the taeniolella-like hyphomycetes of *Chaetorostrum* have been widely accepted. The asexual morph is characterized by micronematous, mononematous conidiophores, and monoblastic, elongate cylindrical, euseptate, brown conidia (Hyde et al. 2020d).

History

The type family *Annulatascaceae* was established by Wong et al. (1998b) for a group of freshwater species. Ranghoo et al. (1999) first reported that *Annulatascaceae* was a distinct family based on a phylogenetic analysis of LSU sequence data. However, with numerous freshwater species being sequenced and incorporated into phylogenetic analyses, *Annulatascaceae* has been shown to be a polyphyletic family (Raja et al. 2003, Campbell & Shearer 2004, Abdel-Wahab et al. 2011, Luo et al. 2015c). For instance, species exhibiting the characteristic features of *Annulatascaceae*, such as *Annulatascus biatriisporus*, *Diluviicola capensis*, and *Fluminicola coronata*, form several distinct clades that are phylogenetically distant from the *Annulatascaceae*. Consequently, they have been assigned to several other families including *Xenospadicoidaceae*, *Pseudoproboscisporaceae*, and *Papulosaceae* (Zhang et al. 2017a). Nevertheless, *Annulatascaceae* remains a large family encompassing approximately 20 diverse genera. This complex group has been well-resolved by Zhang et al. (2017a) through the introduction of a new order *Atractosporales* and six new families, *Atractosporaceae*, *Barbatosphaeriaceae*, *Conlariaceae*, *Lentomitellaceae*, *Pseudoproboscisporaceae* and *Woswasiaceae*. Although these taxonomic changes have been carried out, many remain questionable or their classification are unstable due to a lack of DNA sequence data. Dong et al. (2021a) conducted a further survey on freshwater species resembling *Annulatascaceae*, resulting in the identification of 23 new taxa. A comprehensive review on *Annulatascaceae* and its related families has been carried out by Hyde et al. (2020d). Consequent studies lead to the reduction of the

families within the order and is presently accommodates a single family *Atractosporaceae* (Hyde et al. 2024b).

General description

Sexual morph: *Ascomata* perithecial, scattered or densely aggregated, immersed, partially superficial, brown to black, ostiolate, unilocular, globose to subglobose, ellipsoidal. *Ostiolar necks* cylindrical to conical, black, glabrous, rarely with setae, hyphae or hairs. *Peridium* carbonaceous or coriaceous. *Paraphyses* numerous, septate, tapering. *Asci* 8-spored, unitunicate, cylindrical, pedicellate, usually with a massive J-, refractive, cylindrical to flaring, doughnut-shaped, apical ring. *Ascospores* uniseriate, mostly hyaline, to pale yellow, or occasionally brown, fusiform, ellipsoidal, oval, unicellular or transversely septate, with or without appendages, mucilaginous sheaths. Asexual morph: hyphomycetous. taeniolella-like for *Chaetorostrum* where *Conidiophores* are micronematous, mononematous. *Conidia* monoblastic, elongate cylindrical, transversely septate, euseptate, brown. *Conidial secession* schizolytic (Fig. 184).

Families included in *Annulatascales*

Annulatascaceae S.W. Wong, K.D. Hyde & E.B.G. Jones

Annulatascales genera *incertae sedis*
Clohiesia K.D. Hyde

Evolution

Hyde et al. (2017a) reported the stem age of *Annulatascales* as 122 MYA. Later, it was found as 113 MYA (Hyde et al. 2020d) and consequently, Hyde et al. (2021a) reported the stem age as 157 MYA in the subclass *Diaporthomycetidae*.

Justification of order and problems

Although several higher rankings have been established to accommodate the Annulatascaceae-like taxa (Zhang et al. 2017a), the family placement of several genera within the *Annulatascales*/*Annulatascaceae* remains uncertain due to lack of sequence data, such as *Aqualignicola*, *Ayria*, *Cataractispora*, *Chaetorostrum*, *Clohiesia*, and *Vertexicola* (Hyde et al. 2020d).

Significance

Ecological and economic roles

The majority of species within the order are isolated from submerged wood in freshwater habitats, which indicates that they are important saprobes in carbon cycling in freshwater systems. The economic roles have not yet been documented.

Chemical diversity

There is no report on the chemical diversity of the species in this order.

Other relevant data and future recommendations

The most distinctive features for this order are that the asci have a massive, J-, refractive, apical ring, and fusiform, hyaline ascospores which are often equipped with appendages or sheaths. These characteristics have also been observed in many other freshwater genera, resulting in taxonomic confusion within this extensive group. We hypothesize that these important structures are closely associated with their aquatic habitats and may have evolved repeatedly; however, the biology of freshwater fungi remains poorly studied and necessitates further investigations in the future.

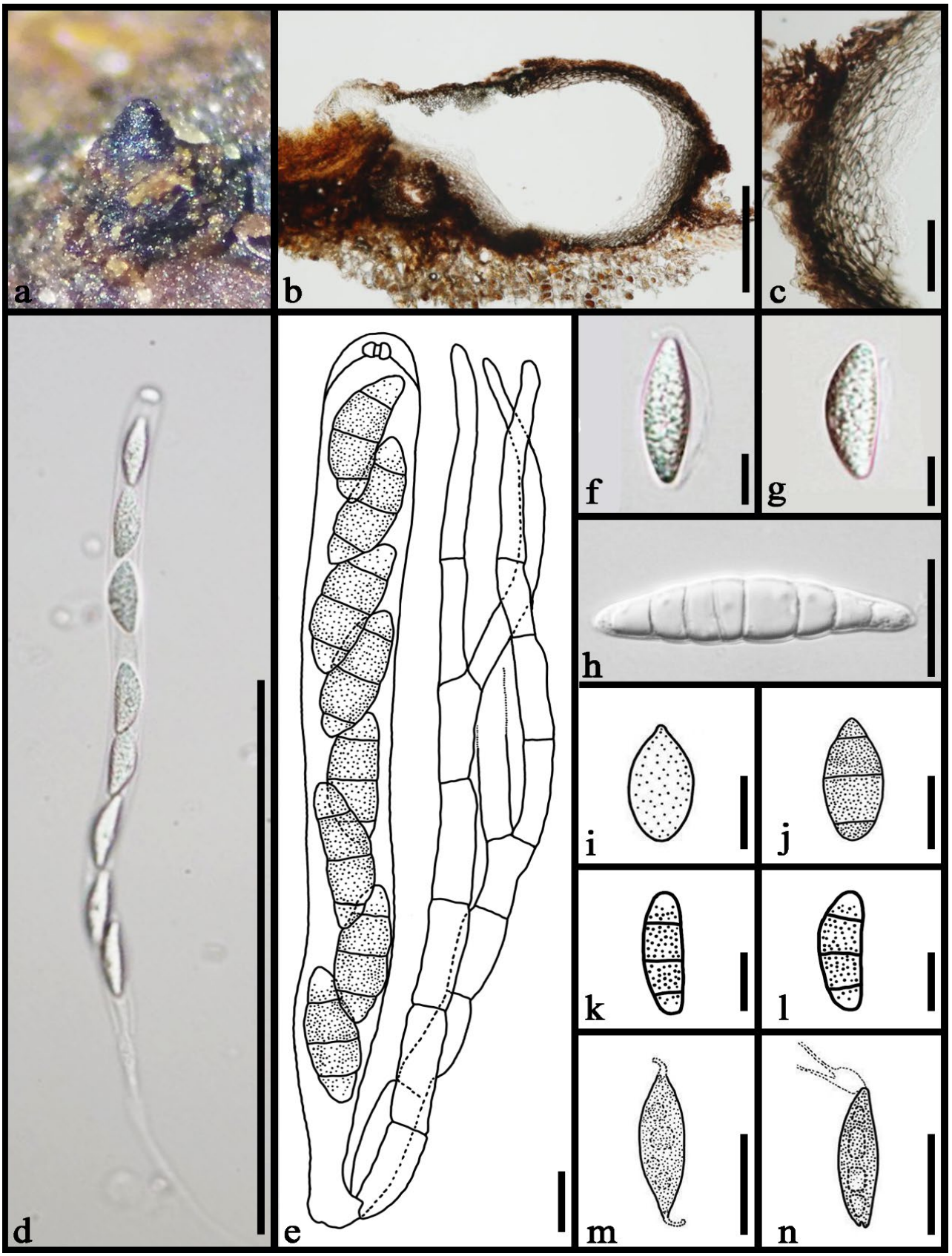


Figure 184 – Morphology of *Annulatascales*. a–d, f, g *Annulatascus nakhonensis* (MFLU 18-1543, holotype). e *Ascitendus austriacus* (PRM 842991, holotype). h *Fusoidigranularius nilensis* (IMI 397966, holotype). i, j *Paoayensis lignicola* (HKU(M) 17516, holotype). k, l *Longivarius aquatorbae* (SS2424.01, holotype). m, n *Submersisphaeria bambusicola* (HKU(M) 9045, holotype). Scale bars: b, d = 200 µm, c = 50 µm, e, k, l = 10 µm, f–h, m, n = 20 µm, i, j = 40 µm.

Atractosporales **Huang Zhang, K.D. Hyde & Maharachch., Fungal Diversity 85: 88 (2017)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Atractosporales, an order within the subclass *Diaporthomycetidae*, was established by Zhang et al. (2017a) with *Atractosporaceae* as the type family. This order is primarily associated with aquatic habitats, particularly decaying submerged wood in freshwater environments (Ho et al. 1999, Réblová et al. 2016a, Zhang et al. 2017a). Species within *Atractosporales* are mainly geographically distributed in Europe, Asia, and North America (Campbell & Shearer 2004, Réblová et al. 2016a, Zhang et al. 2017a, Luo et al. 2019b). It currently comprises only a single family, *Atractosporaceae*, which includes two genera: *Atractospora* and *Rubellisphaeria* (Dong et al. 2021a, Hyde et al. 2021a).

History

Atractospora and *Rubellisphaeria*, introduced by Réblová et al. (2016a) from decaying submerged wood in freshwater habitats, were found to have a sister relationship in phylogenetic analyses. Zhang et al. (2017a) introduced *Atractosporales* to accommodate three newly introduced families, *Atractosporaceae*, *Conlariaceae*, and *Pseudoproboscisporaceae*. However, later phylogenetic analyses conducted by Luo et al. (2019b) and Dong et al. (2021a) suggested that *Conlariaceae* and *Pseudoproboscisporaceae* should be classified as distinct monophyletic lineages. As a result, *Pseudoproboscisporaceae* was reclassified under *Diaporthomycetidae* families *incertae sedis*, and *Conlariaceae* was elevated to the order *Conlariales* (Hyde et al. 2021a). Presently, *Atractosporales* includes only *Atractosporaceae*.

General description

Rubellisphaeria differs from *Atractospora* in having subhyaline to reddish-brown ascomata, short-stipitate asci and ellipsoidal, slightly inequilateral, thin-walled, aseptate ascospores with delayed formation of a middle septum (Réblová et al. 2016a).

Sexual morph: *Ascomata* perithecial, astromatic, immersed to superficial, globose, subglobose to conical with a lateral neck, dark brown to black (*Atractospora*) or subhyaline to dark reddish-brown (*Rubellisphaeria*). *Ostiole* periphysate. *Ascomatal wall* leathery to fragile or waxy, two-layered. *Paraphyses* abundant, persistent, septate. *Asci* unitunicate, stipitate, eight-spored, apex with a inamyloid apical ring. *Ascospores* fusiform or ellipsoidal, hyaline or pale brown, aseptate or transversely septate, smooth or ornamented, without sheath or appendages (adapted from (Réblová et al. 2016a, Zhang et al. 2017a, Luo et al. 2019b)). Asexual morph: (*in vitro*) *Hyphae* in *vitro* subhyaline to pale brown. *Conidiogenous cells* blastic. *Conidia* monilioid, consisting of three to five ellipsoidal to subglobose cells, brown, thick-walled (adapted from Réblová et al. (2016)) (Figs. 185, 186).

Families included in *Atractosporales*

Atractosporaceae Huang Zhang, K.D. Hyde & Maharachch.

Evolution

Hyde et al. (2020d) found the stem ae of *Atractosporales* as 106 MYA. Consequently, Hyde et al. (2021a) found the stem age as 128 MYA in the subclass *Diaporthomycetidae*.

Justification of order and problems

The order recovered in the crown clade and showed the close phylogenetic relationship to *Conlariales* based on LSU, SSU, TEF1-α and RPB2 sequence data. However, the clade was not supported and the taxon sampling was conducted mainly focusing freshwater *Diaporthomycetidae* (Hyde et al. 2021a). Thus, broad taxon sampling with extant genera of freshwater species in *Sordariomycetes* can provide better taxonomic resolution of this order.

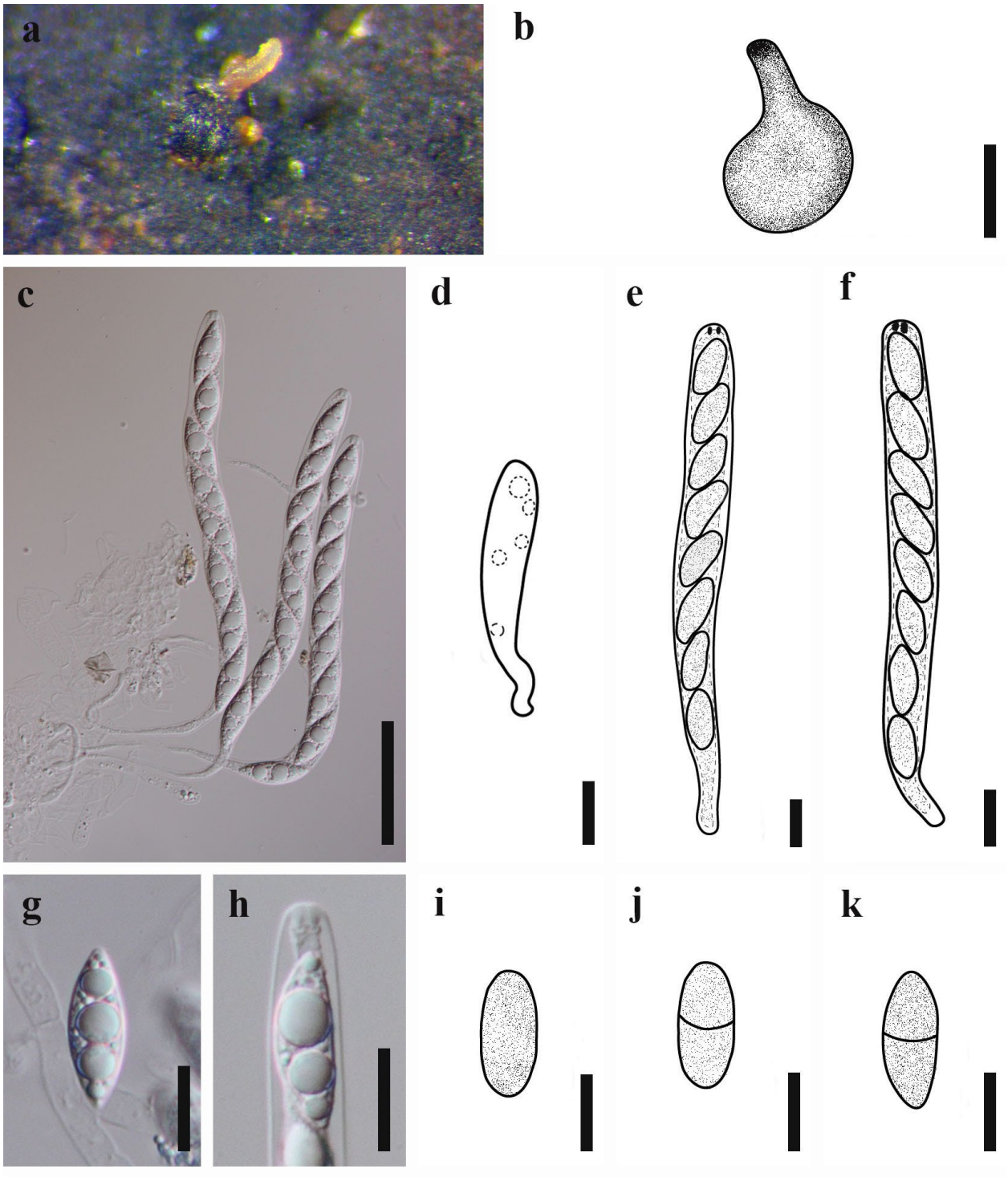


Figure 185 – Sexual morph of *Atractosporales*. a, c, g, h *Atractospora* sp. b, d–f, i–k *Rubellisphaeria* sp. Scale bars: b = 200 µm, c = 40 µm, d–k = 10 µm.

Significance

Ecological and economic roles

All species of *Atractosporales* are reported from freshwater habitats, which play important roles in decomposition of lignocellulose in wood.

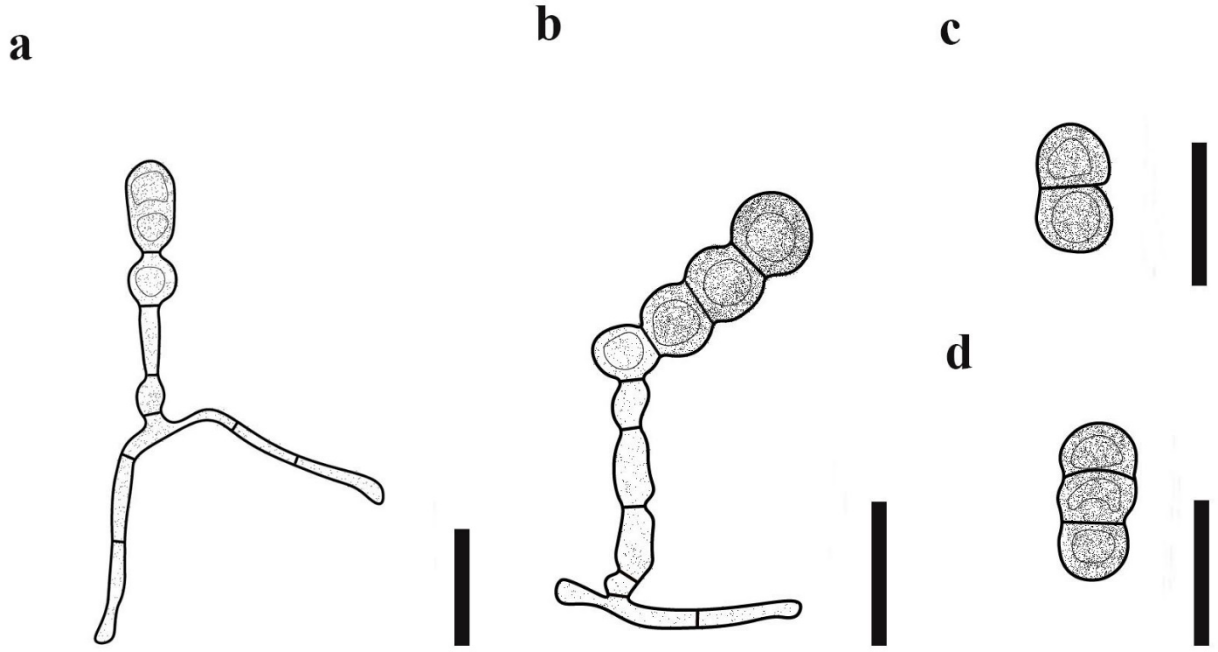


Figure 186 – Asexual morph of *Atractosporales.* a–d *Atractospora* sp. Scale bars: b–n = 10 µm.

Barbatosphaeriales **K.D. Hyde & Hongsanan, Fungal Diversity 107: 85 (2021)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Barbatosphaeriales was introduced to accommodate a single family *Barbatosphaeriaceae* based on phylogeny and divergence time estimate (Hyde et al. 2021a).

History

Barbatosphaeriales accommodates a single family *Barbatosphaeriaceae* that was originally introduced by Zhang et al. (2017a) to encompass three genera including *Barbatosphaeria*, *Ceratostomella* and *Xylomelasma*. The generic type *Barbatosphaeria* was established to accommodate *Barbatosphaeria barbirostris* which was previously placed in *Calosphaeria barbirostris*. The genus shares similar morphology to *Lentomitella* in ascospores features, partly perithecial characters and holoblastic-denticulate conidiogenesis. However, LSU phylogeny showed they are distinct and further morphologically differ in ascomatal formation, and ascus morphology (Réblová 2007). *Barbatosphaeria* clustered together with *Aquaticola* and *Cataractispora* in the phylogenetic analyses that were considered as core genera of the freshwater family *Annulatascaceae* (Réblová 2007). The remaining genera of *Annulatascaceae* that were sampled including *Annulatascus*, *Annulusmagnus* and *Aniptodera* were grouped and formed a monophyletic clade and clearly separated from *Aquaticola* and *Cataractispora*. Thus, the familial placement of the genus was not designated. *Ceratostomella* was introduced to accommodate two species *C. vestita* and *C. cirrhosa* (Saccardo 1878). Höhnel (1905) established *Lentomitella* based on *Ceratostomella vestita* which differs from extant species of *Ceratostomella* in having ornamented (longitudinally striate) ascospore walls and suggested that *Ceratostomella* belongs to *Lentomita* or *Ceratosphaeria*. However, the taxonomic placement of *Ceratostomella* underwent several changes. The genus was also placed under *Endoxyla* within *Diaporthaceae* (von Arx 1952, von Arx & Müller 1954, Munk 1957, Müller & von Arx 1973) but later was treated under *Clypeosphaeriaceae* of the *Xylariales* (Untereiner 1993, Eriksson et al. 2003b). Réblová (2006) redescribed the genus based on the lectotype species *C. rostrata* and defined the generic concept by accepting four species.

The genus formed a close phylogenetic clade to the newly established genus *Xylomelasma* and they share similarities in having pigmented ascospores before discharge, asci floating within the centrum at maturity and a similar branching pattern of ascogenous hyphae. However, they differ in the thickness of the perithecial wall, paraphyses that are cylindrical and only slightly constricted at the septa, and cylindrical and generally larger asci with a distinct, refractive apical ring, and ellipsoidal ascospores that are obliquely uniseriate within the ascus. Zhang et al. (2017a) established the family *Barbatosphaeriaceae* to accommodate *Barbatosphaeria*, *Ceratostomella* and *Xylomelasma* based on morpho-molecular analyses. The family formed a sister clade to *Natantiella ligneola* and *Ophiostomatales* and was placed in *Diaporthomycetidae* family *incertae sedis*. The family formed a distinct clade within *Diaporthomycetidae* with a stem age 177 MYA in the study of Hyde et al. (2021a). Thus, the order *Barbatosphaeriales* was established to accommodate this family and presently accommodates four genera (Hyde et al. 2024b).

General description

The members of the order are commonly characterized by having dark, long-necked, astromatic ascomata, mostly surrounded by sparse mycelium, clavate or cylindrical-clavate asci, arising from autogenous hyphae and mostly ellipsoidal ascospore (Zhang et al. 2017a).

Sexual morph: *Ascomata* astromatic, leathery to fragile, solitary or aggregated in circular to oval nests or in short rows, globose to subglobose, dark brown to black, glabrous or roughened, with elongate necks, venter or neck are sparsely covered with a pubescence that disappears with age. *Necks* cylindrical, central or lateral, straight to slightly fexuous, when in circular groups decumbent to perpendicular, covering, piercing the periderm in a group. *Ostiole* periphysate. *Peridium* two-layered. *Paraphyses* abundant, persistent, cylindrical, unbranched, septate, constricted at the septa, tapering to the apex. *Asci* 8-spored, unitunicate, clavate or cylindrical, tapering towards the pedicel, with a distinct or indistinct, refractive, J-, apical ring, foating freely in centrum at maturity. *Ascospores* 1- or 2-seriate, oblong to ellipsoid, subcylindrical, reniform, straight or slightly curved, allantoid, U- to horseshoe-shaped or 3/4 circular, aseptate or septate, not- or slightly constricted at the septum, smooth-walled. Asexual morph: *Hyphomycetous* ramichloridium and sporothrix-like. *Conidiophores* semi-micronematous to macronematous, unbranched or branched, cylindrical to fask or irregularly-shaped, brown or hyaline. *Conidiogenous cells* polyblastic, integrated, terminal, sympodially elongating with several denticles or forming rachis producing conidia holoblastically. *Conidia* ellipsoidal to suballantoid, straight or curved, unicellular, hyaline (adapted from Hyde et al. 2021a) (Fig. 187).

Families included in *Barbatosphaeriales*

Barbatosphaeriaceae H. Zhang, K.D. Hyde & Maharachch

Evolution

The stem age for *Barbatosphaeriales* is reported as 177 MYA (Hyde et al. 2021a) and the stem age of *Barbatosphaeriaceae* was reported as ca 110 MYA by Zhang et al. (2017a).

Justification of order and problems

Barbatosphaeriales is established within *Diaporthomycetidae* which formed a distinct clade based on phylogenetic and divergence time estimate analyses (Hyde et al. 2021a). However, a detailed investigation of the morphological features of the members needs further studies.

Significance

Ecological and economic roles

The members of the order are reported as saprobic on decaying wood and bark (Hyde et al. 2020d). Lai et al. (2021) reported *Xylomelasma* sp. as an endophytic fungus from the medicinal plant *Salvia miltiorrhiza*.

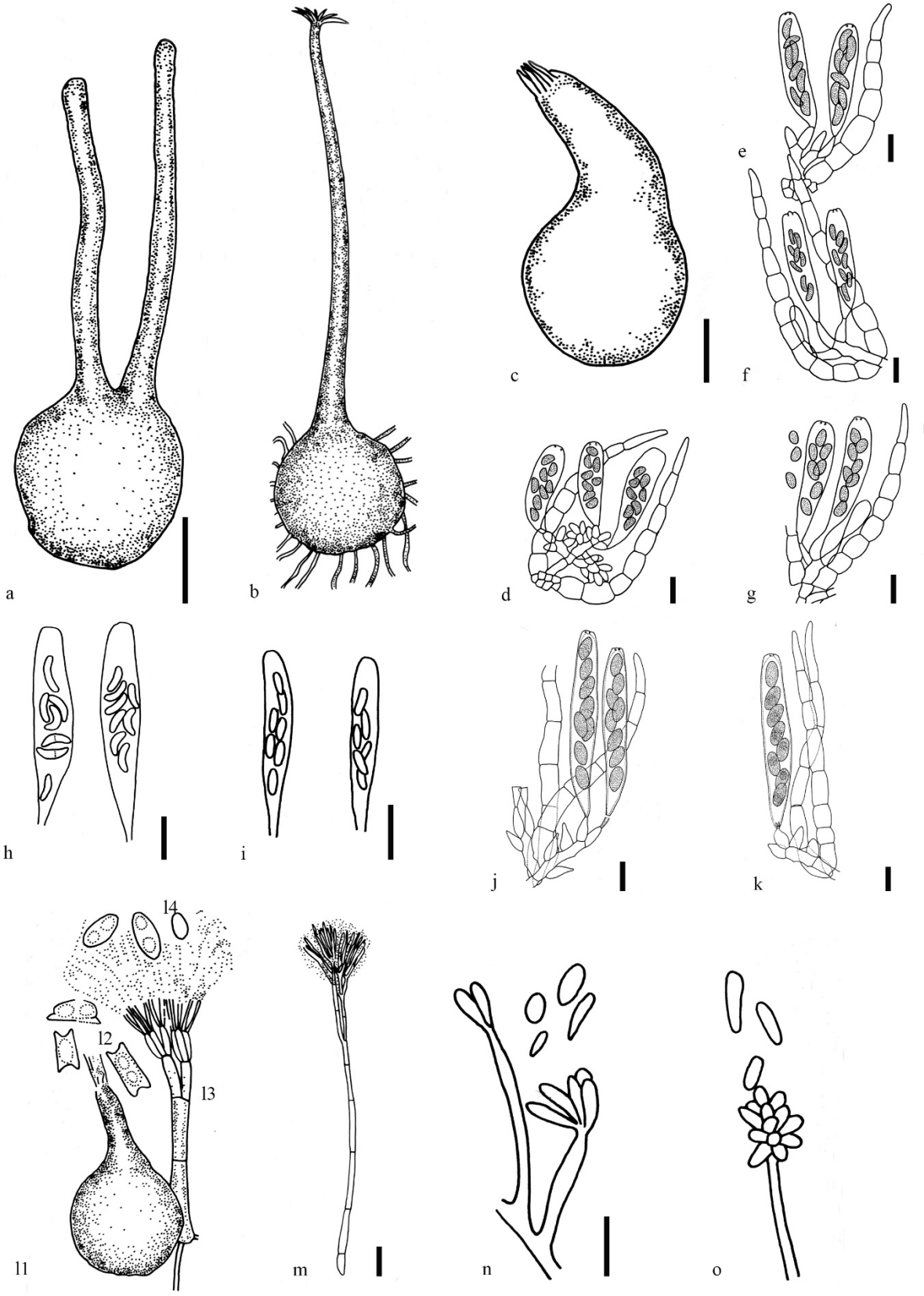


Figure 187 – Sexual and asexual morphs of *Barbatosphaeriales*. a–c Morphology of perithecia (a, *C. rostrocylindrica*, b *C. stenoceras*). d–g, j, k Asci with ascospores, ascogenous hyphae, paraphyses (d *Ceratostomella cuspidata*, e *C. pyrenaica*, f *C. rostrata*, g C. *rhynchophora*, j *Xylomelasma novaezelandiae*, k *X. sordida*). Asci (h *Barbatosphaeria dryina*, i *B. barbirostris*). l1 Perithecium l2

Ascospores. l3 Conidiophore. l4 conidia (l1, l2, l3, l4 *Ceratostomella leptographioide*), m Conidiophore (*Ceratostomella rostrocylindrica*). n, o Conidia and conidiophore (j *Ceratostomela minutum*, k *Ceratostomella stenoceras*) (redrawn from Davidson 1942, Réblová 2006, drawn from Réblová et al. 2015). Scale bars: a = 184 µm, b = x 1500, d–k = 10 µm, l1 X 240, l2 X 2000, l3 X 600, l4 X 2000, m = 17 µm, c, n = 8 µm.

Chemical diversity

Lai et al. (2021) extracted five chromone derivatives, including 2,6-dimethyl-5-methoxyl-7-hydroxylchromone, 6-hydroxymethyleugenin, 6-methoxymethyleugenin, chaetoquadrin D (4), and isoeugenitol, and three isocoumarin congeners, namely diaporthin, 8-hydroxy-6-methoxy-3-methylisocoumarin, and 6-methoxymellein from the culture of the endophytic fungus *Xylomelasma* sp. Among these, some compounds showed antibacterial and antioxidant activities (Lai et al. 2021).

Other relevant data and future recommendations

A detailed investigation of the members of the order has not been done yet. Index Fungorum (2025) showed 111 epithets linked to *Ceratostomella,* but molecular data are available for only a few species. Thus, detailed morphological analysis along with phylogenetic analyses can provide a better resolution of the taxonomy of the members.

Boliniales **P.F. Cannon, Ainsworth & Bisby's Dictionary of the Fungi, Edn 9 (Wallingford): x (2001)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Sordariomycetidae*

Introduction

Boliniales, belonging to subclass *Sordariomycetidae* comprises only one family (*Boliniaceae*) and nine genera (Wijayawardene et al. 2022a). This order was established by Kirk et al. (2001), in the Dictionary of Fungi 9th edition (Kirk et al. 2001). Andersson et al. (1995) demonstrated that *Boliniaceae*, formerly grouped with *Xylariales* (Munk 1953, Barr 1990b, Romero & Samuels 1991), are more closely related to the *Sordariales* based on the analysis of SSU DNA sequences. The family was later included in *Boliniales* along with *Catabotrydaceae*. However, the latter family is currently placed in *Catabotryales* (Hyde et al. 2020d). *Boliniaceae* which was introduced by Rick (1931) and revised by Untereiner et al. (2013), is distributed worldwide and mostly saprobic on wood in terrestrial habitats. *Apiorhynchostoma*, *Camaropella*, *Camarops*, *Cornipulvina*, *Endoxyla*, and *Pseudovalsaria* are six of the nine accepted genera in this family with molecular data. *Camarops* as the type genus which contains 28 species, with two important species, *Camarops hypoxyloides* and *C. tubulina* known as bioindicators of natural forest ecosystems (Holec 2005, Huhndorf & Miller 2008, Raja et al. 2011, Untereiner et al. 2013, Maharachchikumbura et al. 2015, 2016, Vu et al. 2019, Hyde et al. 2020d, Wijayawardene et al. 2020). Membranaceous ascomata, cylindrical asci, and ellipsoidal ascospores were considered as the preliminary features of *Boliniales* (Kirk et al. 2001). Consequently, this order was assigned to certain species characterized by carbonaceous ascomata (Zhang et al. 2006). Accordingly, the monophyletic *Boliniales*, characterized by cylindrical asci and smooth-walled ellipsoidal ascospores with germ pore(s), formed a sister relationships to *Phyllachorales* in the *Sordariomycetidae* (Maharachchikumbura et al. 2016, Hongsanan et al. 2017a, Hyde et al. 2017b, Huang et al. 2021b).

History

Most *Boliniales* were discovered mainly on wood in America and Europe. The asexual morph has not been determined (Zhang et al. 2006, Huang et al. 2019). Based on some morphological similarities, such as carbonaceous ascomata, *Boliniaceae* was previously assigned to *Xylariales*. Later, this family was placed in *Boliniales* according to the morphological characteristics of the genus *Bolinia* typified by *B. tubulina* (Kirk et al. 2001). *Bolinia* was initially described by Nitschke (1867)

and then upgraded to the generic rank by Saccardo (1882b). Previously, *Camarops* was stated by Karsten (1873) based on *C. hypoxyloides* P. Karst. *Bolinia* and *Camarops* have frequently been mentioned together in the research due to their close similarities. By analyzing the taxonomy of these taxa, Munk (1957) and von Arx & Müller (1954) reached the conclusion that *Camarops* and *Bolinia* were two separate genera with the same characteristics and one notable difference was that the former had monostichous ascomata while the latter had polystichous ascomata. Shear (1938) and Svrček (1969) indicated that *Sphaeria tubulina* might belong to *Camarops* (*C. tubulina*). However, Nannfeldt (1972) revised the species of *Camarops* and *Bolinia*, and recommended that these two genera should be merged because of their similar characteristics. Although *Bolinia tubulina* was reclassified as *Camarops tubulina*, it remains the type species for its order and family, as both *Boliniales* and *Boliniaceae* were originally established based on *Bolinia tubulina* (Maharachchikumbura et al. 2016, Huang et al. 2021b).

General description

Members of *Boliniales* are generally distinguished based on the morphology of stromata, ascomata, and ascospores. However, these characteristics differ significantly within some genera resulting in it being unclear whether the validity of this approach of taxonomic separation is correct. For instance, the most species-rich genus in the order, *Camarops*, produces stromata that can be applanate, peltate, or turbinate, hard and strongly carbonized or soft, and dark to lightly or brightly colored. Species of *Camaropella* are characterized by immersed, valsoid stromata and clustered long-necked ascomata (Vasilyeva 1997). The species of *Endoxyla*, the second-largest genus in the order *Boliniales*, contains ascospores which may be either aseptate, one- or two-septate, or in some cases, they can have a hyaline cell. The hyaline cap, a noncellular appendage that covers the germ pore of the ascospores, is one of the important characteristics of some *Boliniales* species that needs to be taken into consideration in further phylogenetic analyses. This feature, which appears to reflect a localized thickening of the ascospore wall, has been reported in one species of the genus *Camarops* and is present in all species of *Apiorhynchostoma* and *Neohypodiscus* (Winter 1886, Müller & von Arx 1962, Rogers et al. 1994, 2006, Rappaz 1995).

Sexual morph: *Ascostromata* immersed, irregularly-shaped, superficial or erumpent, pale brown to black. *Ascomata* perithecial, immersed, solitary or gregarious, erumpent or superficial, globose to obpyriform, papillate, brown to black. *Peridium* carbonaceous, coriaceous or membranaceous, composed of brown to dark brown cells of *textura intricata* or *textura prismatica*. *Paraphyses* abundant, flamentous, tapering, septate, branched. *Asci* 8-spored, unitunicate, cylindrical to clavate, having round to blunt apex, pedicellate. *Ascospores* 2–3-seriate, normally cells in the center brown to dark brown, and the terminal cells hyaline to pale brown, subglobose to ellipsoidal, 0–2-septate, smooth-walled, guttulate. Asexual morph: Undetermined (Fig. 188).

Families included in *Boliniales*

Boliniaceae Rick

Evolution

The divergence time for *Boliniales* has been estimated at about 158 MYA (Hyde et al. 2020d). Some members of this order were traditionally allied with *Xylariales* based on morphological similarity such as carbonaceous ascomata (Barr 1990b, Romero & Samuels 1991). However, Andersson et al. (1995) concluded that *Boliniaceae* was more closely linked to *Sordariales* based on SSU based phylogenetic analysis.

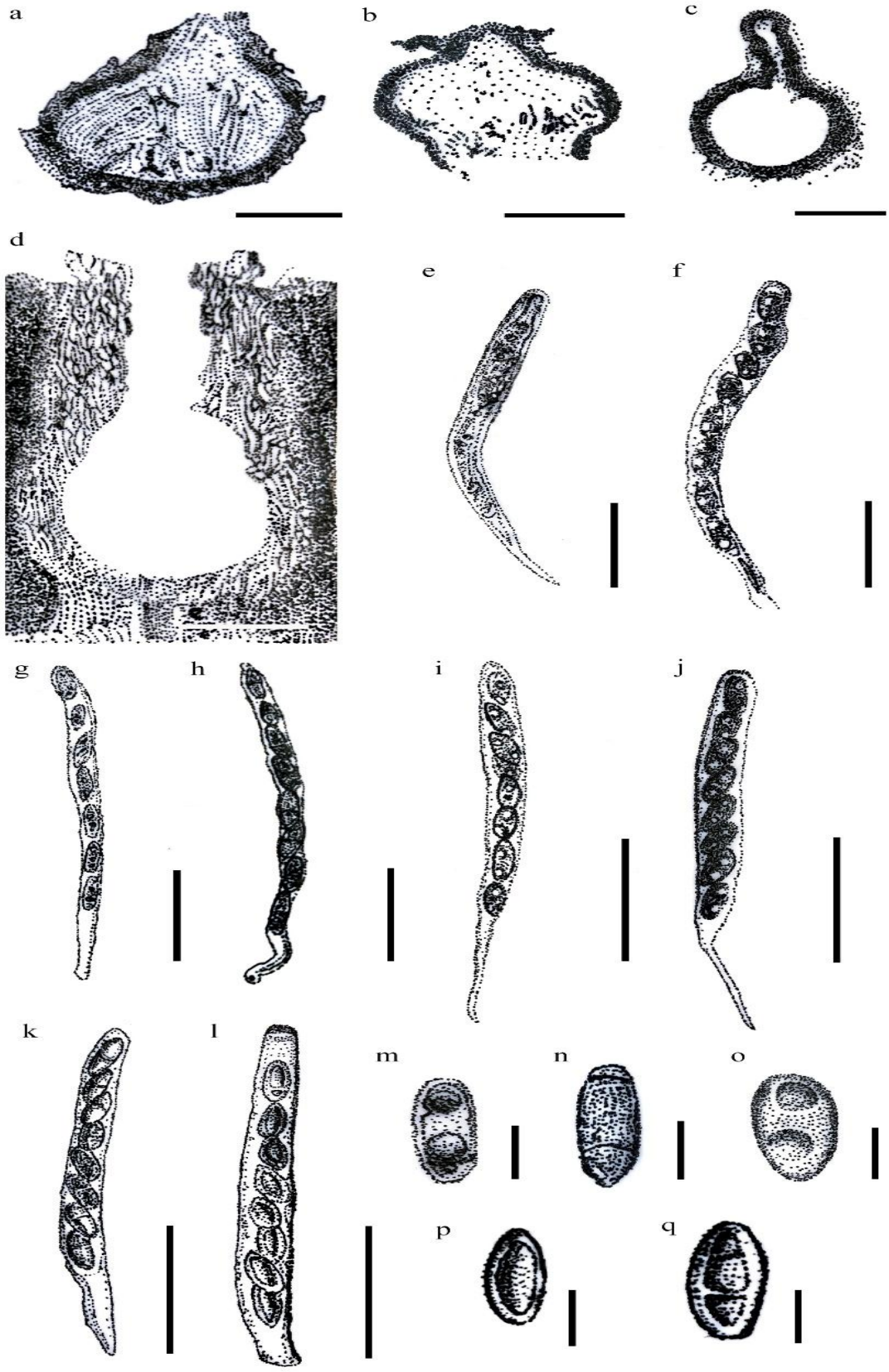


Figure 188 – Appearance of Ascomata of *Boliniales* (a *Apiocamarops* sp., b *Apiorhynchostoma* sp., c *Endoxyla* sp., d *Camarops* sp.). e–l Asci (e–f *Apiocamarops* sp., g–h *Apiorhynchostoma* sp., i–j *Camarops* sp., k–l *Endoxyla* sp.). m–q Ascospores (m *Apiocamarops* sp., n *Apiorhynchostoma* sp., o *Camarops* sp., p–q *Endoxyla* sp.) (drawn from Huang et al. 2021b). Scale bars: a–d = 50 µm, e–h = 20 µm, i–l = 30 µm, m–q = 5 µm.

Justification of order and problems

The classification of *Boliniales* has been challenging due to the atypical production of large stromata in this group. Initially, it was placed within the *Xylariomycetidae* (Munk 1953). Somrithipol et al. (2008) claimed that the *Chaetosphaeriales* were divided into two distinct clades, *Boliniales* and *Coniochaetales*, which had strong support. Phylogenetic analyses based on DNA data have suggested its reassignment to the *Sordariomycetidae* (Huhndorf et al. 2004a). Maharachchikumbura et al. (2015) clarified the position of *Boliniales* which is closest to *Phyllachorales* and *Sordariales*, comprising a single family, *Boliniaceae*, with nine genera.

Significance

Ecological and economic roles

This order comprises an ecologically significant group of fungi, with numerous species commonly found as saprobes on wood and bark in both temperate and tropical regions (Rogers et al. 2006). Many species have been reported to cause rotting wood in Europe, North America and South America (Nannfeldt 1972, Huhndorf & Miller 2008).

Chemical diversity

No relevant studies are available regarding the chemical diversity of *Boliniales.*

***Calosphaeriales* M.E. Barr, Mycologia 75(1): 11 (1983)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Calosphaeriales previously comprised two families, *Calosphaeriaceae* and *Pleurostomataceae* with three genera (*Calosphaeriopsis*, *Enchnoa*, *Kacosphaeria*), and the order was placed in *incertae sedis* (Hyde et al. 2020d). The members are mainly characterized by black ascomata with an eccentric papilla or long neck, conspicuously septate, tapered paraphyses, numerous, clavate or subglobose asci borne from fascicled or spicate ascogenous hyphae, hyaline, allantoid to subcylindrical ascospores with phialidic hyphomycetous asexual morphs (Réblová et al. 2015b, Huang et al. 2021b). The taxa are reported in both sexual and asexual morphs and the sexual and asexual links have been linked to many species including experimentally (Réblová et al. 2015b). *Calosphaeriophora* and *Phaeocrella* were described as asexual morphs of *Calosphaeria* and *Togniniella,* respectively (Réblová et al. 2004). However, *Calosphaeria* and *Togniniella* were adopted as valid names according to the dual nomenclature priority (Réblová et al. 2015b).

History

Calosphaeriaceae was introduced by Munk (1957) and placed in *Sphaeriales* based on having a unique centrum that has small to very small asci, springing in various heights from bundles that are very long and stout, with paraphysis-like hyphae. Wehmeyer (1975) accepted the *Calosphaeriaceae* under *Allantosphaeriales*. Barr (1983b) erected a new order *Calosphaeriales* to accommodate this family. She distinguished the order based on having globose or ampulliform ascomata immersed in the substratum or stroma, ostiole periphyses, unitunicate asci with a shallow apical ring, asci with paraphyses gradually decreasing, ascospores that are hyaline, allantoid or oblong, continuous or septate.

Réblová et al. (2004) added the second family *Pleurostomataceae*, based on the evidence from morphology and phylogeny. *Pleurostomataceae* is a monotypic family introduced to accommodate *Pleurostoma*. It has been reported in both sexual and asexual states. The order formed a close association with *Jobellisiales* and *Togniniales* in the phylogenetic analyses conducted by Maharachchikumbura et al. (2016). *Calosphaeriaceae* formed a sister clade to *Jobellisiales*. Thus, Hongsanan et al. (2017a) considered *Jobellisiales* to be a synonym of *Calosphaeriales* and the order formed a distinct lineage between *Togniniales* and *Diaporthales*. However, *Jobellisiales* was

considered to be a distinct clade. *Calosphaeriales*, *Togniniales* and *Diaporthales* were also recovered as distinct lineages, but phylogenetically they are closely associated orders (Hyde et al. 2020d, Huang et al. 2021b). Despite the distinct phylogeny, the order shares a similar morphology to *Togniniales* in having clavate asci borne from spicate ascogenous hyphae (Réblová et al. 2015, Maharachchikumbura et al. 2016, Hongsanan et al. 2017a). The order presently accommodates two families which comprise five genera and three more genera are treated under *incertae sedis* (Hyde et al. 2024b).

General description

All members are astromatic. However, several *Calosphaeria* and *Jattaea* species have a tomentum that can develop into a thin, compact stromatic layer enclosing one or several ascomata (Réblová et al. 2015b). The ascoma centrum is unique among *Sordariomycetes* and it comprises persistent, sparsely branched, short or elongated ascogenous hyphae with minute cells formed from croziers in sympodial succession, asci in predominantly spicate arrangement and persistent paraphyses (Réblová et al. 2015b). The asexual morphs linked to *Calosphaeria*, *Jattaea*, *Phialophora* and *Pleurostoma* are characterized by phialidic hyphomycetes, semi-macronematous, hyaline, subhyaline to pale yellow-brown conidiophores often reduced to conidiogenous cells such as phialides or adelophialides. Phialides are hyaline, subhyaline or pale brown, sometimes pigmented in the apical region below the collarette; they are short-ampulliform to elongate-ampulliform to cylindrical, tapering, with a more or less conspicuous funnel-shaped collarette (Réblová et al. 2004, Vijaykrishna et al. 2004, Damm et al. 2008a, Réblová 2011).

Sexual morph: Astromatic, rarely stromatic. *Ascomata* perithecial, scattered or solitary, dark brown to black, immersed, globose to subglobose, coriaceous or membranous, tuberculate or smooth or with hyphal coating, papillate; papilla positioned laterally, ostiolate. *Neck* long or short, periphysate. *Peridium* thick, outer layer coriaceous or membranous, composed of two to four layers, composed of *textura intricate*, *angularis epidermoidea* or *prismatica*. *Ascogenous hyphae* discrete, hyaline, smooth, branched, producing a sympodial sequence of hyaline, ovoid to ellipsoidal cells, often with mucronate apex, in dense clusters, each giving rise to an ascus. *Paraphyses* numerous, hyaline, filamentous, broad, septate, unbranched, tapering, and deliquescing. *Asci* 8-spored or polysporous, unitunicate, clavate, reniform or oval long or short pedicellate, sessile, mostly in fascicles, apical ring distinct or absent. *Ascospores* 2–3-seriate or overlapping, hyaline, oblong, allantoid or ellipsoid, straight to slightly curved, aseptate, smooth-walled, sometimes with guttules. Asexual morph: *Hyphomycetous*, Acremonium- and phialophora-like. *Conidiophores* micronematous or semi-macronematous, brown or hyaline, straight or flexuous, 0-septate, branched, unbranched, tuberculate or smooth- walled. *Conidiogenous cells* phialides or adelophialdes, mono- or polyphialidic, terminal, intercalary or lateral, hyaline to subhyaline, ampulliform, cylindrical to subcylindrical, smooth-walled. *Conidia* aseptate, oblong, allantoid, or subcylindrical, hyaline, smooth, with or without guttules (adapted from Hyde et al. 2020d) (Fig. 189).

Families included in *Calosphaeriales*

Calosphaeriaceae Munk
Pleurostomataceae Réblová, L. Mostert, W. Gams & Crous

Calosphaeriales genera *Incertae sedis*
Calosphaeriopsis Petr.
Enchnoa Fr.
Kacosphaeria Speg.

Evolution

The divergence time for *Calosphaeriales* has been estimated as 160 MYA (Hyde et al. 2020d). In the subsequent study, it has been estimated as 155 MYA (Hyde et al. 2021a).

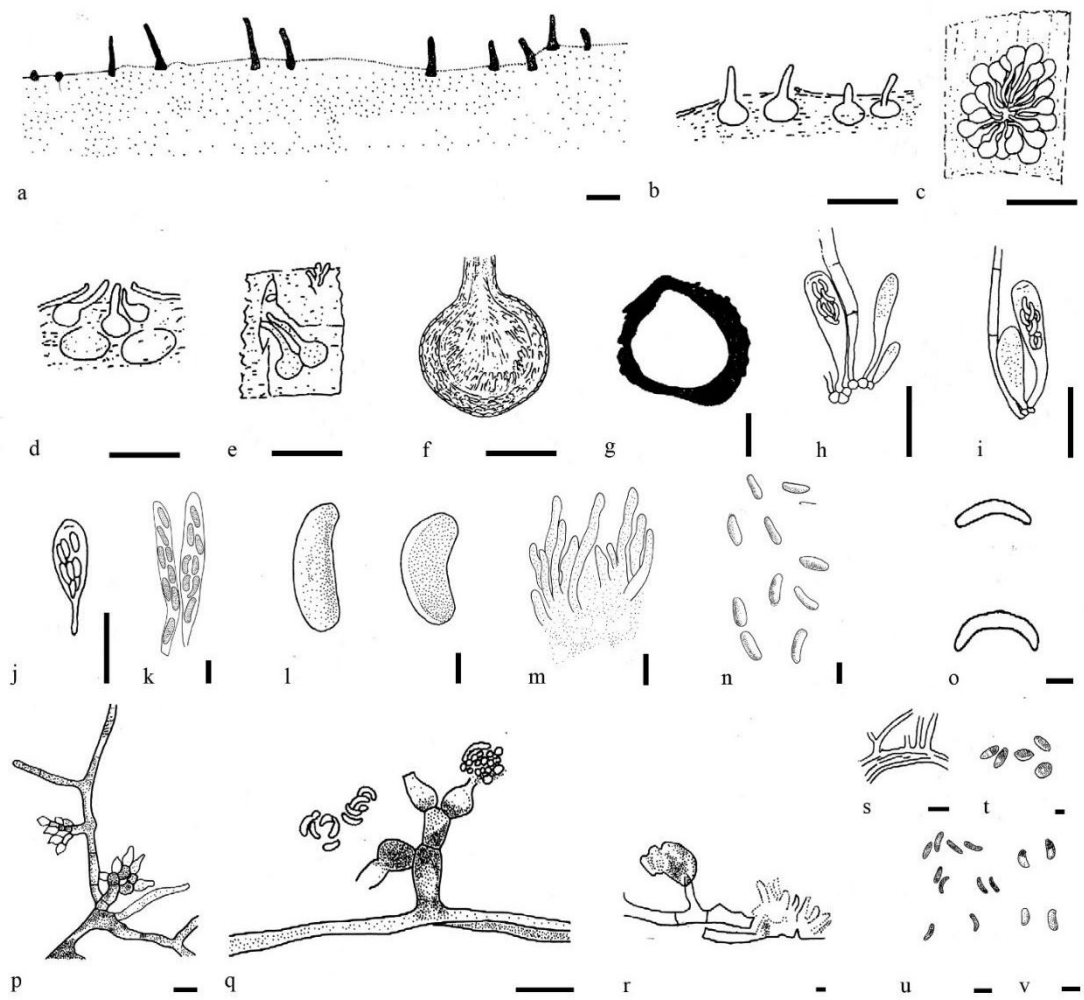


Figure 189 – Morphology of *Calosphaeriales*. a–e Ascomata on the substrate (a *Flabellascus tenuirostris*, b *Jattaea discreta*, c *Calosphaeria pulchella*, d *C. microsperma,* e *C. barbirostris*). f, g Vertical section through ascoma (f *Calosphaeria pulchella,* g *Pleurostoma candollei*). h–l Asci (h *Calosphaeria puchelloidea*, i *Jattaea discreta*, j *Calosphaeria barbirostris*, k *Jattaea prunicola*, l *Pleurostoma candollei*). m Paraphyses (*Jattaea prunicola*). n, o Ascospores (n *Jattaea prunicola*, o *Pleurostoma candollei*). p–r Conidiophores with phialides in whorls (p *Flabellascus tenuirostris*, q *Flabellascus tenuirostris*). r Conidiophores and conidia (*Calosphaeria africana*). s Conidiophores (*Calosphaeria africana*). t–v Conidia (t *Calosphaeria Africana*, u *Flabellascus tenuirostris* (Type I conidia). v *Flabellascus tenuirostris* (Type II conidia)) (redrawn from Barr 1985, redrawn from Damm et al. 2008a, Réblová et al. 2015b, Huang et al. 2021a). Scale bars: a = 25 µm, b–e = 1000 µm, f = 150 µm, g = 100 µm, h–j = 15 µm, k–n, r–v = 5 µm, o = 1 µm, p, q = 10 µm.

Justification of order and problems

Calosphaeria is a phenotypically diverse genus that needs further taxonomic revision, even though several species have been transferred to different families, including *Ceratostomataceae*, *Gnomoniaceae*, *Nitschkiaceae*, *Togniniaceae*, *Valsaceae* and *Sordariomycetes incertae sedis* (Réblová et al. 2015b). Only a few species have been studied in culture, hence their asexual morph in culture is unknown and many species lack molecular data (Damm et al. 2008a).

Significance

Ecological and economic roles

Calosphaeriales species are reported as saprobic or hypersaprobic and have been observed together with old stromata and ascomata of other ascomycetes. Globally, their substrates are woody plants, bark and shrubs. They are inconspicuous and are frequently found when searching for other

fungi beneath the periderm, especially beside stromatic ascomycetes of the *Diaporthales* and *Diatrypaceae* (Réblová et al. 2015b). *Phialophora* causes diseases in humans and plants. *Phialophora richardsiae* causes chromoblastomycosis, also known as chromomycosis, which is a subcutaneous chronic mycosis and phaeohyphomycosis in humans (Ikai et al. 1988, Son et al. 2010). Some species have also been isolated from soil, wood and sewage (Schol-Schwarz 1970), grafted unions of nursery vines and diseased vines (Halleen et al. 2006, Halleen & Groenewald 2005, Carlucci et al. 2015). *Pleurostoma repens* was associated with subcutaneous infections with granulomatous nodules in humans (Hironaga et al. 1989). *Pleurostomophora ochracea* causes Eumycetoma with yellow grains in humans (Mhmoud et al. 2012).

Other relevant data and future recommendations

Only a few species of the *Calosphaeriaceae* have thus far been studied in culture, and hence data availability on their respective anamorphs and DNA phylogeny remains sparse (Damm et al. 2008a).

***Cancellidiales* K.D. Hyde & Hongsanan, Fungal Diversity 107: 86 (2021)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Cancellidiales, a monotypic order was established by Hyde et al. (2021a) to accommodate *Cancellidium* with four species based on morphological characters, phylogenetic analysis and divergence time estimates. Dong et al. (2021a) introduced the second genus *Obliquiminima* and a new species *C. thailandense* to the order. Currently, two genera *viz*. *Cancellidium* and *Obliquiminima* with five species are accepted in the order. The order is well-studied and all the species have associated sequence data (Dong et al. 2021a, Hyde et al. 2021a).

History

Cancellidium was established by Tubaki (1975) and is typified by *C. applanatum*. The placement of *Cancellidium* has not been clear since it was established. Phylogenetic analyses placed *Cancellidium* in *Sordariomycetes* genera *incertae sedis*. However, the genus was not monophyletic and phylogenetic analyses showed that the placement of *C. applanatum* was distant from *C. pinicola* (Yeung et al. 2006, Pratibha et al. 2014, Zelski et al et al. 2014). Luo et al. (2019b) showed that *Cancellidium applanatum* clustered within *Diaporthomycetidae*, while *C. pinicola* grouped within *Hypocreaceae* (*Hypocreomycetidae*). Hyde et al. (2021a) obtained a similar result as Luo et al. (2019b), they therefore excluded *C. pinicola* from *Cancellidium*. In addition, their analysis showed that *Cancellidium* formed a distinct, well-supported clade within *Diaporthomycetidae* and the stem age falls in the order range. They introduced a new order (*Cancellidiales*) and a new family (*Cancellidiaceae*) to accommodate this genus, three new *Cancellidium* species were also introduced. Subsequently, Dong et al. (2021a) introduced a monotypic genus *Obliquiminima* and a new species *Cancellidium thailandense* to the family. Currently, the order comprises two genera with five species (Dong et al. 2021a, Hyde et al. 2021a).

General description

Cancellidium is known only by the asexual morphs that are characterized by large, flattened, fan-shaped conidia with many parallel columns of cells and internally contain chains of subhyaline, globose to fusiform cells (Cai et al. 2006a, Seifert et al. 2011). Morphologies of this genus are similar and studies distinguished them based on the size and color of conidia and phylogenetic analysis (Dong et al. 2021a, Hyde et al. 2021a). The sexual morph of *Cancellidiales* is presented by *Obliquiminima,* which comprises a single species (Dong et al. 2021a), thus, further taxon sampling is required to better understand the morphology of this order.

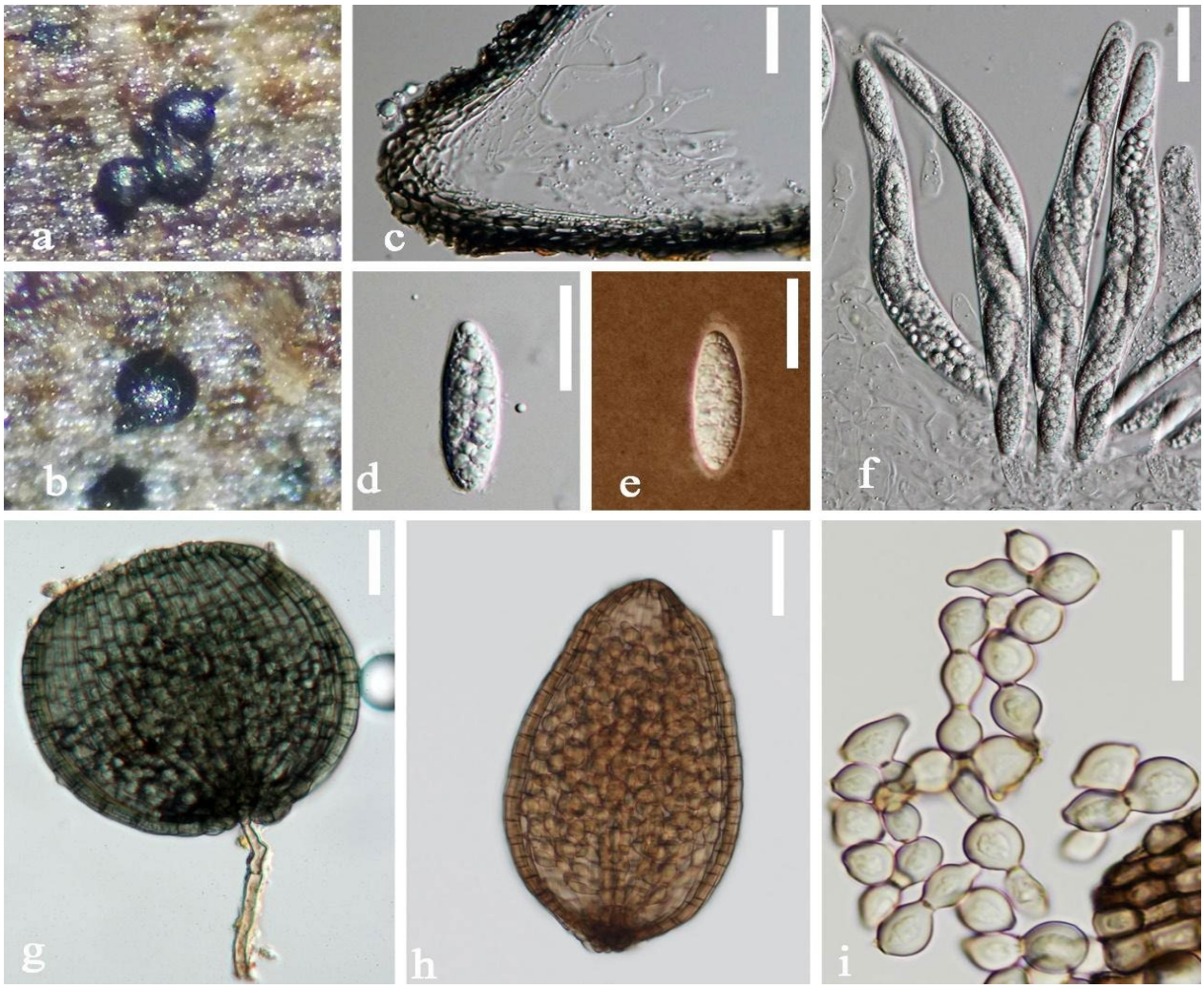


Figure 190 – Sexual and asexual morphs of *Cancellidiales*. a–f *Obliquiminima hyalina*. g *Cancellidium thailandense*. h, i *C. atrobrunneum*. Scale bars: c–g, i = 20 µm, h = 30 µm.

Sexual morph: *Ascomata* tiny, scattered, superficial, ellipsoidal to subglobose, black, coriaceous, ostiolate, with a lateral neck. *Necks* short, black, cylindrical, and oblique to the host substrate. *Peridium* comprising several layers of dark brown to black, thick-walled, compressed cells of *textura angularis*. *Paraphyses* tapering towards the apex, dense, hypha-like, septate, unbranched, hyaline. *Asci* 8-spored, unitunicate, narrowly obclavate, slightly truncate at apex, sessile, with a small, refractive apical ring. *Ascospores* uni- to bi-seriate, oval, narrowly ellipsoidal, straight, aseptate, guttulate, hyaline, thin-walled, smooth, with a thin gelatinous sheath. Asexual morph: *Conidiophores* semi-macronematous to macronematous, mononematous, pale brown to yellowish-brown, smooth, thick-walled, septate, cylindrical, sometimes developed from assimilative hypha. *Conidiogenous cells* monoblastic, integrated, terminal, pale brown to yellowish-brown. *Conidia* acrogenous, holoblastic, solitary, dry, olivaceous to greyish-green, shiny, flattened, obovate or ellipsoidal, fan-shaped, mostly with truncated head, composed of many parallel, septate columns arranged in lines radiating from conidial base, internally contain chains of subhyaline, small moniliform cells (adapted from Dong et al. 2021a, Hyde et al. 2021a) (Fig. 190).

Families included in *Cancellidiales*

Cancellidiaceae K.D. Hyde & Hongsanan

Evolution

Recent studies showed that the ancestors of *Cancellidiales* diverged around 137 MYA during the Cretaceous (145– 66 MYA). *Cancellidium* species are likely to have evolved in streams in one

part of the world and have colonized other continents with time, and they were likely restricted to submerged wood in various river systems. Hyde et al. (2021a) reported four *Cancellidium* species that are morphologically similar to each other but phylogenetically distinct, they therefore suspect that *Cancellidium* species may have speciated over time.

Justification of order and problems

Cancellidiales is a well-resolved order with all the species associated with sequence data. The order comprises two genera *Cancellidium* and *Obliquiminima*. However, *Cancellidium* is known by the asexual morphs, while *Obliquiminima* comprises a single sexual species. Thus, it is not possible to compare the morphological differences of these two genera. Dong et al. (2021a) introduced *Obliquiminima* based on phylogenetic analysis. Hence, further fresh collections are required to better understand the morphological characters of this order.

Significance

Ecological and economic roles

Cancellidiales species are cosmopolitan and distributed in many countries (Australia, Brazil, Brunei, China, India, Japan, Malaysia, Peru and Thailand) and are exclusively known as saprobes from freshwater habitats (Fryar et al. 2004, Pinnoi et al. 2006, Zhao et al. 2012, Zelski et al. 2014, Dong et al. 2021a, Hyde et al. 2021a). Lignicolous freshwater fungi play an important role in nutrient and carbon cycling, biological diversity and ecosystem functioning and they can decompose lignocellulose in woody litter, softening the wood and releasing nutrients (Hyde et al. 2016a).

Chemical diversity

There were no reports of chemical compounds or secondary metabolites from *Cancellidiales* species.

Other relevant data and future recommendations

Only two genera *viz*. *Cancellidium* and *Obliquiminima* are accepted in this order. However, only asexual morphs are known for *Cancellidium*, while *Obliquiminima* is known only by the sexual morph with a single species. *Obliquiminima* was accepted in the order based on only phylogenetic analysis. However, limited samples and species in *Cancellidiales* have hampered our understanding of this group. Thus, additional research, such as more sampling, is required to better understand the morphological characteristics and sexual and asexual connections of this order.

Catabotryales **K.D. Hyde, Mycosphere 11(1): 374 (2020)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Incertae sedis*

Introduction

Catabotryales was formally introduced by Hyde et al. (2020d). This order is distinct from its sister orders in having astromatic ascomata, broad, cylindrical asci and ellipsoidal to cylindrical ascospores without a mucilaginous sheath (Hyde et al. 2020a).

History

Catabotrydaceae (Barr 1990b) accommodates a single genus *Catabotrys* (Theissen & Sydow 1915), which comprises two species, including the type species *C. deciduum* and *C. chandrapurensis*. The family is characterized by pulvinate, superficial stromata on substrates, long ostiolar ascomata embedded in stromatic columns, and hyaline, 1-celled, ellipsoidal ascospores (Seaver & Waterston 1946, Barr 1990b). *Catabotryaceae* was placed in *Amplistromatales* based on DNA sequence analyses (Maharachchikumbura et al. 2015, 2016). However, this family was later placed in the *Sordariomycetes* family *incertae sedis* based on phylogeny and molecular clock evidence (Hongsanan et al. 2017a). *Catabotryaceae* has few strains representing its taxonomic placement.

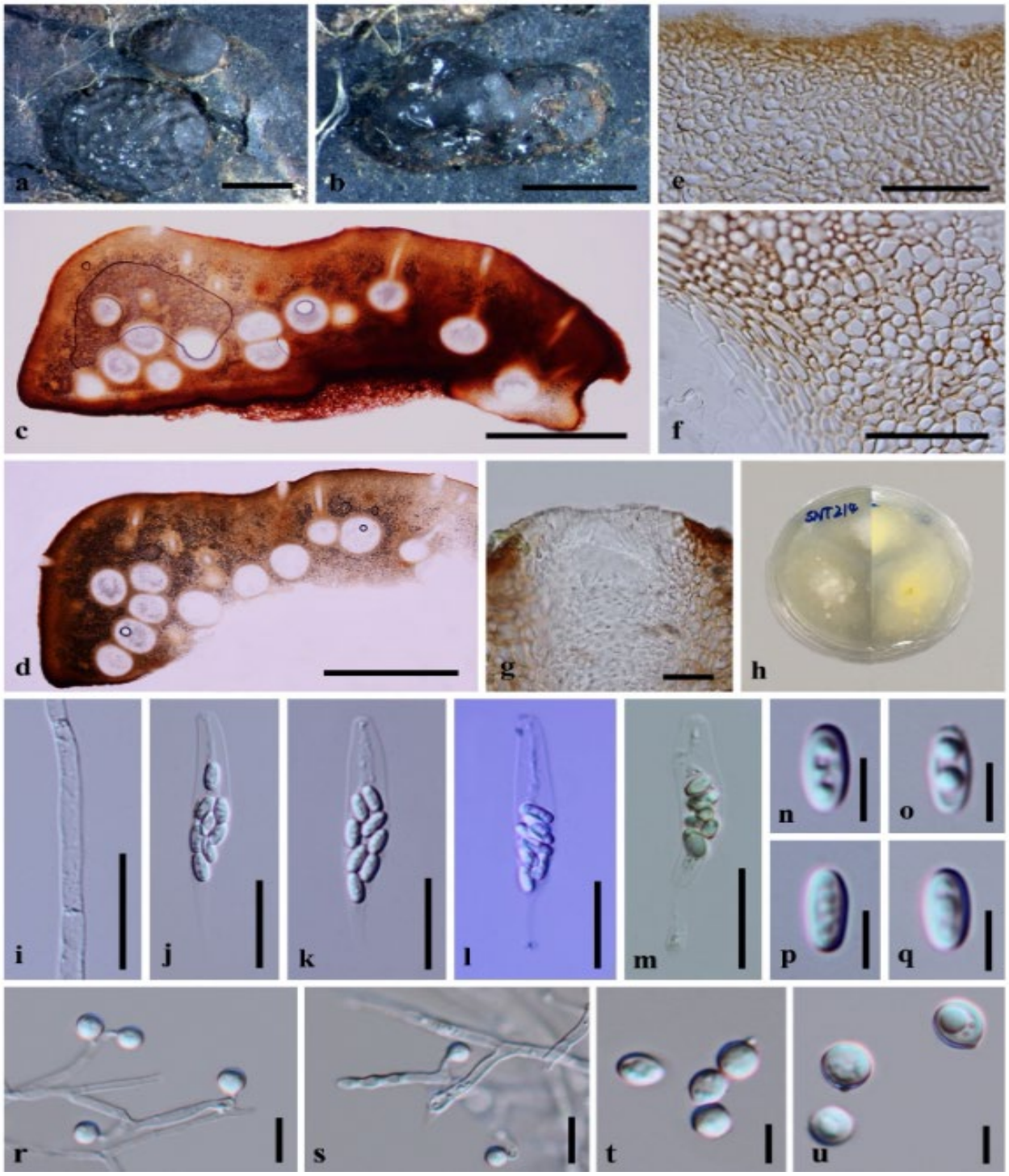


Figure 191 – Sexual and asexual morphs of *Catabotryales* (*Catabotrys deciduum* (MFLU 18-1073)). a, b Appearance of stromata on host surface. c, d Vertical sections through the stromata. e, f Structure of peridium. g Ostiole with periphyses. h Colonies on PDA. i Paraphyses. j–m Asci. l Ascus in Cotton blue. m Ascus apex in Melzer's reagent, J- subapical ring. n–q Ascospores. r–u Sporulation in culture. t, u Conidia in culture. Scale bars: a, b = 2 mm, c, d = 1000 µm, e, f = 50 µm, g–m = 20 µm, r, s = 10 µm, r, n–q, t, u = 5 µm.

General description

Sexual morph: *Stromata* solitary or irregularly scattered, conspicuous, multi-loculate, superficial, with base slightly penetrating the epidermis at regular intervals, discoid to pulvinate, reddish-brown to black, surface scurfy, flat or slightly convex. *Ascomata* deeply imbedded in stromatic columns, globose, with a long, periphysate, ostiolar neck. *Peridium* thick, composed of

several reddish-brown outer layer cells of *textura globosa* and *textura epidermoidea*, with pale brown to hyaline internal cells of *textura angularis*. *Paraphyses* hypha-like, numerous, tapering towards the apex, not embedded in a gelatinous matrix. *Asci* 8-spored, unitunicate, broad cylindrical, short-pedicellate, apically rounded or truncate, with a J-, discoid, refractive, apical ring. *Ascospores* bi-seriate, hyaline, 1-celled, ellipsoidal to cylindrical, smooth-walled. Asexual morph: hyphomycetous. *Vegetative hyphae* hyaline, septate, smooth-walled. *Conidiophores* micronematous. *Conidiogenous cells* holoblastic, terminal and intercalary. *Conidia* globose or obovoid, hyaline, 1-celled and smooth-walled, often with denticles from conidiogenous cells (Fig. 191).

Families included in *Catabotryales*

Catabotryaceae Petr. ex M.E. Barr

Evolution

Hyde et al. (2017a), suggested that family *Catabotryaceae* represent an order based on divergent time estimations. The divergence time for *Catabotryales* has been estimated at 172 MYA (Hyde et al. 2020a).

Justification of order and problems

This order was established based on morphology and phylogeny. However, it is necessary to analyse molecular data with broad taxon sampling using polyphasic approaches to confirm its taxonomic status.

Significance

Ecological and economic roles

Species of *Catabotrys* reported from India, Panama (Huhndorf et al. 2004a), and Thailand (Hyde et al. 2020d) on *Salacca* sp., *Elaeis guineensis*, and *Rhizophora mucronata*. *Catabotrys* species are reported from many localities and mostly found from palms (Theissen & Sydow 1915, Seaver & Waterston 1946, Huhndorf et al. 2004a). All species in this order are saprobes involved in litter decay. *Catabotrys* species have a pantropical distribution, and mainly appear on dead plant material with striking superficial stromata. Wu et al. (2014c) reported endophytic isolates of *Catabotrys* from *Fortunearia sinensis* in China. However, the frequent appearance on dead plant tissue indicates that saprobic nutrition may dominate and occupy a large part of its life cycle, while it may also at first be an endophyte within living plant tissues.

Chemical diversity

No chemical compounds and secondary metabolites were reported from species in *Catabotryales*.

Other relevant data and future recommendations

Further collections are needed to delimit the species boundaries in this order. Sequence data are only available for one *Catabotrys* species.

***Cephalothecales* Maharachch. & K.D. Hyde, Mycosphere 11 (1): 375 (2020)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Sordariomycetidae*

Introduction

Cephalothecales is a order of *Sordariomycetes*, which comprises the family *Cephalothecaceae* (Hyde et al. 2020d). *Cephalothecaceae* was introduced by Höhnel (1917a) that includes six genera *viz*. *Albertiniella*, *Cephalotheca* (type), *Cryptendoxyla*, *Phialemonium*, *Scaptona* and *Victoriomyces* (Fuckel 1872, Kirschstein 1936, Malloch & Cain 1970b, Gams & McGinnis 1983b, Maharachchikumbura et al. 2016, Davolos et al. 2019, Hyde et al. 2024b). The order is

characterized by ascomata with a cephalothecoid peridium; peripheral cells forming plate-like complexes composed of radial clusters of cells, each plate separated by a well-defined line of dehiscence. The species in this order are saprobic or epiphytic, often growing on rotten wood, dead plants, or fungi, and cause mycotic infection in humans (Perdomo et al. 2012, Maharachchikumbura et al. 2016).

History

The family *Cephalothecaceae* was erected with the type *Cephalotheca* and other cleistothecial ascomycetes with a cephalothecoid (plate-like) peridium (Höhnel 1917a). *Cephalothecaceae* was previously classified in the order *Sordariales* by Suh & Blackwell (1999) based on SSU and LSU sequence analysis. Maharachchikumbura et al. (2016) tentatively referred *Cephalothecaceae* to the families *incertae sedis* in *Sordariomycetes* since its uncertain phylogenetic placement and distinct morphology. Hongsanan et al. (2017a) reported that the divergence time of *Cephalothecaceae* was at 175 MYA. Hyde et al. (2020d) placed the family *Cephalothecaceae* in a newly established order *Cephalothecales*, which belongs to the class *Sordariomycetes*.

Cephalotheca was established by Fuckel in 1872. During the taxonomic history of the genus *Cephalotheca*, it has been placed in two families: *Pseudeurotiaceae* (Malloch & Cain 1970b) and *Cephalothecaceae* (Benny & Kimbrough 1980). Hawksworth et al. (1995) maintained both families in the order *Eurotiales* and included 14 genera in *Pseudeurotiaceae* and only *Cephalotheca* in *Cephalothecaceae*. Suh & Blackwell (1999), based on rDNA analysis of species from these two families, suggested that all these fungi be excluded from *Eurotiales* and that they can be referred to six different orders of *Ascomycota*. *Albertiniella* was introduced by Kirschstein (1936) based on the type *Albertiniella reticulata*. The other species of this genus, *Albertiniella polyporicola*, was initially described as a species of *Cephalotheca* (Jaczevski 1922), but Malloch & Cain (1970b, 1972) transferred it to *Albertiniella*. *Cryptendoxyla* was introduced by Malloch & Cain (1970b) in the family of *Pseudeurotiaceae*, which was typified by *Cryptendoxyla hypophloia*. Based on phylogenetic investigations, *Cryptendoxyla* was placed in *Cephalothecaceae* (Wijayawardene et al. 2012a, Maharachchikumbura et al. 2016). *Phialemonium*, typified by *P. obovatum*, was introduced by Gams & McGinnis (1983b) to accommodate three species. The genus *Phialemonium* was included in *Cephalothecaceae* as an asexual morph based on phylogenetic analysis (Perdomo et al. 2013). Considering the results of molecular investigations supplemented by morphological and ultrastructural studies, the family *Cephalothecaceae* is considered to comprise four genera: *Albertiniella*, *Cephalotheca*, *Cryptendoxyla*, and *Phialemonium* (Lumbsch & Huhndorf 2010, Wijayawardene et al. 2012a, Maharachchikumbura et al. 2016). *Victoriomyces* was described and added by Davolos et al. (2019) with the type species *V. antarcticus*. It was confirmed by phylogenetic analysis of the LSU, SSU and RPB2 datasets (Davolos et al. 2019). *Scaptona* was recently established and accepted under *Cephalothecaceae* in Hyde et al. (2024b).

General description

Albertiniella and *Cephalotheca* form subglobose to globose sexual structures containing asci (Suh et al. 2006, Akulov 2013, Hyde et al. 2020d). The ascospores of *Cephalothecales* are variously-shaped; they can be ovate to globose and hyaline to yellowish or kidney-shaped with numerous foveolae on the surface or cylindrical to oblong and brown to dark brown with small guttules (Suh et al. 2006, Akulov 2013, Lysková et al. 2014, Hyde et al. 2020d). Thus, the ascospore morphology is not a good indication of the relationship of these genera in *Cephalothecales*. *Cephalotheca* and *Phialemonium* have similar morphologies found in *Cephalothecales*; *Cephalotheca* taxa form hyaline, smooth, limoniform conidia frequently found in long chains; *Phialemonium* taxa include hyaline or pigmented, one-celled, cylindrical, smooth-walled conidia arranged in slimy heads or long chains (Hamayun et al. 2012, Perdomo et al. 2013). The type of conidiophores and conidia supports the close association with *Cephalothecales*.

Sexual morph: *Ascomata* perithecial, solitary to gregarious, superficial, dark brown to black, carbonaceous, covered by sulphureous hyphae, without periphyses. *Peridium* cephalothecoid,

comprising 2–3 layers, outer layer composed of dark brown cells of *textura angularis* to *prismatica*, inner layer composed of elongated, hyaline cells of *textura prismatica*. *Ascogenous* hyphae septate. *Asci* 8-spored, unitunicate pyriform to subglobose to globose, evanescent, apedicellate, without an apical ring. *Ascospores* irregularly arranged, brown, variously-shaped, without germ pores. Asexual morph: Hyphomycetous. *Mycelium* branched septate. *Conidiophores* long, stiffly upright, cylindrical, septate. *Conidiogenous cells* phialidic, cylindrical, strongly tapering and thick-walled. *Conidia* in chains, cylindrical, hyaline to brown, ovate or obovate, with or without an apiculate or truncate base, 1-celled (adapted from Maharachchikumbura et al. 2016, Davolos et al. 2019, Hyde et al. 2020d) (Figs. 192, 193).

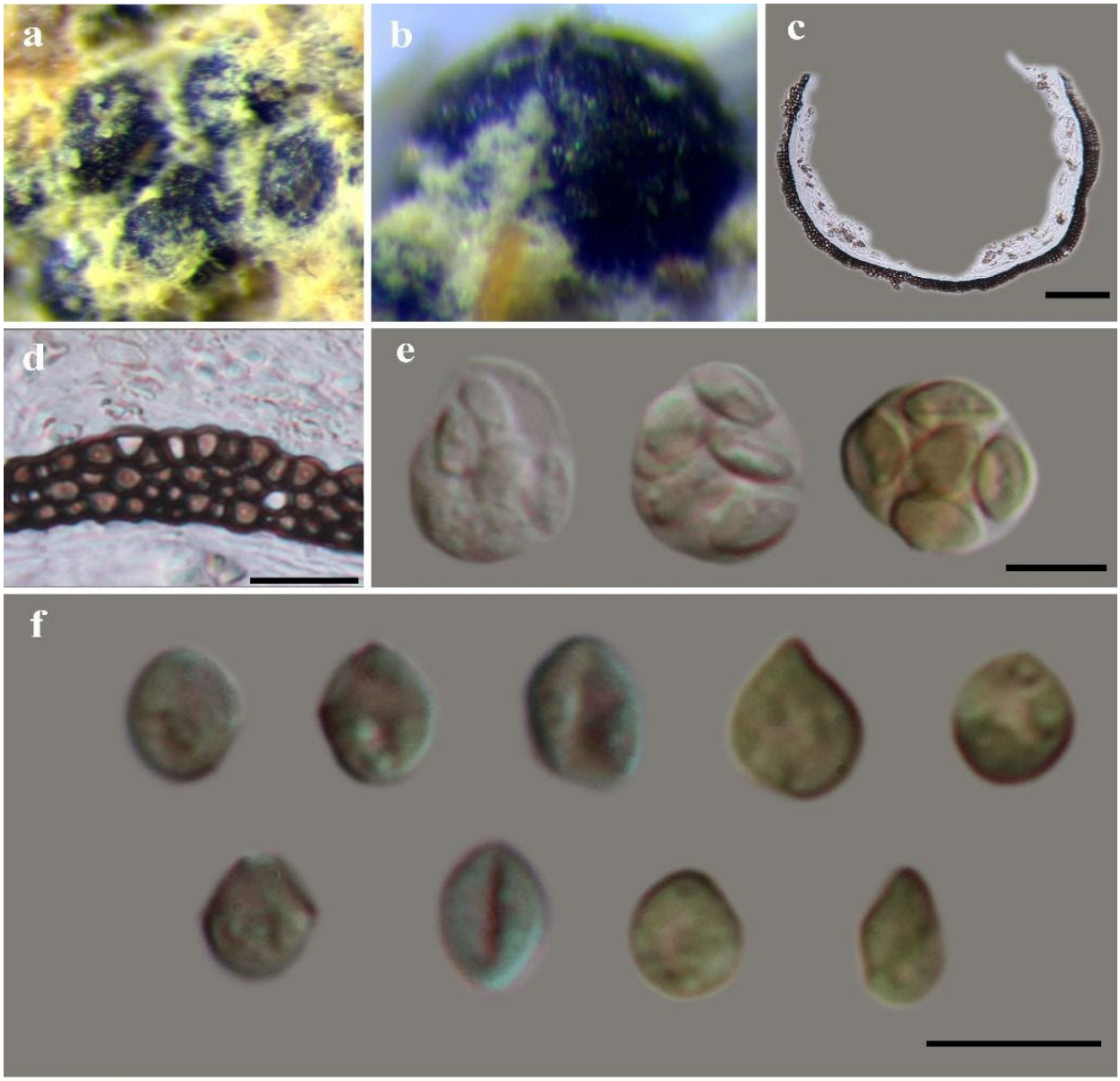


Figure 192 – Morphology of *Cephalotheca sulfurea* (G00266459, holotype). a, b Ascomata. c Cross section of ascoma. d Peridium. e Asci. f Ascospores. Scale bars: a, b = 100 µm, c = 50 µm, d = 10 µm, e, f = 5 µm.

Families included in *Cephalothecales*

Cephalothecaceae Höhn.

Evolution

Cephalothecaceae is a monotypic family of *Sordariomycetes*, strongly supported by its stem age, ca. 175 MYA (Hongsanan et al. 2017a). Subsequently, Hyde et al. (2020d) re-established the divergence time of *Cephalothecaceae* at 154 MYA and raised it to the ordinal status.

Justification of order and problems

Cephalothecaceae was introduced by Höhnel (1917a) and is characterized by ascomata with a cephalothecoid peridium. The peridial cells form plate-like complexes made up of radiating groups of cells, where each plate is separated by well-defined lines of dehiscence (Malloch & Cain 1970b). *Cephalothecaceae* was previously accommodated in the *Sordariales* by Suh & Blackwell (1999), but this study was based only on SSU and LSU sequence analysis. This has been revised with time, and based on its uncertain phylogenetic placement and different morphology, Maharachchikumbura et al. (2015) tentatively referred the *Cephalothecaceae* to *Sordariomycetes* family *incertae sedis*.

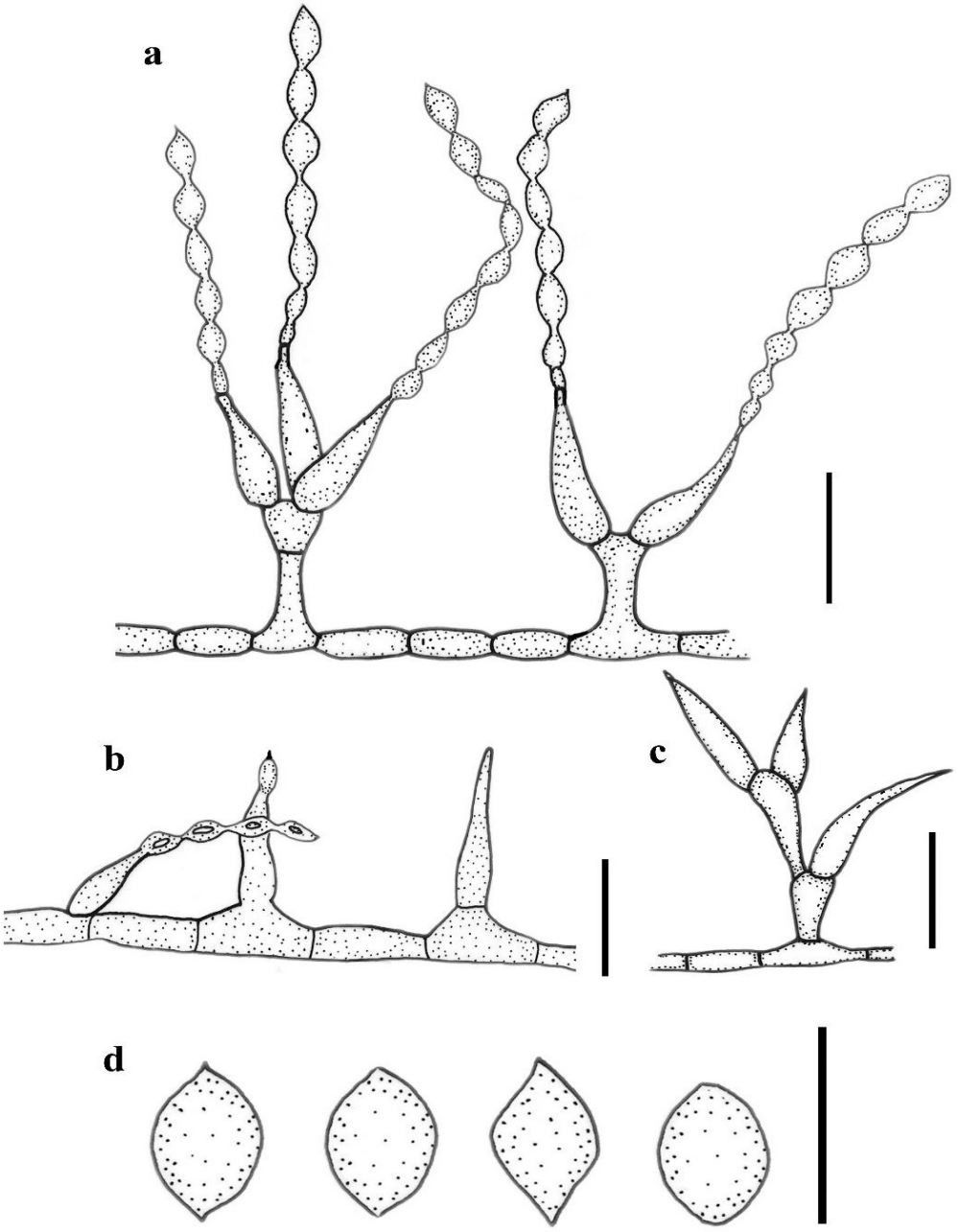


Figure 193 – Morphology of *Cephalotheca sulfurea.* a, b Conidiophores with conidiogenous cells and conidia. c Conidiogenesis. d Conidia. Scale bars: a–c =10 μm, d = 5 μm.

Although the placement of *Cephalothecaceae* is not stable within the subclass *Sordariomycetidae*, it has high support in the MCC tree (Hongsanan et al. 2017a).

Significance

Ecological and economic roles

Some species of *Cephalothecaceae* can cause diseases in humans and animals (Řehulka et al. 2016, Hyde et al. 2020d). Some *Phialemonium* species are responsible for opportunistic infections in immunocompromised hosts, resulting in diseases such as peritonitis, endocarditis, osteomyelitis, and skin infections in post-burn wounds (King et al. 1993, Guarro et al. 1999, Sigler 2002, Rivero et al. 2009, Perdomo et al. 2011). Saprobic fungi in the genus *Cephalotheca* have rarely been reported to cause human diseases. Nevertheless, *Cephalotheca foveolata* has been reported to cause subcutaneous infection, subcutaneous hyalohyphomycosis, localized skin infection, and bloodstream infection (Suh et al. 2005, 2006, Yaguchi et al. 2006, Lu et al. 2015). In addition, *C. sulfurea* can produce gibberellins like phytohormones and significantly promote the growth of soybean biomass (Hamayun et al. 2012).

Chemical diversity

No relevant studies are available regarding the chemical diversity of *Cephalothecales.*

Other relevant data and future recommendations

Hamayun et al. (2012) suggested that in future studies, *Cephalotheca sulfurea* mycelia could be applied to field crops to explore their interaction with crops under field conditions. Genes encoding gibberellins can also be further studied and identified to optimize *C. sulfurea* gas-producing medium.

Ceratolentales **K.D. Hyde & Hongsanan, Fungal Diversity 107: 94 (2021)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Ceratolentales was introduced to accommodate two newly described families, *Bullimycetaceae* and *Ceratolentaceae* and each family accommodates a single genus (Hyde et al. 2021a).

History

Bullimycetaceae was introduced to accommodate a single genus *Bullimyces,* with three freshwater fungi (*B. communis*, *B. costaricensis* and *B. aurisporus)* from Costa Rica. However, the familial placement of the genus remained uncertain yet formed a distinct clade with high bootstrap support within *Sordariomycetidae* based on LSU sequence data (Ferrer et al. 2012). Luo et al. (2019b) transferred the genus to *Diaporthomycetidae* genera *incertae sedis* based on the phylogenetic analyses, where the *Bullimyces* formed a distinct clade with *Ceratolenta*. *Ceratolenta* was introduced by Réblová (2013) to accommodate a single species *Ceratolenta caudata*. The genus formed a close phylogenetic clade to *Ophiostomatales*, *Papulosaceae* and *Annulatascaceae* (Réblová 2013).

The same phylogenetic result was also obtained in the study of Hyde et al. (2021a) but with low statistical support. However, the divergence time estimate analysis showed the stem age as 81 MYA for both generic clades, which falls inside the family range. Subsequently, *Bullimycetaceae* and *Ceratolentaceae* were established to accommodate *Bullimyces* and *Ceratolenta,* respectively. Further, the stem age obtained for these family clades was 147 MYA. Based on morpho-molecular evidence along with divergence time estimates, the order *Ceratolentales* was established to accommodate these families (Hyde et al. 2021a).

General description

Bullimycetaceae and *Ceratolentaceae* share similar morphologies in having globose to subglobose ascomata with a long neck, unitunicate, cylindrical asci and fusiform, hyaline, septate

ascospores but differ in several other characters. *Ceratolentaceae* has guttulate, filiform paraphyses, cylindrical to clavate, long-pedicellate asci with a refringent, J-, apical ring and uniseriate or biseriate, hyaline, fusiform ascospores without a gelatinous sheath whereas *Bullimycetaceae* has globose, hyaline cells paraphyses, cylindrical asci that lack apical ring and ascospores are uniseriate, broadly ellipsoidal-fusiform to ellipsoidal, hyaline becoming dark yellow with age and some species have a gelatinous sheath or appendages (Hyde et al. 2021a).

Sexual morph: *Ascomata* astromatic, immersed to erumpent, subglobose to globose, ostiolate, some species with a long neck. *Neck* cylindrical emerging above the substratum, straight or slightly curved, ostiolate, periphysate. *Peridium* leathery, two-layered. *Paraphyses* hyaline, septate, guttulate, fliform, tapering toward the tip, longer than the asci. *Asci* 8-spored, unitunicate, cylindrical to clavate, long-stipitate, broadly rounded at the apex with or without apical ring. *Ascospores* uniseriate or biseriate, fusiform, ellipsoidal-fusiform to ellipsoidal hyaline, three-septate, without gelatinous sheath. Asexual morph: Undetermined (adapted from Hyde et al. 2021a) (Fig. 194).

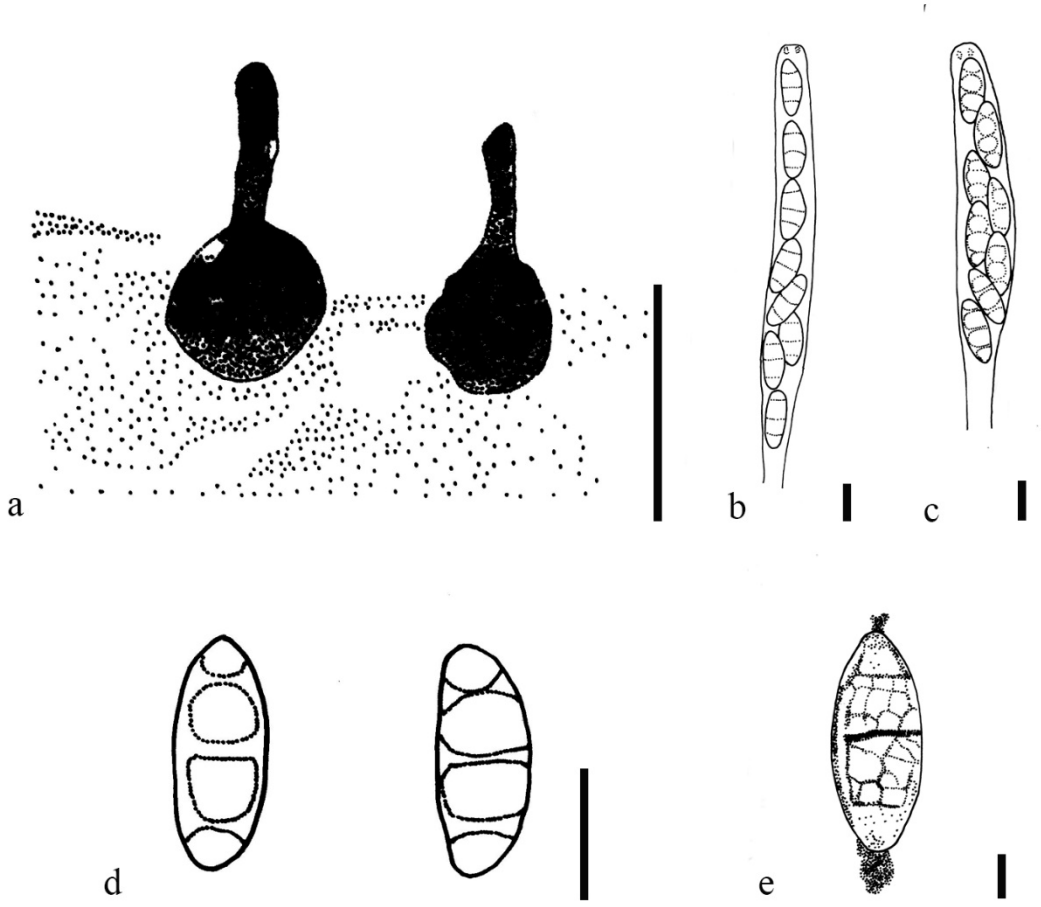


Figure 194 – Morphology of *Ceratolentales*. a–d Perithecia (*Ceratolenta caudata*). b, c Asci (*Ceratolenta caudata*). d, e Ascospores (d *Ceratolenta caudata*, e *Bullimyces communis*). (drawn from Ferrer et al. 2012, Réblová 2013). Scale bars: a = 500 µm, b–e = 10 µm.

Families included in *Ceratolentales*

Bullimycetaceae K.D. Hyde & Hongsanan
Ceratolentaceae K.D. Hyde & Hongsanan

Evolution

The stem age for *Ceratolentales* is reported as 147 MYA while the stem age for the families *Bullimycetaceae* and *Ceratolentaceae* was reported as 81 MYA (Hyde et al. 2021a).

Justification of order and problems

The order was established based on morphological, phylogenetic and time divergence estimates. However, the reinvestigation of holotypes or fresh material of these taxa reported in the order, along with new collections, can provide a better understanding of the taxonomy of the order.

Significance

Ecological and economic roles

Bullimyces was reported from freshwater habitats in Costa Rica and *Ceratolenta* was reported from terrestrial habitats in the Czech Republic and all the taxa are reported as saprobes (Ferrer et al. 2012, Réblová 2013).

Chemical diversity

No relevant studies are available on the chemical diversity of *Ceratolentales.*

***Chaetosphaeriales* Huhndorf, A.N. Mill. & F.A. Fernández, Mycologia 96(2): 378 (2004)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Sordariomycetidae*

Introduction

Chaetosphaeriales is a relatively large order, currently comprising six families (Hyde et al. 2024b). Species of this order are mainly saprobes on decaying plant parts such as decaying leaf, fruit, branch, bark and wood in terrestrial and freshwater habitats, while some are fungicolous (Fernández & Huhndorf 2005, Hyde et al. 2020d, Wu & Diao 2022). Huhndorf et al. (2004a) introduced *Chaetosphaeriales* to accommodate taxa with superficial or semi-immersed, subglobose, globose or obpyriform, ostiolate, glabrous, roughened or setose ascomata with or without subiculum, paraphysate hamathecium, clavate or cylindrical, asci with or without apical ring, ellipsoid to fusiform ascospores and enteroblastic, phialidic conidiogenesis (Huhndorf et al. 2004a). Réblová et al. (2020b, 2021a, b, c, d) and Wu & Diao (2022) in their systematic work of polyphyletic genera recognized several new genera within *Chaetosphaeriaceae*, *Chaetosphaeriales*. Introduction of *Chaetosphaeriales* is supported by molecular clock analysis by Hongsanan et al. (2017a).

History

The species of *Chaetosphaeria* are saprobic on decaying plant material in terrestrial and freshwater habitats (Fernández & Huhndorf 2005, Perera et al. 2016a, Hyde et al. 2020d). *Chaetosphaeria* was placed in *Lasiosphaeriaceae* by Barr (1990b). Later new family *Chaetosphaeriaceae* was established for *Chaetosphaeria* and four other genera (*Loramyces*, *Niesslia*, *Rhagadostoma* and *Zignöella*) (Locquin 1984a). *Chaetosphaeriaceae* was not a validly published name as it was introduced without any description (Locquin 1984a). Therefore, Réblová et al. (1999) re-introduced the family based on *Chaetosphaeria* and added another six genera *viz*. *Ascocodinaea*, *Melanochaeta*, *Melanopsammella*, *Porosphaerella*, *Porosphaerellopsis*, and *Striatosphaeria*. *Chaetosphaeriaceae* is characterized by carbonaceous, coriaceous or membranaceous, dark brown ascomata, unitunicate, J- asci and 0–3-septate, hyaline or brown ascospores (Réblová et al. 1999, Hyde et al. 2020d, Wu & Diao 2022). The asexual morphs of *Chaetosphaeriaceae* are non-phialidic sporidesmium-like, phialidic coelomycetous or phialidic hyphomycetous (Réblová et al. 1999, Hyde et al. 2020d, Wu & Diao 2022). Réblová et al. (1999) accepted *Chaetosphaeriaceae* in *Sordariales* based on morphology. Based on LSU sequence data, Huhndorf et al. (2004a) introduced *Chaetosphaeriales* to accommodate *Chaetosphaeriaceae*. *Helminthosphaeriaceae* was introduced by Samuels et al. (1997) based on species with black, carbonaceous ascomata, apically free paraphyses,

unitunicate asci and greyish-brown ascospores, and accommodated *Helminthosphaeria*. Hyde (1992a) proposed that *Linocarpon* and *Neolinocarpon* are typical to lasiosphaeriaceous taxa based on their apical structure of the asci and in ascospore morphology. Konta et al. (2017) described the saprobic family *Linocarpaceae* within *Chaetosphaeriales*, to accommodate *Neolinocarpon* and *Linocarpon*, which were maintained in *Xylariales*, genera *incertae sedis* (Maharachchikumbura et al. 2015, 2016). *Linocarpaceae* is characterized by black, dome-shaped, slightly raised or flattened circular areas, or immersed ascomata with black shiny papilla, cylindrical asci with a J-, apical ring and filiform ascospores with or without polar appendages (Konta et al. 2017). The asexual morph is phialophora-like (Konta et al. 2017). Konta et al. (2017) also introduced *Leptosporellaceae* to the order to accommodate *Leptosporella*, which was previously accepted in *Chaetosphaeriales* genera *incertae sedis* (Maharachchikumbura et al. 2016). *Leptosporellaceae* is characterized by black, carbonaceous, dome-shaped, raised ascomata, J- asci with wedge-shaped subapical ring and filiform, aseptate ascospores with or without polar mucilaginous appendages (Konta et al. 2017). Lin et al. (2019a) described *Multiguttulispora* and placed it within *Chaetosphaeriaceae*. Réblová et al. (2020b, 2021a, b, c, d) introduced several new genera within the family in their systematic assessment of polyphyletic genera. *Neoleptosporella*, *incertae sedis* taxon, was added to the order by Phukhamsakda et al. (2020). Subsequently more genera were added to the order and Hyde et al. (2020d) accepted four families and 59 genera in the order. *Endophragmiella* was linked to *Helminthosphaeriaceae* based on molecular data by Hernandez-Restrepo et al. (2017). However, Huang et al. (2021b) excluded *Endophragmiella* from *Helminthosphaeriaceae* and accommodated it in *Ascomycota* genus *incertae sedis*. The monotypic genus *Phialolunulospora* was introduced within *Chaetosphaeriaceae* by Zheng et al. (2020). Later, Goh et al. (2021) introduced the monotypic genus *Phaeonawawia* within *Chaetosphaeriaceae*. Thus, Wijayawardene et al. (2022a) accepted 60 genera in *Chaetosphaeriales*. Wu & Diao (2022) provided a comprehensive study of anamorphic *Chaetosphaeriaceae* and accommodated 89 genera in the family. *Bahusutrabeeja*, *Lecythothecium*, *Miyoshiella*, *Phialolunulospora*, *Pyrigemmula* and *Umbrinosphaeria* were synonymized under other genera in *Chaetosphaeriaceae* by Wu & Diao (2022). *Hemicorynespora* and *Ascochalara*, which do not have sequence data, were not treated in the study by Wu & Diao (2022). Presently, seven families are accepted under *Chaetosphaeriales* (Hyde et al. 2024b).

General description

Since the ascomata and asci of *Linocarpon* (*Linocarpaceae*) and *Leptosporella* (*Leptosporellaceae*) species are similar, they are difficult to differentiate (Konta et al. 2017). Based on ascospore morphology, these genera/families can be differentiated (Konta et al. 2017). Sexual morph characters of chaetosphaeriaceous taxa are simple and difficult to detect, while the asexual morph characters are considered as distinctive (Gams & Holubová-Jechová 1976, Huhndorf et al. 2004a). The asexual morphs of *Chaetosphaeriales* are diverse and vary in form from acervuloid to cupulate, sporodochial and synnematous, and solitary or clustered conidiophores (Hyde et al. 2020d, Réblová et al. 2020b, 2021a, b, c, d, Wu & Diao 2022). Most of the anamorphic *Chaetosphaeriales* genera have phialidic conidiogenous cells. They are mostly hyphomycetes, and less commonly coelomycetous genera (eight genera in *Chaetosphaeriaceae*) (Hyde et al. 2020d, Réblová et al. 2020b, 2021a, b, c, d, Wu & Diao 2022). A few genera and species in *Chaetosphaeriaceae* form non-phialidic conidiogenous cells and holoblastic conidia (Luo et al. 2019b, Wu & Diao 2022). These asexual morphs are sporidesmium-like taxa. Conidia of chaetosphaeriaceous taxa vary the most in shape, color, septation and appendage, and are important characters for genus level identification (Hyde et al. 2020d, Wu & Diao 2022). The sterile or fertile setae are usually found in some genera while some genera possess microawns.

Sexual morph: *Ascomata* perithecial, gregarious or scattered, solitary, superficial or basally immersed on a thin stroma or on a thin subiculum, ovoid, globose to subglobose, sometimes dome-shaped, carbonaceous, coriaceous or membranaceous, dark brown to black, rough, smooth or with short setae, papillate. *Ostiole* lined with hyaline periphyses or periphyses absent. *Subiculum* if present composed of thin, scanty, brown to dark brown, septate unbranched hyphae. *Peridium* composed of

one or two layers. *Hamathecium* of septate paraphyses, sparse or abundant. *Asci* 8-spored, unitunicate, clavate to cylindrical, with J-, apical ring. *Ascospores* fusiform, cylindrical to ellipsoid, filiform, aseptate or 1–3-septate, hyaline, brown or becoming dark colored, smooth-walled or striate, guttulate, with sheath or appendages. Asexual morph: Hyphomycetous (sporodochial and synnematous, and solitary or grouped conidiophores) or coelomycetous (acervuloid to cupulate). *Acervuloid to cupulate conidiomata* usually superficial, globose to navicular, unilocular, with variable excipular development and adorned with sterile hyphae or setae, basal stroma of these cupulate conidiomata are usually well-developed. *Sporodochial conidiomata* usually with a basal stroma, generally associated with dark brown, septate setae arising from basal stroma, sometimes sterile microawns present, conidia are embedded in wet spore mass covering the upper part of sporodochia. *Synnematous conidiomata* consisting of a compacted group of erect and fused hyphae, the apices and occasionally intercalary cells of which function as conidiophores and conidiogenous cells, sometimes setose. *Setae* sterile or fertile, pale to dark brown, septate, and thin- or thick-walled, simple, or branched, and formed from hyphae or stroma. *Conidiophores of all coelomycetous genera and some sporodochial hyphomycetous genera* pale brown to brown, branched or unbranched, arising from inner layer cells of cavity, terminated with 1 to several hyaline to very pale brown conidiogenous cells. *Conidiophores of hyphomycetous genera* with synnemata closely compacted group of erect and fused hyphae, the apices and occasionally intercalary cells of which function as conidiophores and conidiogenous cells. *Conidiophores of other hyphomycetous genera* macronematous or mononematous, brown, septate, branched or unbranched, straight, or slightly flexuous, solitary, or formed in clusters and arising directly from hyphae or basal stroma, sometimes setiform. *Conidiogenous cells* usually phialidic, sometimes non-phialidic with holoblastic conidia, terminal, intercalary or lateral, ampulliform, cylindrical, lageniform or ellipsoidal, usually straight, hyaline, pale brown to dark brown, thin- or thick-walled, smooth- or rough-walled with different ornamentation on the cell wall, monophialidic without or with a single apical collarette or polyphialidic with several collarettes. *Conidia* amerosporous, didymosporous, phragmosporous, dictyosporous or rarely scolecosporous, globose, ellipsoid, cuneiform, pyramidal, fusiform, falcate, cylindrical, flamentous, star-shaped, aseptate, uniseptate, to multiseptated, euseptate or distoseptate, hyaline, subhyaline, pale brown to dark brown, with or without tubular appendage. Tubular appendage single to multiple, branched or unbranched, bipolar and/or lateral, sometimes mucilaginous balls at the conidial ends. Microconidia produced in pure cultures (adapted from Konta et al. 2017, Hyde et al. 2020d, Wu & Diao 2022) (Figs. 195, 196, 197, 198, 199, 200).

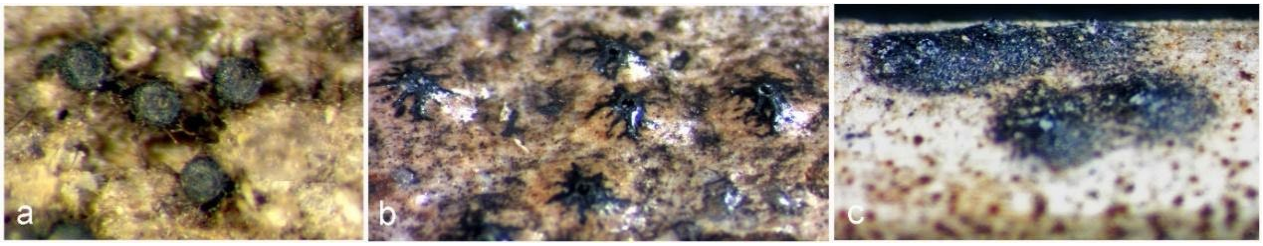


Figure 195 – Ascomata morphology of *Chaetosphaeriales* on the host. a. *Chaetosphaeria jonesii.* b *Leptosporella cocois.* c *Linocarpon arengae*.

Families included in *Chaetosphaeriales*

Chaetosphaeriaceae Réblová, M.E. Barr & Samuels
Helminthosphaeriaceae Samuels, Cand. & Magni.
Leptosporellaceae Konta & K.D. Hyde
Linocarpaceae Konta & K.D. Hyde
Neoleptosporellaceae J.F. Zhang, Y.Y. Chen & Jian K. Liu
Pseudocapsulosporaceae S.N. Zhang, E.B.G. Jones & K.D. Hyde

Chaetosphaeriales genera *Incertae* sedis

Caudatispora J. Fröhl. & K.D. Hyde
Erythromada Huhndorf, A.N. Mill. F.A. Fernández & Lodge
Lasiosphaeriella Sivan.
Neoleptosporella Phukhams. Perera & K.D. Hyde
Rimaconus Huhndorf, F.A. Fernández, Joanne E. Taylor & K.D. Hyde

Justification of order and problems

Current molecular phylogenetic analysis has improved the understanding of both sexually and asexually characterized taxa of *Chaetosphaeriales* (Liu et al. 2016a, Perera et al. 2016a, Luo et al. 2019b, Réblová et al. 2020b, 2021b, Wu & Diao 2022). Maharachchikumbura et al. (2016) acknowledged the need for a monograph with molecular support for *Chaetosphaeriaceae* to overcome the taxonomic confusion. Wu & Diao (2022) provided a comprehensive monograph of anamorphic *Chaetosphaeriaceae* and the family was expanded to accommodate 89 genera, including 22 new genera and 10 newly assigned genera. Polyphyletic *Codinaea*/*Dictyochaeta*/*Tainosphaeria* complex was resolved with a taxonomic outline of 28 monophyletic genera and accepted *Codinaea* and *Dictyochaeta* with narrower sense in their work. Further, non-phialidic sporidesmium-like taxa were divided into 10 genera by Wu & Diao (2022). Réblová & Nekvindová (2023) introduced seven new chloridium-like genera in *Chaetosphaeriaceae*.

Significance

Ecological and economic roles

Species of *Chaetosphaeriales* are saprobes on decaying plant material in terrestrial and freshwater habitats while some are fungicolous (Fernández & Huhndorf 2005, Hyde et al. 2020d, Wu & Diao 2022). *Adautomilanezia*, *Chaetosphaeria*, *Leptosporella* and *Linocarpon* are examples for terrestrial saprobes while *Dictyochaeta*, *Sporoschisma*, *Tainosphaeria* and *Menisporopsis* are aquatic (Réblová et al. 1999, Liu et al. 2016a, Perera et al. 2016a, Konta et al. 2017). Saprobic *Chaetosphaeriales* species play an important role in nutrient and carbon cycling and ecosystem functioning by decomposing plant material (Hyde et al. 2016a).

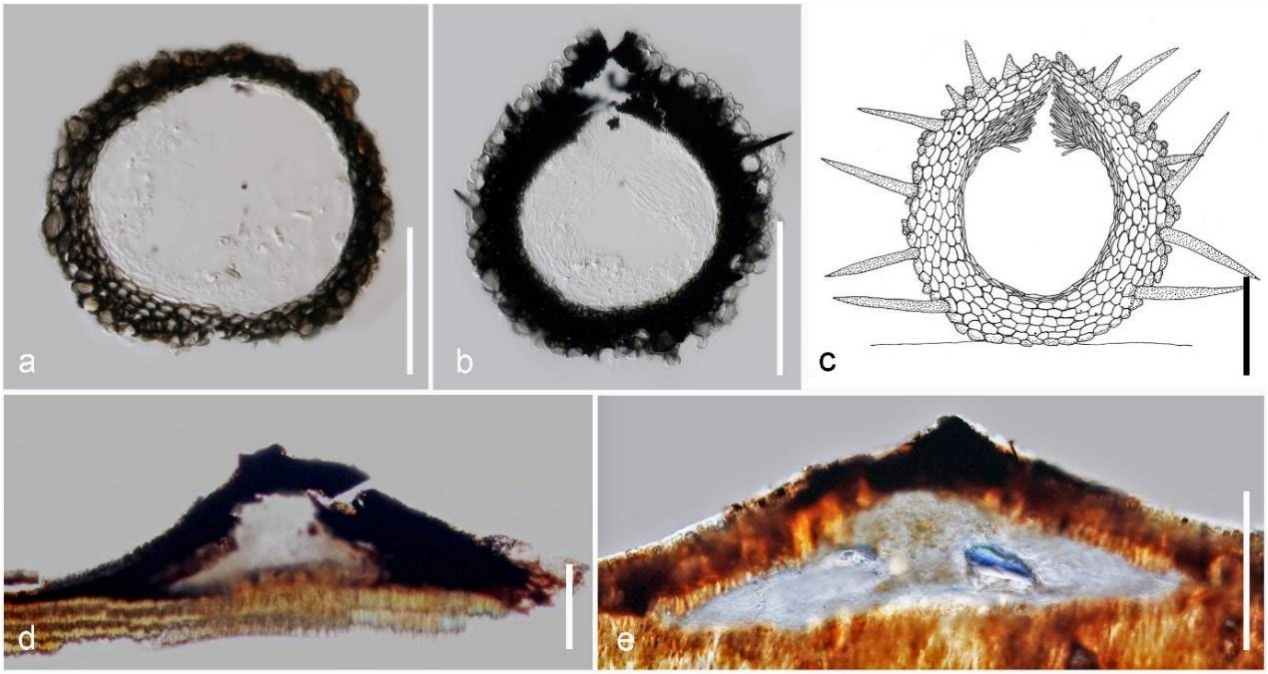


Figure 196 – Ascomata morphology of *Chaetosphaeriales.* a *Chaetosphaeria jonesii.* b *Chaetosphaeria garethjonesii.* c *Helminthosphaeria pilifera* (Réblová 1999d). d *Linocarpon arengae* e *Leptosporella cocois*. Scale bars: a = 50 μm, b = 100 μm, c = 50 μm, d, e = 200 μm.

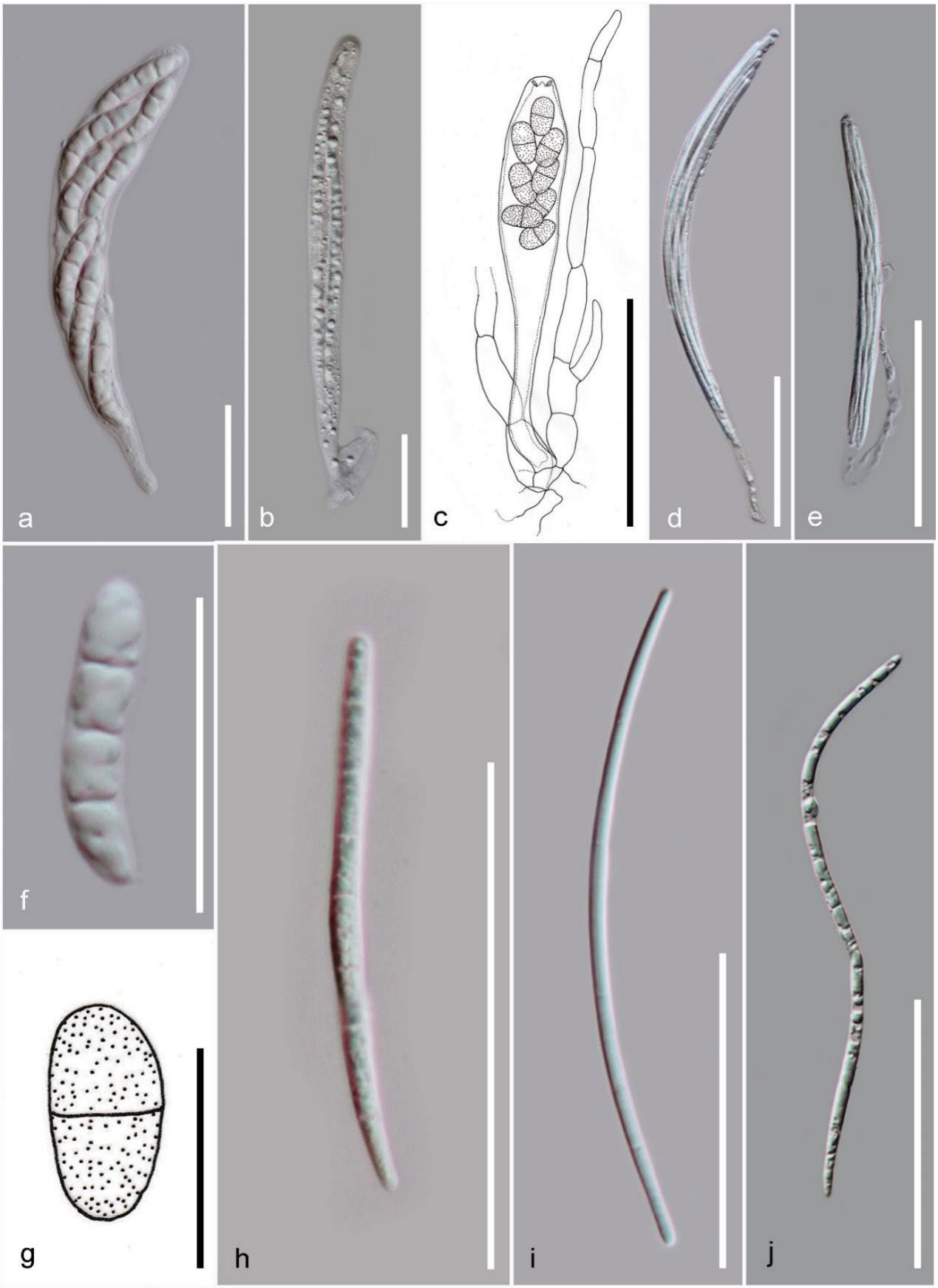


Figure 197 – Asci and ascospores morphology of *Chaetosphaeriales.* a, f *Chaetosphaeria jonesii.* b, h *Chaetosphaeria garethjonesii.* c, g *Helminthosphaeria pilifera* (Réblová 1999d). d, i *Linocarpon arengae.* e, j *Leptosporella cocois*. Scale bars: a–e = 50 µm, f = 20 µm, g = 10 µm, h–j = 50 µm.

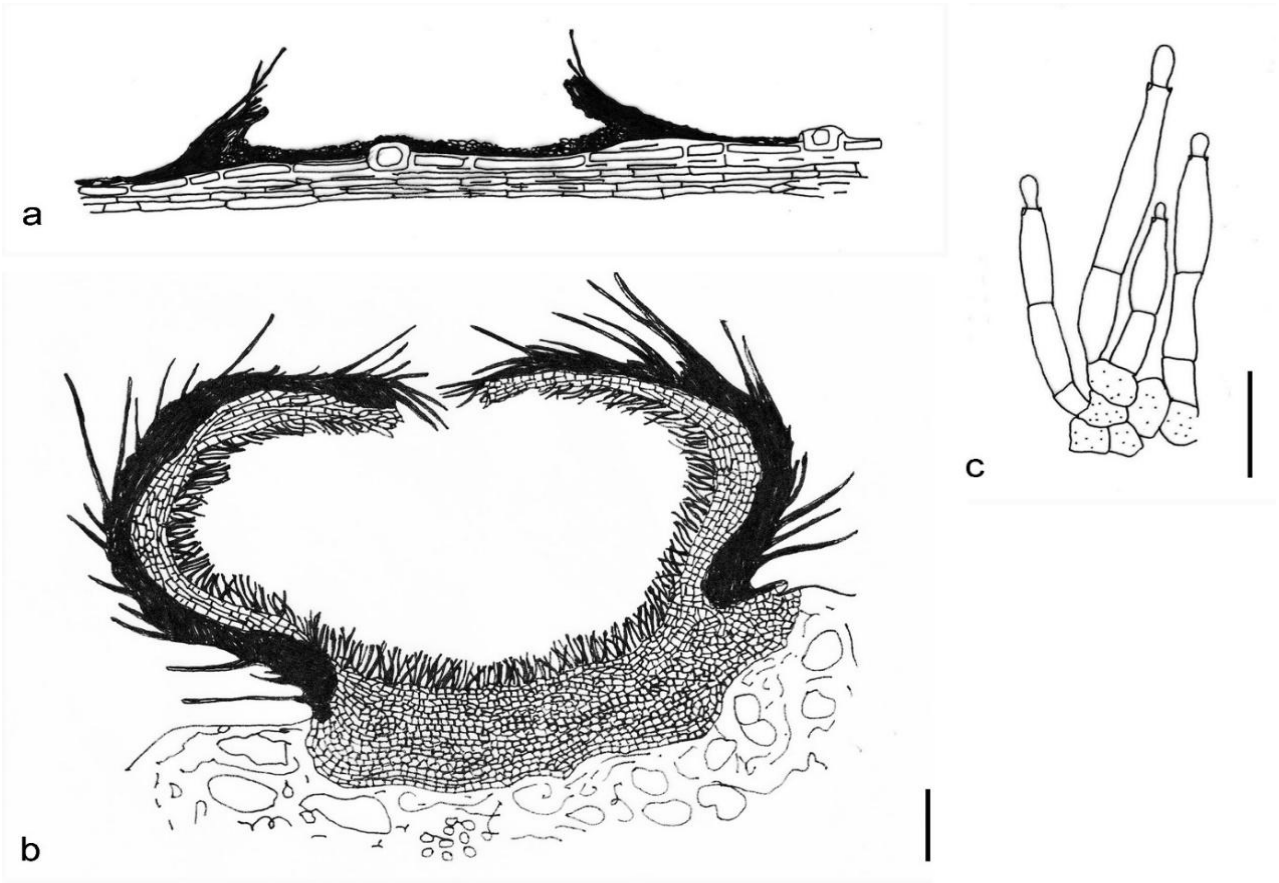


Figure 198 – Conidiomata and conidiophore morphology of *Chaetosphaeriales*. a, c *Dinemasporium fusiforme* (Duan et al. 2007). b *Pseudolachnella tengii* (Wu & Diao 2022). Scale bars: b, c = 20 μm.

Eucalyptostroma eucalypti and *E. eucalyptorum* were isolated from leaf spots of *Eucalyptus* (Crous et al. 2016a, 2018b). However, there is no study confirming any pathogenicity in *Eucalyptostroma*. Species of the *Helminthosphaeria* are fungicolous, occurring on basidiomata of species of the *Aphyllophorales* (Samuels et al. 1997). Species of *Tainosphaeria* are saprobes, usually occurring on erumpent stromata of over-matured ascomycetes (Fernández & Huhndorf 2005).

Chemical diversity

Dinemasporium produces bioactive metabolites (Dinemasones A, B and C) while Dinemasones A and B exhibited antibacterial, antifungal, and antialgal activities (Krohn et al. 2008). A new compound 'Decatransin' with potent bioactivity on mammalian and yeast cells was isolated from *Chaetosphaeria tulasneorum* by Junne et al. (2015).

Conlariales K.D. Hyde & Hongsanan, Fungal Diversity 107: 94 (2021)

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Conlariales comprises *Conlarium* and *Riomyces* and is presently placed in *Diaporthomycetidae* (Hyde et al. 2021a).

History

Conlariales was established by Hyde & Hongsanan (Hyde et al. 2020d) to accommodate a single family *Conlariaceae* and two genera, *Conlarium* and *Riomyces*. *Conlarium* was originally introduced by Liu et al. (2012a) based on morpho-molecular analyses and was placed in

Annulatascaceae sensu lato. The genus comprised a single species *Conlarium duplumascospora,* that was reported on submerged wood in China. The taxon showed distinguishing features among the members of *Annulatascaceae sensu lato* in having gregarious, dark brown to black ascomata with long neck, biseriate ascospores with or without globose or papillary appendages at one or both end, and muriform conidia in its anamorphic stage. Maharachchikumbura et al. (2016) treated the genus under *Sordariomycetidae*, genera *incertae sedis*. Zhang et al. (2017a) established a new family *Conlariaceae* to accommodate *Conlarium* with an additional species *Conlarium aquaticum* based on morphology and phylogeny.

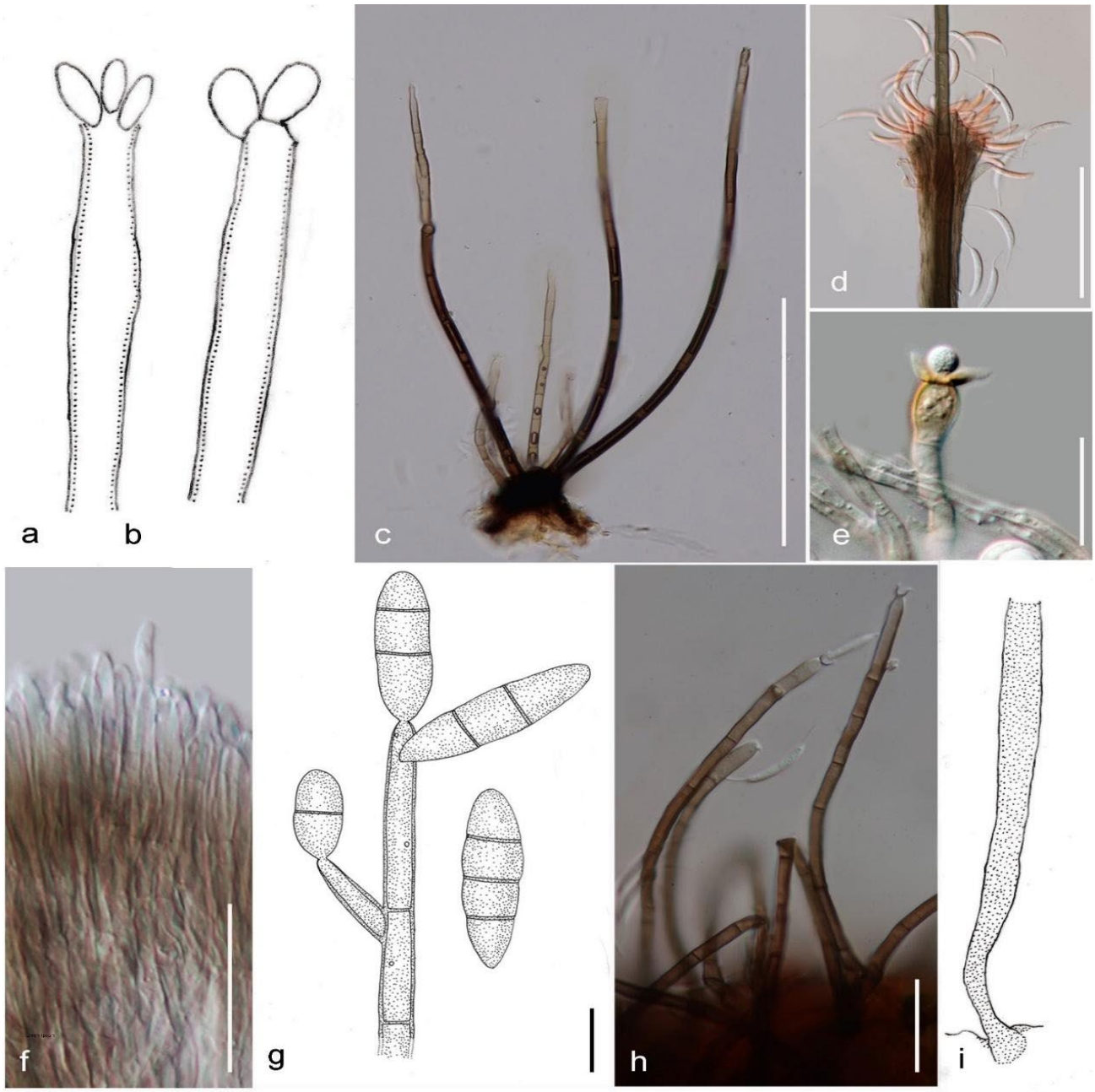


Figure 199 – Conidiophore morphology of *Chaetosphaeriales.* a *Chloridium jinghongense.* b *Chloridium culmicola.* c *Dictyochaeta lithocarpi.* d *Menisporopsis theobromae.* e *Chaetosphaeria panamensis.* f *Thozetella fabacearum.* g *Helminthosphaeria pilifera* (Réblová 1999d). h *Tainosphaeria siamensis.* i *Sporoschisma nigroseptatum* (a, b, i: Wu & Diao 2022). Scale bars: c = 10 µm, d = 50 µm, e = 20 µm, f, g = 10 µm, h = 20 µm.

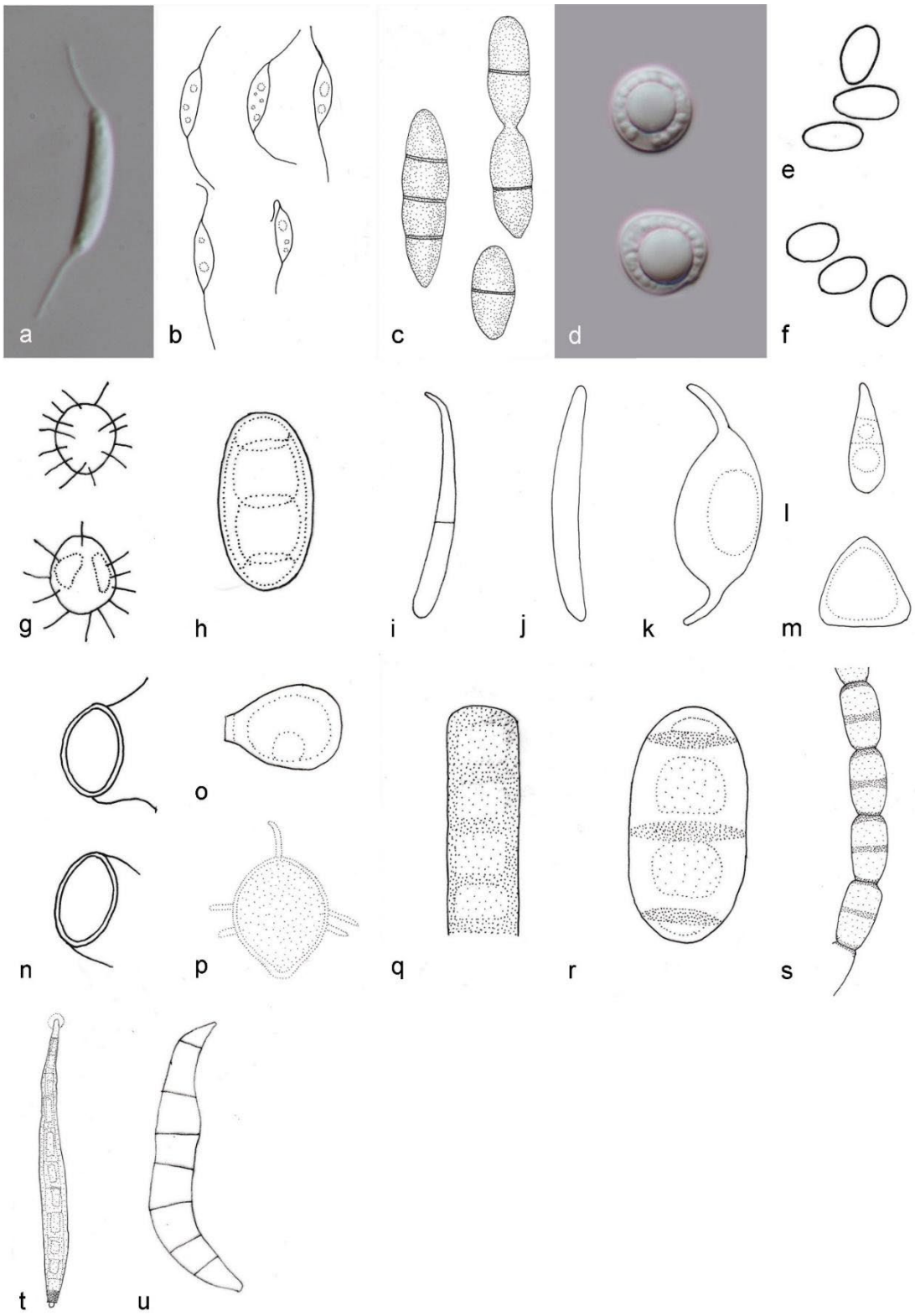


Figure 200 – Conidia morphology of *Chaetosphaeriales*. a *Thozetella fabacearum*. b *Dinemasporium fusiforme* (Duan et al. 2007). c *Helminthosphaeria pilifera* (Réblová 1999d). d *Chaetosphaeria panamensis*. e *Chloridium proliferatum*. f *Chloridium gonytrichii*. g *Codinaea dwaya*. h *Exserticlava vasiformis*. i *Cryptophiale udagawae*. j *Zanclospora novae-zelandiae*. k *Codinaea leomaiae* (Barbosa et al. 2016). l *Phialogeniculata guadalcanalensis* (Luo et al. 2019b). m *Paragaeumannomyces nawawii*. n *Calceisporiella sinensis*. o *Fuscocatenula variegata*. p *Nawawia oviformis* (Peng et al. 2016). q *Sporoschisma mirabile*. r *Monosporoschisma elegans*. s *Sporoschisma parcicuneatum*. t *Linkosia subramanianii*. u *Phialoturbella lunata* (e–j, m–o, q–u: Wu & Diao 2022).

Conlariaceae clustered together with two newly established families *Atractosporaceae* and *Pseudoproboscisporaceae,* without strong statistical support in the combined LSU, SSU, ITS and RPB2 sequence alignment and was treated under a newly established order *Atractosporales*. However, these three families shared similarities in having perithecial, astromatic, immersed to semi-immersed ascomata with necks, unitunicate, eight-spored asci with apical rings and hyaline, fusiform ascospores. However, *Conlariaceae* recovered outside of *Atractosporales* in the phylogenetic analysis conducted by Luo et al. (2019b). Consequently, the author accepted *Conlariaceae* with two genera; *Conlarium* and *Riomyces* under *Diaporthomycetidae* family *incertae sedis*. *Conlarium* also formed a distinct clade in the phylogenetic analyses conducted by Hyde et al. (2020d). Hyde et al. (2021a) investigated freshwater *Diaporthomycetidae* based on phylogenetic and evolutionary analyses and established *Conlariales* to accommodate *Conlariaceae*.

General description

Riomyces is only known from its sexual morph whereas *Conlarium* species are reported in both sexual and asexual states. The sexual members are distinguished by gregarious ascomata and the asexual morph shows subglobose or irregular, brown, clathrate and muriform conidia (Zhang et al. 2017a).

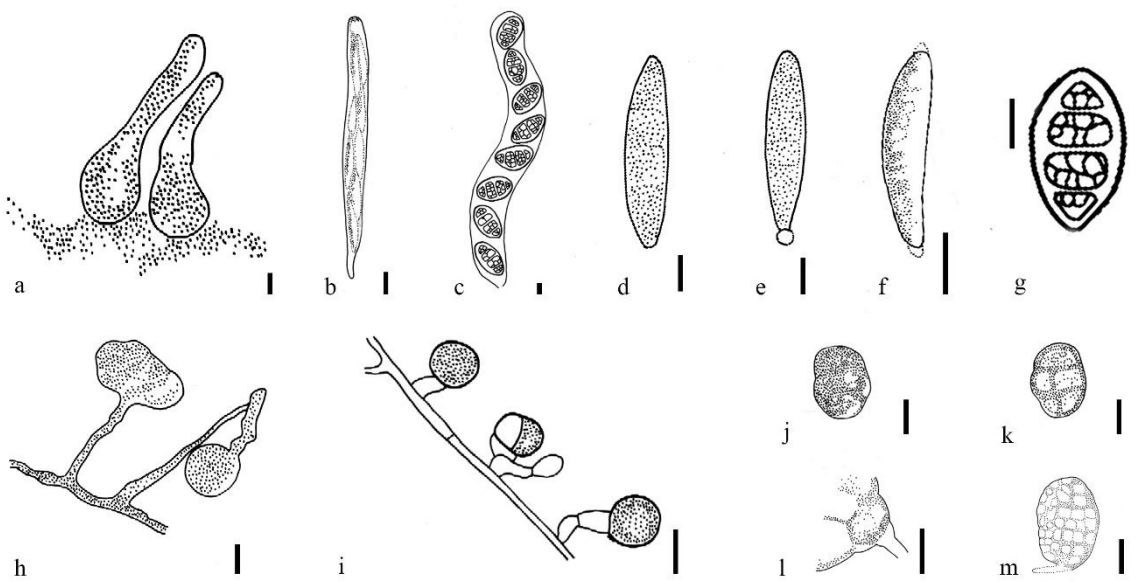


Figure 201 – Morphology of *Conlariales.* a Ascomata on natural substrate (*Conlarium duplumascospora*). b, c Asci (b *Conlarium duplumascospora*, c *Riomyces rotundus*). d–g (d–f *Conlarium duplumascospora*, g *Riomyces rotundus*). h Conidiophore bearing mature (left) and immature (right) conidium (*Conlarium duplumascospora*). i Conidiophores, conidiogenous cells and conidia (*Conlarium baiseense*). j, k, m Conidium (j, k *Conlarium duplumascospora*, m *Conlarium aquaticum*). l Conidiogenous cells (*Conlarium aquaticum*) (drawn from Ferrer et al. 2012, Liu et al. 2012a, Zhang et al. 2017a, Xie et al. 2019). Scale bars: a = 100 μm, b–m = 10 μm.

Sexual morph: *Ascomata* perithecioid, gregarious, coriaceous or membranous, immersed to erumpent or superficial, dark brown to black, globose to subglobose, smooth, ostiolate. *Neck* short or elongated, cylindrical, straight or slightly flexuous. *Peridium* composed of several layers of cells of *textura angularis*. *Paraphyses* cylindrical or globose, hyaline, septate. *Asci* 8-spored, unitunicate, cylindrical, short pedicellate, apically rounded, with a distinct, refractive, massive, barrel-shaped, apical ring or lacking apical structures. *Ascospores* uni- to bi-seriate, hyaline, fusiform or ellipsoidal-

fusiform, straight or slightly curved, aseptate to multi-septate, guttulate, thin- or thick-walled, with or without appendages or appendages at one or both ends or surrounded by an irregular gelatinous sheath. Asexual morph: Hyphomycetous. *Colonies* dark brown to black. *Mycelium* mostly immersed, consisting of branched, septate, thin-walled, smooth, pale brown to brown hyphae. *Conidiophores* micronematous or semi-macronematous, mononematous, septate or aseptate, unbranched or irregularly branched, straight or flexuous, hyaline, becoming brown when old. *Conidiogenous cells* holoblastic, determinate, doliiform, cylindrical. *Conidia* brown, muriform or columnar conidia (more transverse and less longitudinal septa) or simple, irregularly globose or subglobose, septate, constricted at the septa (adapted from Xie et al. 2019, Hyde et al. 2021a) (Fig. 201).

Families included in *Conlariales*

Conlariaceae Huang Zhang, K.D. Hyde & Maharachch.

Evolution

The divergence time estimate analyses, conducted by Hyde et al. (2021a), revealed the stem age of the order as 138 MYA.

Significance

Ecological and economic roles

Conlariales are primarily reported from freshwater habitats in Costa Rica, China, and Thailand. The taxa are reported as saprobes in submerged wood, dead wood or soil (Ferrer et al. 2012, Liu et al. 2012a, Zhang et al. 2017a, Phookamsak et al. 2019, Xie et al. 2019, Hyde et al. 2021a). Xie et al. (2019) reported three species that are reported as endophytes in sugarcane rhizosphere including *Conlarium baiseense*, *C. nanningense* and *C. sacchari* (Xie et al. 2019).

Chemical diversity

No relevant studies are available on the chemical diversity of *Conlariales*.

Other relevant data and future recommendations

Riomyces formed a close clade to *Magnaporthales* when it was established based on the SSU and LSU sequence data (Ferrer et al. 2012). However, a close relationship to *Magnaporthales* was not observed in the study of Luo et al. (2019b) and Hyde et al. (2021a). *Riomyces* was not treated in the phylogenetic analysis conducted by Zhang et al. (2017a) when they established the family *Conlariaceae*. In addition, the genus nested with *Conlarium* in the study of Yu et al. (2024b), who investigated the phylogenetic relationship of these genera by including all the available sequence data. Thus, the reevaluation of *Riomyces* and *Conlarium* is required.

***Coniochaetales* Huhndorf, A.N. Mill. & F.A. Fernández, Mycologia 96(2): 378 (2004)**

= *Cordanales* M. Hern.-Rest. & Crous
Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Sordariomycetidae*

Introduction

Coniochaetales comprises two families (*Coniochaetaceae* and *Cordanaceae*). The taxa are widely distributed as saprobic in dung (Doveri 2016) and soil (Phookamsak et al. 2019), pathogenic in plants (Damm et al. 2010), rarely on humans (Khan et al. 2013, Kabtani et al. 2022) and endophytes in various plants (Kokaew et al. 2011, Nasr et al. 2018, Harrington et al. 2019). They are also found in acidic water with high concentrations of heavy metals (Vázquez-Campos et al. 2014, Dayarathne et al. 2020).

Some taxa occur as yeasts and are classified within dematiaceous fungi due to the presence of melanin in their cell walls. They are known for emitting dark pigments in culture, which is perceived as a virulence factor (Nosanchuk & Casadevall 2006). The sexual morph is characterized by 4 to 8,

or multi-spored asci and ascospores with longitudinal germ slits. They differ from *Sordariaceae* and allied families in having ascospores with elongate germ slits (Malloch & Cain 1971a). The asexual morph possesses phialidic or polyblastic conidiogenous cells (Asgari & Zare 2006, Asgari et al. 2007). The anamorph of *C. lignicola* was introduced as *Lecythophora* (Nannfeldt 1934), but the genus was later transferred elsewhere. Gams & McGinnis (1983a) reintroduced this generic name for anamorphs of *Coniochaeta*. The sexual-asexual connection was re-emphasized by Weber et al. (2002). *Lecythophora* was synonymized with *Coniochaeta* following the "one fungus, one name" rules of nomenclature (Khan et al. 2013).

History

Coniochaetales was established by Huhndorf et al. (2004b) to accommodate a single family *Coniochaetaceae* in the subclass *Sordariomycetidae*. *Coniochaetaceae* was previously placed in *Sordariales* and the family formed a strongly supported sister clade to *Chaetomiaceae*/*Sordariaceae*, according to SSU sequence data (Lee & Hanlin 1999). Later, the family was recovered as a distinct clade to *Sordariales* and clustered with *Xylariales* in phylogenetic analyses, which were conducted based on LSU sequence data with broad taxon sampling (Weber et al. 2002). However, there was insufficient statistical support for the establishment of a new order. García et al. (2006) revised the order, recovered it as a well-supported clade within *Sordariomycetidae* and synonymized *Coniochaetidium*, *Ephemeroascus*, and *Poroconiochaeta* under *Coniochaeta*. *Coniochaetaceae* formed a monophyletic clade within *Sordariomycetidae* in the phylogenetic analyses based on LSU sequence data. Consequently, a new order, *Coniochaetales* was introduced. The order formed a sister clade to *Cordanaceae* (*Cordanales*) in the multigene phylogenetic analysis and was paced in *Diaporthomycetidae* (Maharachchikumbura et al. 2015). *Coniochaetales* differs from *Cordanales* by having a basal stroma, ascospores without germ slits and polyblastic asexual morphs (Hernández-Restrepo et al. 2015). The ordinal position of *Coniochaetales* became uncertain in the subsequent phylogenetic studies conducted by Yang et al. (2015) and Su et al. (2016a). Maharachchikumbura et al. (2016) placed this order in *Sordariomycetes*, order *incertae sedis*. *Cordanaceae* and *Coniochaetaceae* were recovered as sisters with a common ancestor at 77 MYA in the phylogenetic analyses conducted by Hongsanan et al. (2017a) but their ordinal position was not supported. In their study, *Cordanales* was suggested to combine under *Coniochaetales* based on the most recent common ancestor (77 MYA). The stem age of the new *Coniochaetales* was 176 MYA. *Cordanales* was established to accommodate *Cordanaceae* (Hernández-Restrepo et al. 2015). Hyde et al. (2020d) combined *Cordanales* under *Coniochaetales* following Hongsanan et al. (2017a). This classification has been accepted until now (Hyde et al. 2024b).

General description

The type of ascomata (cleistothecial or perithecial) and the ornamentation of the ascospore walls were of little taxonomic value at the generic level. Phialidic anamorphs were considered as an informative phylogenetic character in *Coniochaetales* (García et al. 2006). A nodulisporium-like anamorph has also been reported for a few *Coniochaeta* species (Hawksworth 1978, Asgari & Zare 2006, Asgari et al. 2007). In phialidic hyphomycetes, the phialide is often reduced to a collarette laterally positioned on a hyphal cell (Gams 2000, Weber 2002, Weber et al. 2002, Seifert et al. 2011), while *Nodulisporium* has long, mononematous conidiophores with holoblastic, polyblastic, hyaline conidia in a sympodial sequence, which gives rise to the characteristic nodulous appearance of the conidiogenous cell (Jong & Rogers 1972, Seifert et al. 2011).

Sexual morph: *Ascomata* perithecial or cleistothecial, solitary to gregarious, superficial, semi-immersed or immersed, subglobose to globose, pyriform, ovoid, dark brown to black, setose, glabrous or hairy, ostiolate or lacking ostiole, sometimes surrounded by a crown of setae. *Ostiole* periphysate, papillate. *Peridium* membranaceous to pseudoparenchymatous, rarely coriaceous; composed of several layers of cells of *textura angularis* or *textura intricata*, *textura prismatica* or less frequently cephalothecoid. *Paraphyses* septate, unbranched, filiform, simple. *Asci* (4-), 8- to multi-spored, unitunicate, cylindrical to fusoid or clavate, globose to subglobose, short pedicellate,

with a truncate to rounded apex, with or without a J-, apical ring, evanescent. *Ascospores* uniseriate or irregularly arranged, initially hyaline, brown to dark brown or olive-greenish to dark olivaceous or black at maturity, or pale brown to brown, ellipsoid to fusiform, broadly ellipsoidal to globose, lenticular or cruciform, with rounded to apiculate ends, flattened on one or both sides, sometimes with pores at both ends, 1-celled or 1-septate with or without a germ slit, smooth-walled or pitted. Asexual morph: hyphomycetous or yeast-like. *Colonies* dark brown to black, pink or orange and a yeast-like appearance. *Conidiophores* mononematous, macronematous or semi-macronematous. *Conidiogenous cells* phialidic, polyblastic, various size and morphology, terminal or intercalary, denticulate, somewhat ampulliform, subulate or indistinguishable from a normal hyphal cell, collarettes present, but usually indistinct, occasionally somewhat flared. *Conidia* accumulating near the point of formation (in chains), hyaline, orange or pink in mass, pale brown to brown, elliptical to oblong-elliptical to reniform, obovoid to ellipsoidal, sometimes with germ pores at the ends, 1-celled or 1-septate, smooth-walled (adapted from Hernández-Restrepo et al. 2014, Hyde et al. 2020d) (Figs. 202, 203).

Families included in *Coniochaetales*

Coniochaetaceae Malloch & Cain
Cordanaceae Nann.

Coniochaetales genera *incertae sedis*
Cannonia J.E. Taylor & K.D. Hyde
Pseudogliomastix W. Gams

Justification of order and problems

Coniochaeta is a highly diverse genus. *Coniochaeta* sequences are either robustly identified or some are misidentified, voucher specimens are often lacking and the ITS sequences between closely related species are similar or identical. Multigene phylogenetic analyses are necessary to distinguish closely related taxa (Harrington et al. 2019). The members of *Coniochaeta* are highly plastic with taxonomically uninformative anamorphs and the delineation of *Coniochaeta* is challenging (Gams & Weber 2002, Asgari et al. 2007, Wanasinghe et al. 2018, Phookamsak et al. 2019, Manawasinghe et al. 2022, Jayawardena et al. 2023, Senanayake et al. 2023). *Cannonia* was introduced as a monotypic genus and was originally placed in *Xylariaceae* based on the ascomata being immersed beneath a clypeus and surrounded by some stromatic tissues (Taylor & Hyde 1999).

However, the close relationship of asci and ascospores between *Cannonia* and *Coniochaetaceae* was mentioned when the genus was introduced. Daranagama et al. (2018) therefore transferred this genus to *Coniochaetales* based on morphology. *Pseudogliomastix* was introduced to accommodate an asexual species that was reported as a phialidic asexual morph (Gams & Boekhout 1985). *Coniochaeta ligniaria* was described as a sexual morph of *C. hoffmannii* (de Hoog et al. 2000). However, these species clustered into different clades in the phylogenetic analyses conducted by Kabtani et al. (2022), indicating a large distance between the teleomorphic and anamorphic species. Multigene phylogenetic analyses (Friebes et al. 2016) along with sexual and asexual characters are important to resolve their taxonomy (Checa et al. 1988, Weber et al. 2002).

Significance

Ecological and economic roles

The taxa are saprobic on dung, plant litter or in soil, water, and wood and are also reported as endophytes, endolichens and pathogens (Hyde et al. 2020d). *Coniochaeta* is a highly diverse genus and occurs on butter, dung, wood, soil, uranium mine wastewater, plants and lichen thalli (Harrington et al. 2019) and are commonly reported in Europe and Eastern Asia (Asgari et al. 2007) but less frequently reported in Central Asian regions (Samarakoon et al. 2018). Temperate and boreal plants and lichens frequently harbor endophytes in the genus *Coniochaeta* (Hyde et al. 2020d).

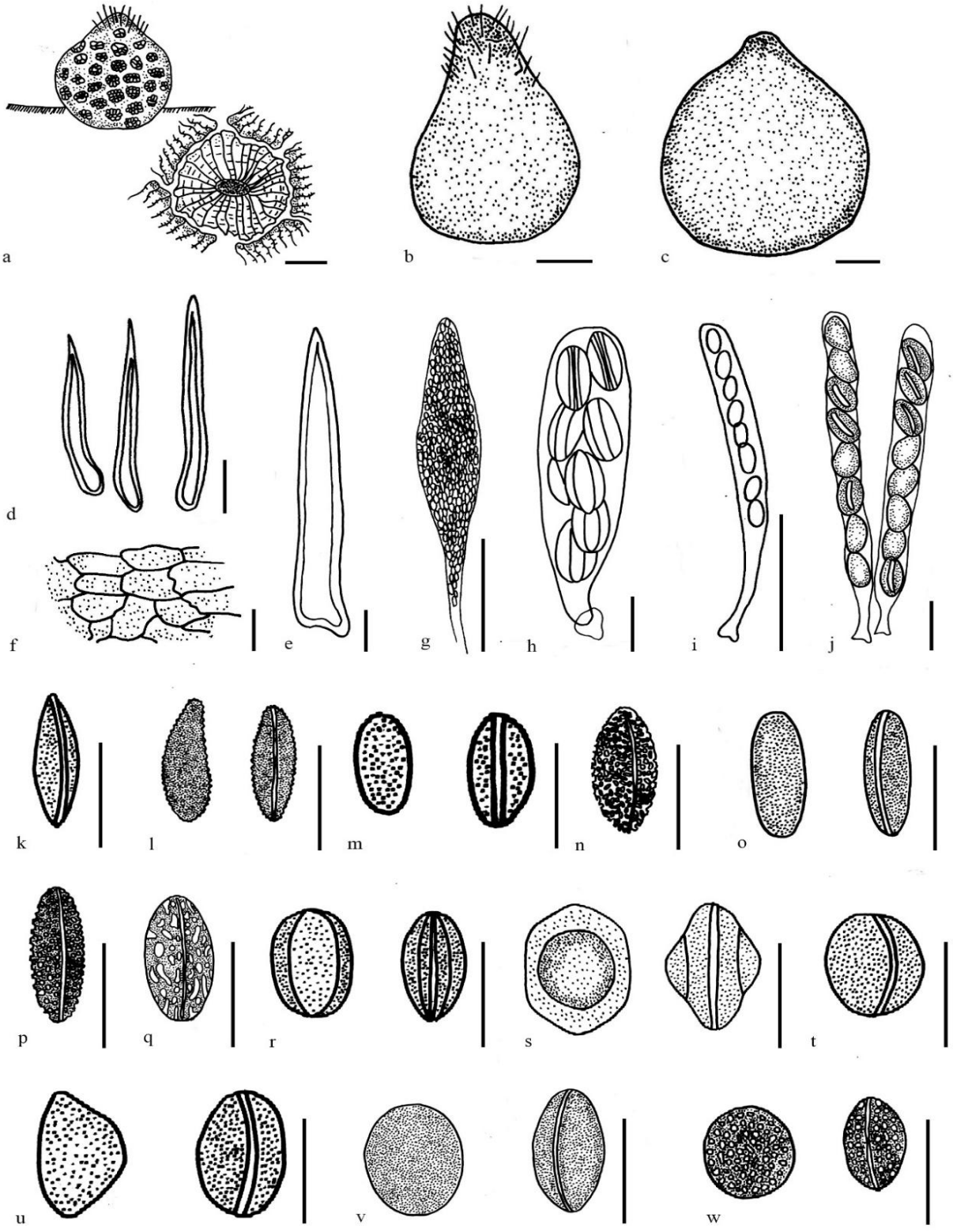


Figure 202 – Sexual morph of *Coniochaetales*. a–b Ascoma (a *Coniochaeta areolanirubra*, b *C. hansenii*, c *C. alkalivirens*. d, e Setae (d *C. hansenii*, e *C. areolanirubra*). f Peridial cells (*C. alkalivirens*). g–j Asci (g *C. hansenii*, h *C. cruciata*, i *C. alkalivirens*. j *C. emodensis*). k–w Ascospores (k *C. angustispora*, l *C. ovata*, m *C. ostrea*, n *C. punctulata*. o C. *saccardoi*, p *C. savoryi*, q *C. ornata*, r *C. cruciata*, s *C. nuciforme*, t *C. malacotricha*) (redrawn from Checa et al. 1988, Hernández-Restrepo et al. 2014). Scale bars: a–c = 100 µm, d = 25 µm, e = 5 µm, f = 10 µm, g = 50 µm, i = 25 µm, h, j–w = 10 µm.

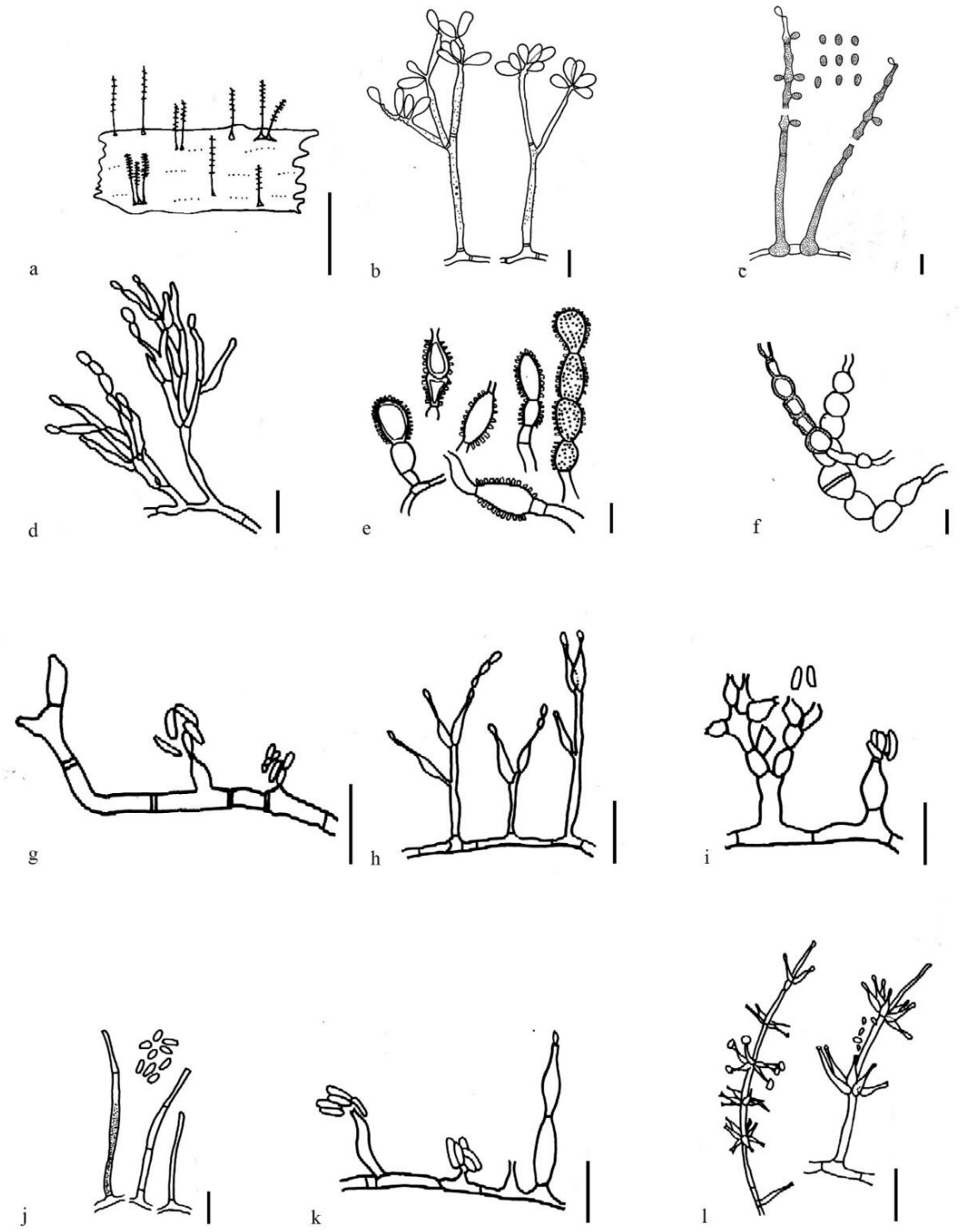


Figure 203 – Asexual morph of *Coniochaetales*. a Habit of *Cordana mercadiana.* b Conidiophores, conidiogenous cells, and conidia of *Coniochaeta emodensis*. c Conidiophores and conidia of *Cordana verruculosa*. d *Coniochaeta mirabile* (cladobotryum- like). e *Coniochaeta boothii* (chlamydospores). f *Coniochaeta ostrea* (clamydospores). g *Barrina polyspora* (lecythophora-like). h *Coniochaeta cypraespora* (paecilomyces-like). i *Coniochaeta vetulina* (*Lecythophora* sp.). j *Wallrothiella subiculosa* (*Pseudogliomastix protea*). k *Coniochaeta ligniaria* (*Lecythophora* sp.). l *Coniochaeta verticillata* (verticillium-like) (redrawn from García et al. 2006, Hernández-Restrepo et al. 2014). Scale bars: a = 200 µm, b–l = 10 µm.

The endophytes of *Coniochaeta* have been suggested to have the capacity to expand and reshape the generic concept and are of research importance because the genus is also reported as human pathogens, and produces biologically active compounds (Weber et al. 2002, Damm & Crous 2010, Khan et al. 2013). Asexually producing *Coniochaeta* yeasts occur as human pathogens which cause invasive fungal infections, occasionally with fatal outcomes, particularly in immunocompromised patients (de Hoog et al. 2000). *Coniochaeta hoffmannii* and *C. mutabilis* are considered as severe human pathogens. *Coniochaeta hoffmannii* has also been described as a plant pathogen (Gams & McGinnis 1983a) and the cause of canine osteomyelitis (Sakaeyama et al. 2007). It has also been involved in emerging human fungal infections, including subcutaneous abscesses (Gams & McGinnis 1983a), keratitis (Fintelmann 2011), and sinusitis (Marriott 1997). *Coniochaeta mutabilis* is considered as a severe pathogen causing human peritonitis (Ahmad et al. 1985), endocarditis (Slifkin & Bowers 1975, Drees et al. 2007), septic shock (Taniguchi et al. 2009), endophthalmitis (Marcus et al. 1999, Scott et al. 2004) and keratomycosis (Ho et al. 1991). *Cordana* species have been recorded from various temperate and tropical regions in the world (Hernández-Restrepo et al. 2014, Zelski et al. 2014, Ai et al. 2019). *Cordana* species cause leaf spots on banana and *Canna* spp. (Ellis 1976b, Markovskaja 2003, Cai et al. 2004, Hernández-Restrepo et al. 2014).

Chemical diversity

Otašević et al. (2020) investigated the bioactivity profiles of endophytic *Coniochaetaceae* species. Trichothecin (TCN) was extracted from *Cordana musae,* which was isolated from banana trees in the Yunnan Mountain plateau (Yang et al. 2014). Antibacterial and antifungal metabolites such as coniosetin and coniochaetone-a and -b are reported in *Coniochaeta ellipsoidea* (Segeth et al. 2003) and *Coniochaeta saccardoi* (Wang et al. 1995) respectively.

Conioscyphales **Réblifert, Persoonia 37: 63 (2015) [2016]**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Savoryellomycetidae*

Introduction

Conioscyphales belong in the subclass *Savoryellomycetidae* in *Sordariomycetes* (Hyde et al. 2020d). The order was introduced by Réblová et al. (2016c) to accommodate the monotypic family *Conioscyphaceae* and genus *Conioscypha*. It comprises taxa from both the terrestrial and freshwater habitats, expanding a large geographical area and collected mainly from decaying leaf and woody substrates, with few others from soil or mammal (Höhnel 1904, Shearer 1973, Matsushima 1975, 1993, 1996, Udagawa & Toyazaki 1983, Kirk 1984, Chen & Tzean 2000, Réblová and Seifert 2004, Zelski et al. 2015, Chuaseeharonnachai et al. 2017, Crous et al. 2018a, Luo et al. 2019b, Li et al. 2024, Xu et al. 2024b, Yu et al. 2024b). The taxa accommodated are mainly saprobic, except for one species, *Conioscypha japonica*, which has also been reported as a parasite in mammals (isolated from the hair of *Canis*) (Udagawa & Toyazaki 1983). The majority of *Conioscypha* species have been reported in their asexual morphs (Höhnel 1904, Shearer 1973, Matsushima 1975, 1993, 1996, Udagawa & Toyazaki 1983, Kirk 1984, Chen & Tzean 2000, Chuaseeharonnachai et al. 2017, Crous et al. 2018a, Luo et al. 2019b, Li et al. 2024, Xu et al. 2024b, Yu et al. 2024b), with the sexual morph described for *C. gracilis*, *C. peruviana* and *C. varia* (Réblová & Seifert 2004, Zelski et al. 2015).

History

The hyphomycetous genus *Conioscypha* was introduced by Höhnel (1904), with *C. lignicola* as the type species. Later, Shearer (1973) reviewed this genus by re-describing and illustrating the type species based on the holotype and three other collections (Goh & Hyde 1998). At the same time, Shearer (1973) introduced another taxon, *C. varia*. Other taxa were subsequently introduced in the genus, based on morphological support (Matsushima 1975, 1993, Udagawa & Toyazaki 1983, Kirk 1984). Réblová & Seifert (2004) introduced the ascomycetous genus *Conioscyphascus* to

accommodate *Conioscyphascus varius*. Interestingly, the former was observed to produce *Conioscypha varia* asexual morph *in vitro*. Phylogenetic analyses based on the LSU sequence data confirmed this connection between the two species (Réblová & Seifert 2004), indicating that they were congeneric. *Conioscyphascus* was then synonymized to *Conioscypha* based on the "one fungus / one name" nomenclatural priority (Zelski et al. 2015, Réblová et al. 2016c). In the multi-locus phylogenetic analyses carried out by Réblová et al. (2016c), it was observed that five *Conioscypha* species (*incertae sedis* taxa) formed a separate monophyletic clade, closely related to *Pleurotheciales* (Réblová et al. 2016c) and *Savoryellales* (Boonyuen et al. 2011). Réblová et al. (2016c) consequently accommodated these five species in a new family, *Conioscyphaceae*, and a new order, *Conioscyphales,* in the subclass *Hypocreomycetidae*. Hongsanan et al. (2017a) later raised *Savoryellales* to *Savoryellomycetidae* and *Conioscyphales* was subsequently accommodated in the latter subclass.

General description

Conioscyphales accommodates a single genus, following which, the taxa in the genus do not show prominent morphological differences from each other, either in their sexual or asexual morph (Réblová et al. 2016c, Hyde et al. 2020d). The order is characterized as follows:

Sexual morph: *Ascomata* immersed to superficial, astromatic, perithecial, papillate or comprising a long neck. *Ostioles* periphysate. *Ascomatal wall* two-layered, waxy, leathery. *Paraphyses* filiform, septate, unbranched, longer than the asci. *Asci* unitunicate, 8-spored, cylindrical-clavate, pedicellate, comprising a conspicuous inamyloid apical ring. *Ascospores* 2–4-seriate, hyaline to subhyaline, ellipsoid to fusiform or fusiform-navicular, transversely multi-septate, lacking a mucilaginous sheath or appendages. Asexual morph: *Conidiophores* mononematous, micronematous, hyaline or pigmented. *Conidiogenous cells* blastic, cyathiform to doliiform, comprising hyaline, cup-like collarettes. *Conidia* brown, unicellular, aseptate, varying in shape, thick-walled, smooth, with a basal pore at the point of attachment to the conidiogenous cells, produced individually and successively by percurrent regeneration of the conidiogenous cell's apex, liberated upon rupture of the outer wall of the conidiogenous cell's apex (Fig. 204).

Families included in *Conioscyphales*

Conioscyphaceae Réblová & Seifert

Evolution

The divergence time for the order has been estimated as 128.5 MYA (Hyde et al. 2020d).

Justification of order and problems

Conioscyphales has been introduced based on its distinct morphological characteristics as well as multi-locus phylogenetic evidence (Réblová et al. 2016c). The order is a small one with no taxonomic ambiguities being evidenced. Conidiogenous cells in the order are rather unique in their possession of cup-like collarettes, resulting from imbricated layers of remnant walls being cast off with every successive conidial secession (Shearer & Motta 1973, Goh & Hyde 1998). The asexual characteristic of the order also distinguishes it from its phylogenetically sister orders and *Pleurotheciales* and *Savoryellales* (Réblová et al. 2016c), which otherwise evidence similar sexual characteristics as *Conioscyphales*.

Significance

Ecological and economic roles

The order comprises mostly saprobic species isolated from decaying plant materials from both the terrestrial and aquatic habitats (Hyde et al. 2020d). While taxa in the order do not appear to be host-specific, *C. bambusicola* has apparently so far only been reported from bamboo (*Phyllostachys* sp.) (Matsushima 1975, Chen & Tzean 2000). *Conioscypha japonica* is the only species in the genus to have been retrieved from the cuticular scrapings and hairs of a living animal (Goh & Hyde 1998).

Other relevant data and future recommendations

So far, only a biphasic approach has been undertaken vis-à-vis the taxonomic circumscription of *Conioscyphales*. Future studies can tap into other biological aspects of the taxa, including exploring, for instance, the metabolite profile of the species or the relationship of the taxa with their surrounding environment or substrates.

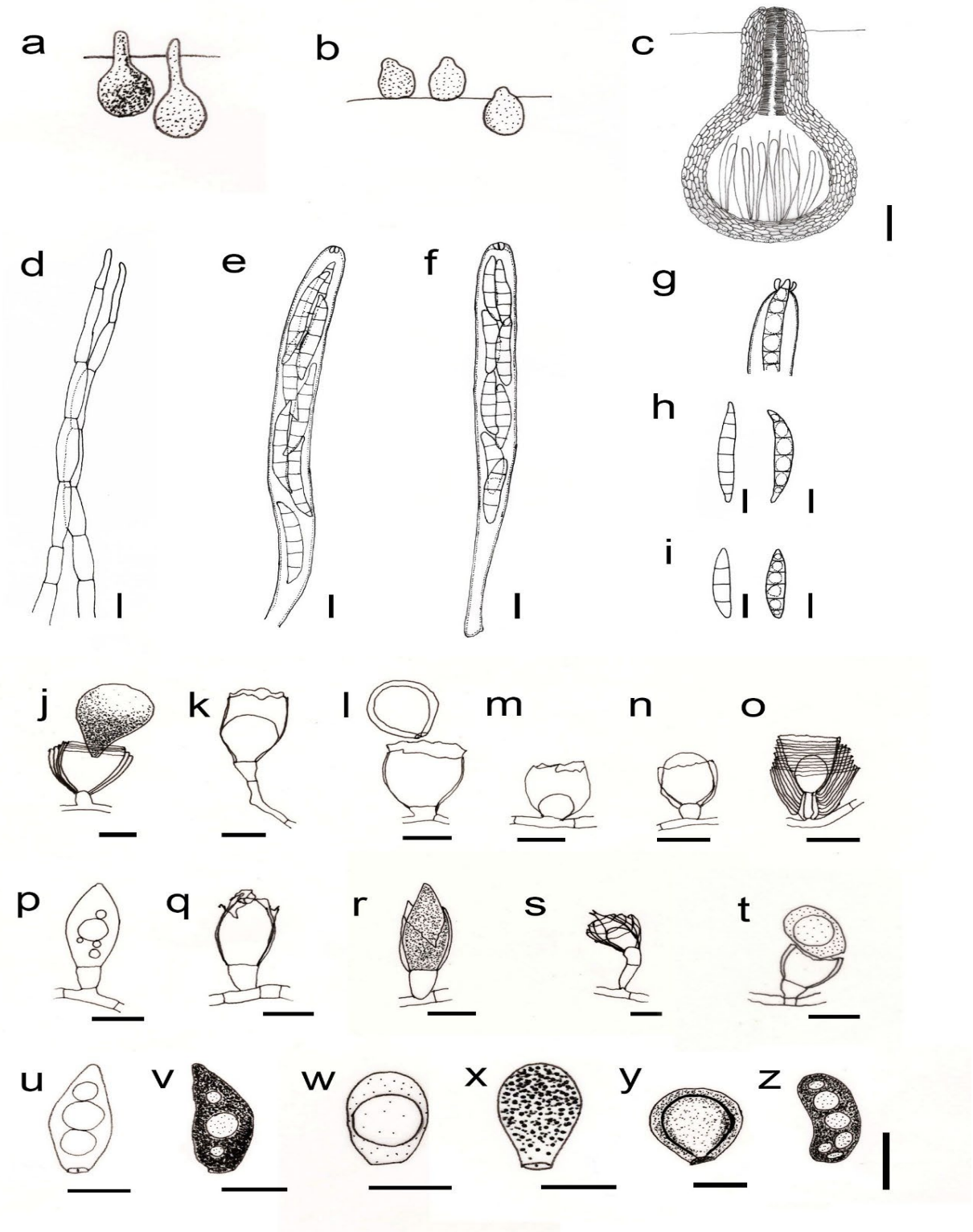


Figure 204 – Morphology of *Conioscyphales*. a Ascomata of *Conioscypha varia*. b Perithecia of *Conioscypha gracilis*. c Longitudinal section of an ascoma (*C. varia*). d Paraphyses (*C. varia*). e, f Asci (e *C. varia*, f *C. gracilis*). g Ascal apex with apical annulus during ascospore discharge (*C. varia*). h,i Ascospores (h *C. varia*, i *C. gracilis*). j–t Conidiophores and conidial development from

conidiogenous cells (j *C. nakagirii*, k,l *C. lignicola*, m–o, t *C. hoehnelii*, p–r *C. bambusicola*, s *C. japonica*). u–z Conidia (u,v *C. bambusicola*, w *C. hoehnelii*, x *C. japonica*, y *C. lignicola*, z *C. peruviana*) (a–i redrawn from Réblová & Seifert 2004, j redrawn from Chuaseeharonnachai et al. 2017, k–y redrawn from Chen & Tzean 2000, z drawn from Zelski et al. 2015). Scale bars: c = 100 μm, d–f, h,i, k–y = 10 μm, j = 15 μm, z = 5 μm.

Coronophorales **Nannf., Nova Acta Regiae Societatis Scientiarum Upsaliensis Ser. 4 8(no. 2): 54 (1932)**

= *Melanosporales* N. Zhang & M. Blackw.
= *Parasympodiellales* Hern.-Restr., Gené, R.F. Castañeda & Crous
Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Hypocreomycetidae*

Introduction

Coronophorales is a monophyletic order that includes 26 genera distributed in six families, which are both phenotypically and phylogenetically distinct (Bundhun et al. 2021b, Huang et al. 2021a). It is a poorly studied order which has recently been well scrutinized by Huang et al. (2021a). Taxa belonging to the order are saprobic, inhabiting woody substrates worldwide, in both temperate and tropical regions (Mugambi & Huhndorf 2010, Maharachchikumbura et al. 2016, Hyde et al. 2020d, Bundhun et al. 2021b). The order is uniquely characterized by turbinate or globose ascomata with long necks or Quellkörper structures and/or Munk pores in the cells of the ascoma wall (Mugambi & Huhndorf 2010, Carneiro de Almeida et al. 2016). The taxa in *Ceratostomataceae* generally comprise long-necked ascomata and ellipsoidal to broadly fusiform ascospores (Marin-Felix et al. 2018, Hyde et al. 2020d). *Bertiaceae*, *Chaetosphaerellaceae*, *Coronophoraceae* and *Nitschkiaceae* have black, tuberculate ascomata with or lacking ostioles, and obconical Quellkörper structures (Saccardo 1882b, Patouillard & Lagerheim 1895b, Subramanian & Sekar 1990, Réblová 1999a, b). *Scortechiniaceae* is mainly characterized by Quellkörper structures in the turbinate ascomata and allantoid to ellipsoidal ascospores (Huhndorf et al. 2004). *Parasympodiellaceae* accommodates taxa which have so far only been reported in their asexual morph (Bundhun et al. 2021b). Several taxa belonging to *Coronophorales* have been described in either their sexual or asexual morph. However, many have been reported to not be easily culturable, or they form infertile cultures (Marin-Felix et al. 2018).

History

Several taxa of *Coronophorales*, such as *Nitschkiaceae*, were earlier included in other orders, including *Sordariales* (Nannfeldt 1932, Müller & von Arx 1973, Subramanian & Sekar 1990, Hawksworth et al. 1995). Nannfeldt (1932) also considered *Coronophorales* to be ascohymenial, while Miller (1949) treated the order as loculoascomycetous. Luttrell (1951a, 1955) placed *Coronophorales* in the Pyrenomycetes with unknown affinities. At the same time, *Coronophoraceae* was accommodated in *Plectascales* (von Arx & Müller 1954). *Coronophoraceae* taxa were, however, also accepted as non-ostiolate relatives of *Lasiosphaeriaceae* (Carroll & Munk 1964, Nannfeldt 1975). Huhndorf et al. (2004a), observed that taxa of *Nitschkiaceae* formed a strongly supported clade, sister to the *Hypocreales*, in their phylogenetic analysis using LSU sequence data. The family was accepted in the *Coronophorales* and consequently the order was included in the *Hypocreomycetidae*, as a distinct unit from *Sordariales* and *Lasiosphaeriaceae*. Along the same lines, Huhndorf et al. (2004b) accepted *Bertiaceae* in the order while simultaneously establishing the new families, *Chaetosphaerellaceae* and *Scortechiniaceae*.

Another family, *Ceratostomataceae*, was initially considered a synonym of *Melanosporaceae* based on the similar morphology of the hyphomycetous asexual morph (Cannon & Hawksworth 1983, Horie et al. 1986, Barr 1990b, Hawksworth et al. 1995, Gams 2000). Later, this family was placed in *Coronophorales* based on phylogenetic evidence (Zhang & Blackwell 2002, Zhang et al.

2006, Hibbett et al. 2007, Maharachchikumbura et al. 2015, 2016, Hongsanan et al. 2017a, Hyde et al. 2017a, 2020d, Wijayawardene et al. 2020). *Coronophoraceae*, which included the two genera *Cryptosphaerella* and *Coronophora*, was placed in *Coronophorales* as an independent clade. However, *Cryptosphaerella* was transferred to *Scortechiniaceae*, which left *Coronophoraceae* as a monotypic family (Mugambi & Huhndorf 2010). Huang et al. (2021a) remarked that *Cryptosphaerella* should not be accommodated in *Scortechiniaceae* since its type species does not possess a Quellkörper and Munk pores, characters that primarily define *Scortechiniaceae*. Therefore, *Cryptosphaerella* was transferred to *Sordariomycetes* genera *incertae sedis* (Huang et al. 2021a). Recently, *Parasympodiellaceae* was transferred to *Coronophorales* based on phylogenetic analysis, with *Parasympodiellales* being synonymized under *Coronophorales* (Bundhun et al. 2021b).

General description

Most of the taxa of *Coronophorales* usually comprise superficial ascomata and a well-formed or an inconspicuous subiculum, and Munk pores (Huang et al. 2021a). *Scortechiniaceae* is the only family in the order which accommodates taxa with a well-developed Quellkörper in their centrum (Huhndorf et al. 2004b). Members of *Bertiaceae* do not possess a Quellkörper, while other families, such as, *Chaetosphaerellaceae*, *Coronophoraceae*, *Nitschkiaceae*, have Quellkörper-like structures (Mugambi & Huhndorf 2010). Asci in the order are clavate to subglobose with subcylindrical to ellipsoidal ascospores. Asexual morphs are hyphomycetous and phialidic (Mugambi & Huhndorf 2010, Maharachchikumbura et al. 2016, Hyde et al. 2020d). Members of *Parasympodiellaceae* are only known in their asexual morph and they are mainly characterized by thallic, terminal or intercalary, sympodial conidiophores and thallic-arthric, aseptate or septate conidia with schizolytic secession (Cheewangkoon et al. 2009, Hernández-Restrepo et al. 2017). Synasexual morph, *viz*. stylaspergillus-like or arthrocristula-like, have also been reported for the family (Bundhun et al. 2021b).

Sexual morph: *Subiculum* inconspicuous or composed of brown to dark brown, branched, septate hyphae. *Ascomata* solitary or gregarious, superficial to erumpent or semi-immersed, usually sitting on a subiculum, with or lacking ostioles, globose to subglobose, carbonaceous or coriaceous, collapsing or laterally collapsing when dry, with or without Quellkörper. *Peridium* carbonaceous to coriaceous to membranaceous, Munk pores present or absent. *Paraphyses* present or absent; when present, few, filiform or broadly cylindrical, inflated, evanescent. *Asci* 4 to 8 or multi-spored, unitunicate, clavate to cylindrical, pedicellate or sessile, apex blunt or rounded, apical ring indistinct or absent. *Ascospores* uni- or bi-seriate or overlapping, hyaline to brown, allantoid, ellipsoidal, ovoid or oval or cylindrical, straight to slightly curved, aseptate to septate, smooth-walled, guttules present or absent, sheath or appendages present or absent. Asexual morph: Hyphomycetous. *Conidiophores* semi-macronematous to macronematous, mononematous, hyaline to brown, branched or unbranched, straight to flexuous, brown, smooth or comprising rough swellings along the whole length in some genera or geniculations in others. *Conidiogenous cells* apical, lateral or intercalary, usually hyaline, often sympodial, blastic or thallic. *Conidia* hyaline or brown, aseptate to septate, globose, oval, elliptical, ellipsoidal, pyriform, cylindrical, oblong or spindle-shaped, smooth or verrucose, solitary or produced in branched or unbranched chains. Synasexual morph: stylaspergillus-like or arthrocristula-like (Fig. 205).

Families included in *Coronophorales*

Bertiaceae Smyk
Ceratostomataceae G. Winter
Chaetosphaerellaceae Huhndorf, A.N. Mill. & F.A. Fernández
Coronophoraceae Höhn.
Nitschkiaceae (Fitzp.) Nannf.
Parasympodiellaceae Hern.-Restr., Gené, Guarro & Crous
Scortechiniaceae Huhndorf, A.N. Mill. & F.A. Fernández

Coronophorales genera *incertae sedis*
Papulaspora Preuss
Sphaerodes Clem.
Tengiomyces Réblová

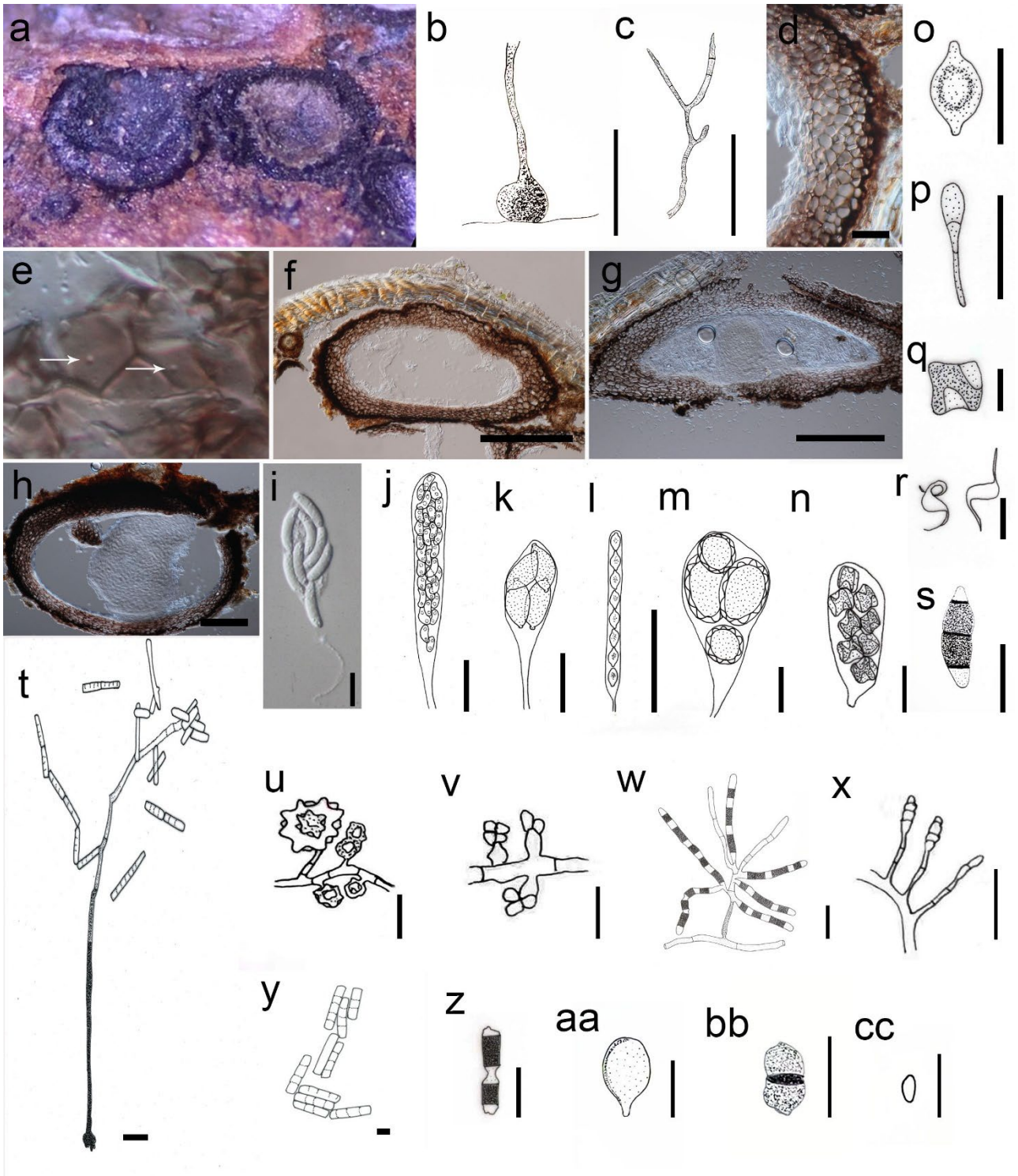


Figure 205 – Morphology of *Coronophorales*. a Ascomata of *Yuxiensis granularis*. b An ascoma of *Arxiomyces vitis*. c Branched hypha (*Chaetosphaerella phaeostroma*). d Section of peridium (*Yuxiensis granularis*). e Munk pores indicated by arrows (*Yuxiensis granularis*). f, g Vertical sections of ascomata (*Yuxiensis granularis*). h Quellkörper (*Yuxiensis granularis*). i–n Asci (i *Yuxiensis granularis*, j *Scortechiniellopsis leonensis*, k *Pustulipora corticola*, l *Erythrocarpon microstomum*, m *Rhytidospora tetraspora*, n *Scopinella barbata*). o–s Ascospores (o *Microthecium*

zobelii, p *Loranitschkia viticola*, q *Scopinella barbata*, r *Biciliosporina karwarensis*, s *Lasiosphaeriopsis salisburyi*). t–x Conidiophores and development of conidia from conidiogenous cells (t *Parasympodiella laxa*, u, x *Erythrocarpon microstomum*, v *Microthecium foveolatum*, w *Parasympodiella hyphenata*). y–cc Conidia (y *Parasympodiella laxa*, z *Parasympodiella hyphenata*, aa *Gonatobotrys simplex*, bb *Chaetosphaerella fusca*, cc *Niesslia nolinae*) (b,c drawn from Huang et al. 2021, j–s, u, v, x, aa–cc redrawn from Huang et al. 2021, t, y drawn from Cheewangkoon et al. 2009, w, z redrawn from Bundhun et al. 2021). Scale bars: b = 500 μm, c,h = 100 μm, d,w = 30 μm, f,g = 200 μm, i, m, n, r, v, y, z, aa, cc = 10 μm, j, l, o, s, t, u, bb = 20 μm, k, p, x = 50 μm, q = 5 μm.

Evolution

Coronophorales have a comparatively faster rate of evolution as compared to other orders, such as *Hypocreales*, in *Hypocreomycetidae*. Families within the order, however, have almost a similar rate of evolution (Huhndorf et al. 2004b). Furthermore, the Quellkörper occurs only in some taxa of this order in *Sordariomycetes* (Huhndorf et al. 2004b, Hyde et al. 2020d).

Justification of order and problems

Coronophorales is a monophyletic order in *Hypocreomycetidae*, justified by multi-locus phylogenetic and evolutionary (MCC) analyses, with *Melanosporales* and *Parasympodiellales* being its synonyms (Hongsanan et al. 2017a, Bundhun et al. 2021b, Huang et al. 2021a). However, Hongsanan et al. (2017a) have stated that the families in *Coronophorales* separate into three main lineages, indicating that they may be three separate orders. In addition, the type family of the order, *Coronophoraceae*, is phylogenetically represented by a single strain, *Coronophora gregaria*, and this familial placement is unstable (Mugambi & Huhndorf 2010, Hongsanan et al. 2017a). Moreover, *Nitschkiaceae* is paraphyletic (Huhndorf et al. 2004b, Mugambi & Huhndorf 2010). Huang et al. (2021a) have also remarked that families in the order cannot be morphologically demarcated by the ascomatal vestiture, ascospore number per ascus or ascospore appendages and that phylogeny is a requisite to support the familial taxonomic demarcation in the order.

Significance

Ecological and economic roles

Most taxa of *Coronophorales* are saprobic on woody substrates, partaking in the decomposition of plant litter, and therefore cycling of nutrients as well as carbon, through secretion of lignocellulolytic enzymes (Baldrian & Valášková 2008, Crowther et al. 2012). Taxa of *Ceratostomataceae* are potential biocontrol agents since they colonize other plant pathogens (Cannon & Kirk 2007). Certain members of *Nitschkiaceae* are mycoparasitic (Hawksworth 1980a, Gonzalez & Martin 1996, Vasilyeva et al. 2010). Some taxa of *Parasympodiellaceae* may cause commercial damage to economically important plants as they often grow on coniferous and dicotyledonous plants (Crous et al. 1995, Cheewangkoon et al. 2009, Seifert et al. 2011).

Other relevant data and future recommendations

While several taxa of *Coronophorales* do have sequence data to support their taxonomic placement, the accurate identification of several others is pending. The latter have solely been identified based on morphology, which is insufficient for their accurate identification (Huang et al. 2021a). Supplementing these species with molecular data is imperative. Recollection of the same taxa to supplement them with accurate or additional morphological information as well as molecular data, is recommended. Sequencing of herbarium material to derive sequence data is also desirable.

Delonicicolales **R.H. Perera, Maharachch. & K.D. Hyde, Cryptogamie, Mycologie 38(3): 329 (2017)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Xylariomycetidae*

Introduction

Delonicicolales was established by Perera et al. (2017) to accommodate *Delonicicolaceae* with the introduction of the monotypic genus, *Delonicicola* (type species: *Delonicicola siamense*). *Delonicicola siamense* was isolated as a saprobe from dried seed pods of *Delonix regia* (*Fabaceae*) in Chiang Rai Province, Thailand. Morphological description, phylogenetic analyses and molecular clock analysis corroborate its taxonomic placement in *Delonicicolales*. Originally, *Delonicicolaceae* consisted of *Delonicicola* and *Liberomyces* (Perera et al. 2017). Subsequently, Voglmayr et al. (2019a) added a new genus, *Furfurella*, to *Delonicicolaceae*. Additionally, *Liberomyces* was synonymized under *Leptosillia*. To date, *Delonicicola* contains a single species, *Furfurella* comprises three species and *Leptosillia* consists of 12 species (Index Fungorum 2024, Species Fungorum 2024).

Delonicicolales taxa are saprobes, pathogens and endophytes (Perera et al. 2017, Voglmayr et al. 2019a) and the order is commonly characterized by hyaline ascospores and conidia (Perera et al. 2017). *Delonicicolales* diverged around 181 MYA (133-234), sharing a common ancestor with *Amphisphaeriales* and *Xylariales* (Perera et al. 2017).

History

Perera et al. (2017) analyzed multiple datasets before proposing the new order. The concatenated ITS-SSU-RPB2 dataset was analyzed to infer the phylogenetic placement of *Delonicicola* in the subclass *Xylariomycetidae*. Furthermore, the individual ITS dataset was analyzed to confirm the phylogenetic placement of *D. siamense* in *Delonicicolaceae*. In their analyses, *Delonicicola* formed a distinct lineage from other orders in *Xylariomycetidae*, thereby validating the establishment of the new order, *Delonicicolales*.

Nonetheless, Vitale et al. (2018) did not accept *Delonicicolales* as a separate order. Instead, the authors classified *Delonicicolaceae* within *Xylariales* based on phylogenetic inferences. In addition, morphological features such as the conidiomata, conidiophores and conidiogenous cells are concordant to some other *Xylariales* taxa. Voglmayr et al. (2019a) also rejected *Delonicicolales* as a separate order based on the phylogenies of different sequence datasets, including the combined ITS-LSU and ITS-LSU-SSU-RPB1-RPB2-TEF1-TUB2. However, in subsequent research, *Delonicicolales* clustered separately from *Amphisphaeriales* and *Xylariales*, supported phylogenetically based on the combined ITS-LSU-BTUB-RPB2 matrices coupled with divergence time estimates (Hyde et al. 2020d). Earlier, *Xylariales* was the sole order in the subclass *Xylariomycetidae* (Maharachchikumbura et al. 2016). To date, besides *Xylariales*, *Amphisphaeriales* and *Delonicicolales* also belong to *Xylariomycetidae* (Wijayawardene et al. 2022a). *Delonicicolales* comprises two families, *Delonicicolaceae* and *Leptosilliaceae* (Hyde et al. 2020d, Wijayawardene et al. 2020, 2022a). *Leptosilliaceae* was established based on phylogenetic analyses and morphological as well as ecological distinctions (Voglmayr et al. 2019a).

General description

Delonicicolales are characterized by perithecial, immersed and ostiolate ascomata, as seen in the currently accepted genera *Delonicicola*, *Furfurella* and *Leptosillia* (Perera et al. 2017, Voglmayr et al. 2019a). Their peridium consists of multiple layers of hyaline or melanized cells forming a *textura angularis* or *prismatica*. As for *Delonicicola*, the peridium comprises around five to eight layers of hyaline cells of *textura angularis* (Perera et al. 2017). Their asci are usually 8-spored, unitunicate and clavate with a short pedicel. However, the asci of *Furfurella* appear bitunicate with a distinct ocular chamber in Lugol solution following treatment with 3 % KOH (Voglmayr et al. 2019a). On the other hand, their conidiomata are pycnidial, uni- or multi-locular, and ostiolate, similar to the ascomata. The conidiomatal walls of these taxa are multi-layered, consisting of dark brown cells outwards (Perera et al. 2017). Their ascospores and conidia are both hyaline. However, ascospores are uni- to bi-seriate and trans-septate (Perera et al. 2017), while the conidia are falcate or filiform, aseptate and allantoid (Voglmayr et al. 2019a). Ascospores of *Leptosillia* may have up to 11 septa (Voglmayr et al. 2019a).

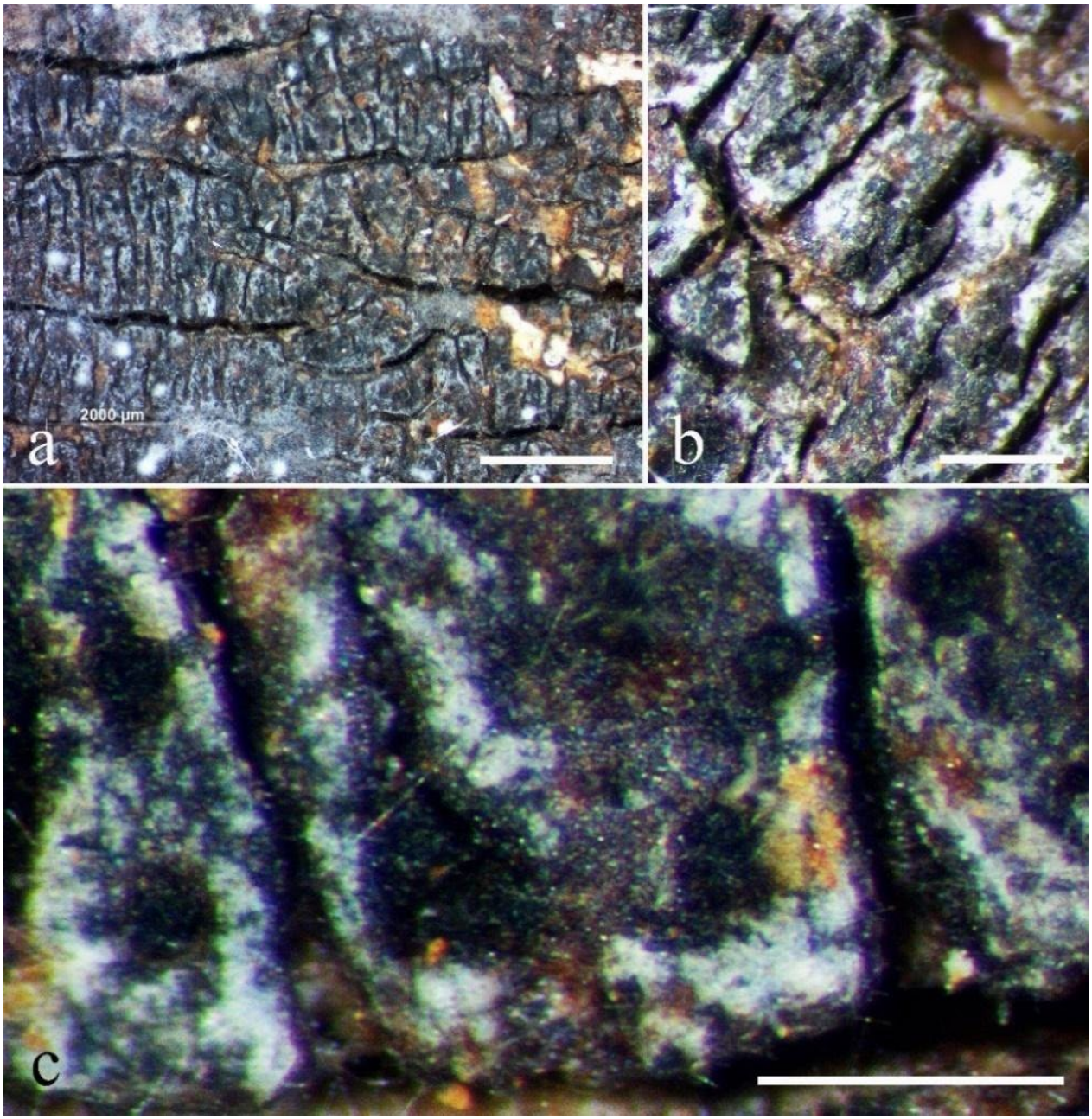


Figure 206 – Appearance of ascomata of *Delonicicolales* on substrate [Permission to use original images obtained by authors; Perera et al. (2017)]. a–c Close up of ascomata of *Delonicicola* sp. on the substrate. Scale bars: a = 2 mm, b, c = 0.5 mm.

Furfurella spp. are easily delineated from *Delonicicola* spp. as they have larger aseptate ascospores, and a yellow-green to turquoise scurf on the stromata and ostioles (Voglmayr et al. 2019a). Despite being part of *Xylariomycetidae*, unlike other xylarialean taxa, germ slits in the ascospores of *Delonicicolales* taxa have not been observed (Samarakoon et al. 2022).

Sexual morph: *Pseudostromata* variable, aggregated, immersed in host tissues, dark brown to black. *Ascomata* perithecial, aggregated, immersed in pseudostromata, ostiolate, papillate. *Peridium* consisting of layers of hyaline or melanized cells of *textura angularis* or *prismatica*. Hamathecium containing aseptate and unbranched paraphyses. *Asci* 8-spored, unitunicate and clavate comprising a short pedicel. *Ascospores* uniseriate or biseriate, trans-septate, hyaline. Asexual morph: *Conidiomata* pycnidial, aggregated or scattered, uni- or multi-locular, ostiolate. *Conidiomatal wall* consisting of multiple layers of dark brown cells outwards. *Conidiophores* branched, hyaline. *Conidiogenous cells* holoblastic with sympodial proliferation. *Conidia* allantoid or bacilloid, falcate or filiform, 1-celled, hyaline (adapted from Perera et al. 2017) (Figs. 206, 207, 208, 209).

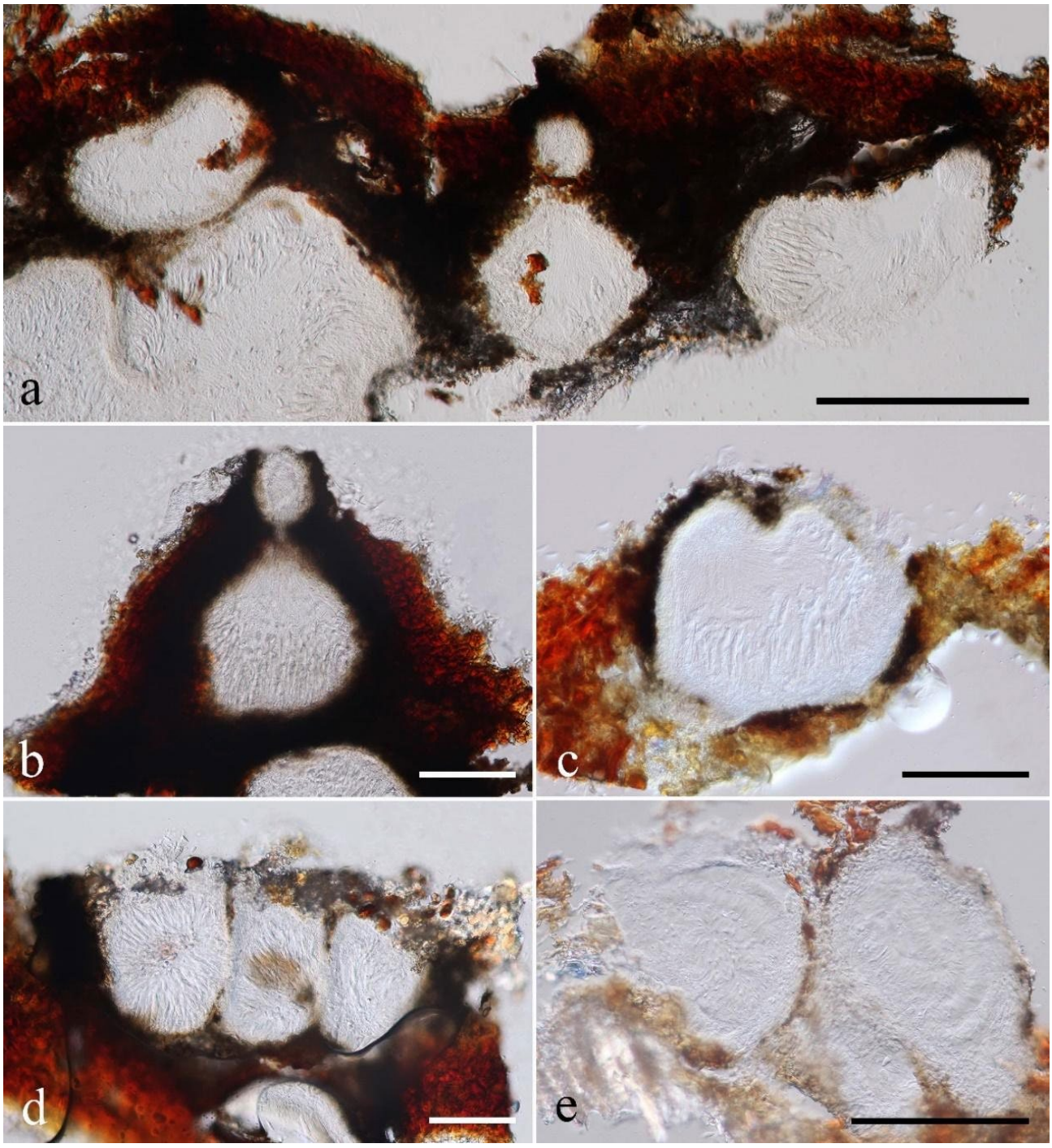


Figure 207 – Ascomata morphology of *Delonicicolales* [Permission to use original images obtained by authors; Perera et al. (2017)] a–d Sectioning through ascomata of *Delonicicola* sp. showing ostiole. e Peridium of *Delonicicola* sp. Scale bars: a = 100 µm, b–e = 50 µm.

Families included in *Delonicicolales*

Delonicicolaceae R.H. Perera, Maharachch. & K.D. Hyde
Leptosilliaceae Voglmayr & Jaklitsch

Evolution

Delonicicolales is the third order in *Xylariomycetidae* (Perera et al. 2017). Similar to *Amphisphaeriales* and *Xylariales*, *Delonicicolales* diverged around 181 MYA (133–234), all sharing a common ancestor (Perera et al. 2017). The estimated stem ages fit within the standard stem ages of an order (150-250 MYA), as proposed by Hyde et al. (2017a).

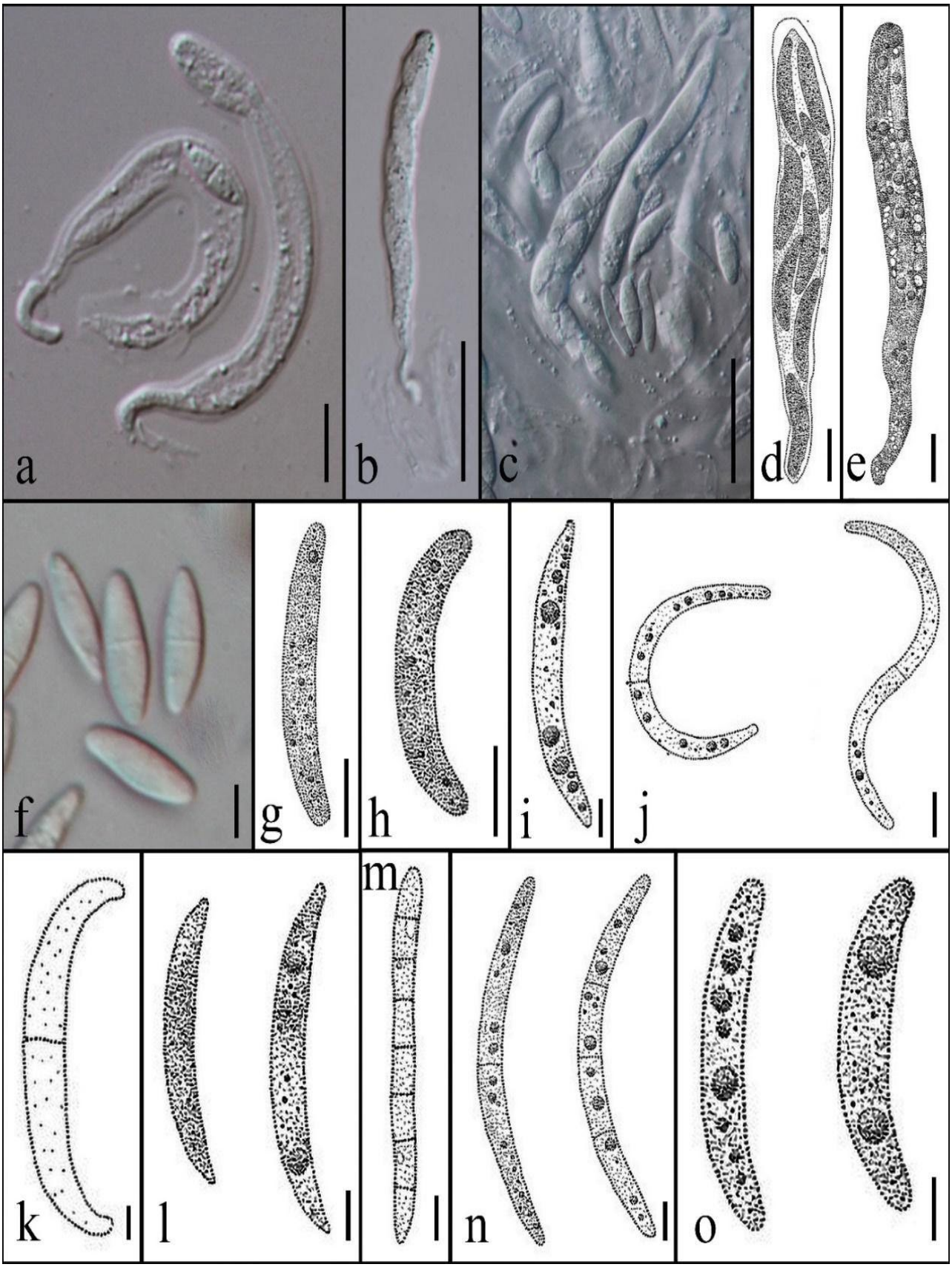


Figure 208 – Asci and ascospore morphologies of *Delonicicolales* [Permission to use original images obtained by authors, Perera et al. (2017)]; redrawn from Voglmayr et al. (2019a)] a–c, f *Delonicicola siamense*. d, g, h *Furfurella nigrescens*. e, l *Leptosillia muelleri*. i *L. acerina*. j *L. macrospora*. k *L. fusariospora*. m *L. pinicola*. n *L. slaptonensis*. o *L. wienkampii*. Scale bars: a–h, j, n = 10 µm. i, k–m, o = 5 µm.

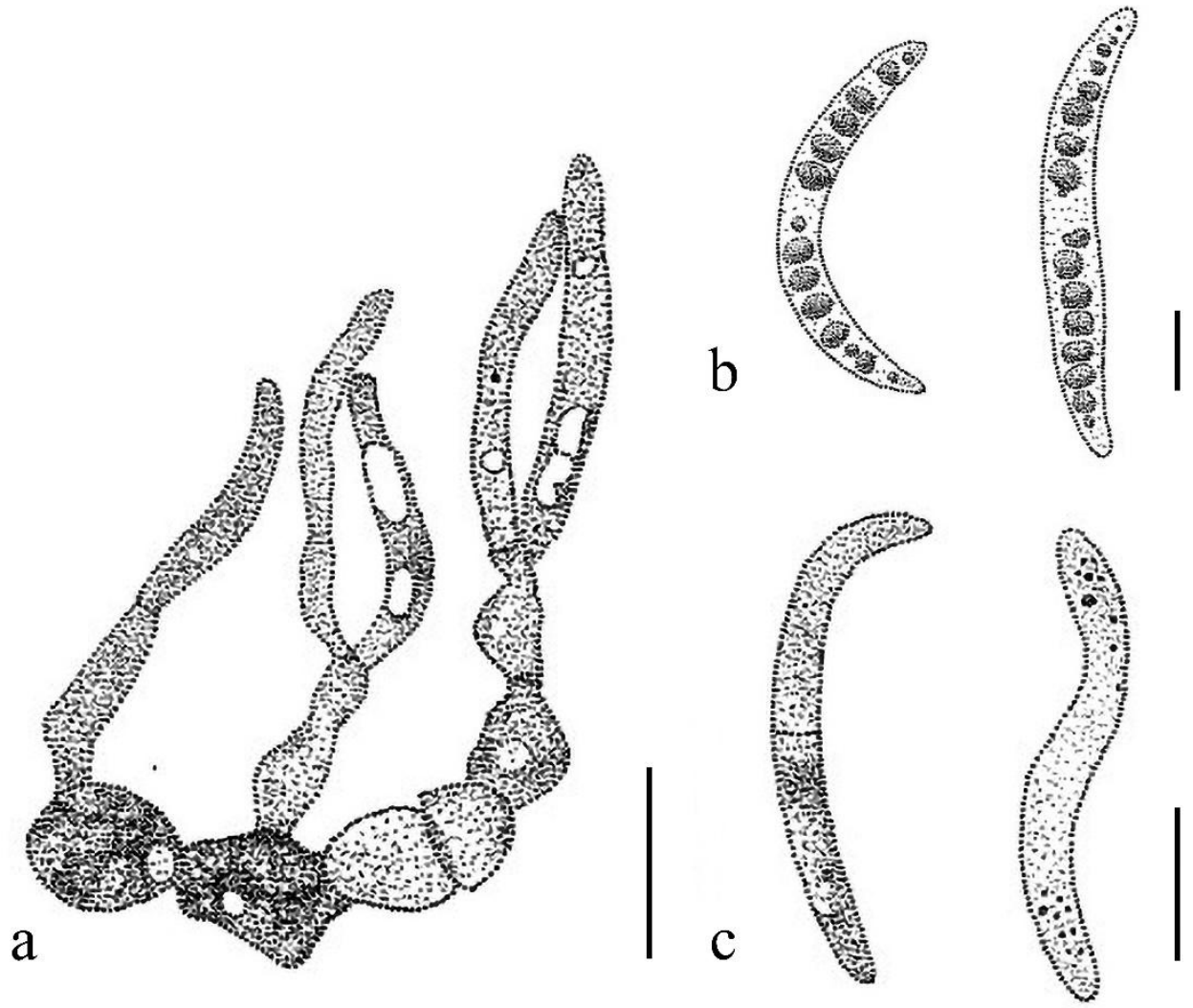


Figure 209 – Conidiogenesis and conidial morphology of *Delonicicolales* [redrawn from Voglmayr et al. (2019a)] a, c *Leptosillia slaptonensis*. b *L. muelleri*. Scale bars: a = 10 µm, b, c = 5 µm.

Justification of order and problems

The lack of phylogenetic support and unstable placement of certain taxa leads to taxonomic confusion, which is common in many families or higher ranks of *Sordariomycetes* (Chen et al. 2023b). Perera et al. (2017) established *Delonicicolales* as a distinct order from *Amphisphaeriales* and *Xylariales*.

Significance

Ecological and economic roles

Delonicicolales taxa have been reported from both living and dead substrates, and play important ecological roles as saprobes, endophytes and pathogens (Perera et al. 2017, Voglmayr et al. 2019a). They are ubiquitous with a cosmopolitan distribution. Further research is required to discover more *Delonicicolales* taxa in different life modes in order to have profound insights about their diversity and distribution.

Chemical diversity

Relevant studies are not available for the chemical diversity of *Delonicicolales* taxa.

Other relevant data and future recommendations

Future research that focuses on gathering additional samples of *Delonicicolales* taxa and generating comprehensive DNA sequence data is crucial for confirming their precise taxonomic classification. Such research is essential to ensure accurate identification and classification within the broader fungal taxonomy. Obtaining more specimens with the provision of DNA sequence data will lead to a more precise and reliable classification system for *Delonicicolales* and contribute to the overall knowledge of their diversity.

Diaporthales **Nannf., Nova Acta Regiae Societatis Scientiarum Upsaliensis, Ser. 4 8(no. 2): 53 (1932)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Diaporthales was introduced by Nannfeldt (1932). Eriksson & Winka (1997) accommodated *Diaporthales* within the subclass *Sordariomycetidae*. The order *Diaporthales* has a worldwide distribution. It contains saprobic, endophytic, and pathogenic taxa that are reported in a variety of hosts and substrates (Barr 1978, Castlebury et al. 2002, Rossman et al. 2007, Senanayake et al. 2017a, b, 2018, 2023, Fan et al. 2018, Jiang et al. 2020b, Hongsanan et al. 2023). The phytopathogenic species in *Diaporthales* cause many diseases in commercial crops and forest trees, which reduce their economic value. These diseases include: chestnut blight, caused by *Cryphonectria parasitica* (*Cryphonectriaceae*) (Gryzenhout et al. 2006a, Rigling & Prospero 2018, Gomdola et al. 2023); poplar and willow canker on *Populus* and *Salix*, caused by *Cytospora chrysosperma* (*Cytosporaceae*) (Fan et al. 2014, 2020b, Wang et al. 2015); and stem-end rot of *Citrus* fruits infected by *Diaporthe citri* (Huang et al. 2013). Medicinal plants host some endophytic species of *Diaporthales* which have been investigated for their antimicrobial activities, e.g., *Diaporthe* spp., which were isolated from the hosts *Copaifera langsdorffii* and *C. pubiflora* (de Carvalho et al. 2021). Antibacterial activity has been demonstrated for extracts from two unidentified *Diaporthe* spp. and *D. miriciae* (Carvalho et al. 2018, Tang et al. 2023). Some studies revealed the secondary metabolites and chemical compounds of *Diaporthaceae* and *Gnomoniaceae* (Chepkirui & Stadler 2017, Wu et al. 2019). As saprobes, they degrade wood. These include: *Apiosporopsis carpinea* on the overwinter leaves of *Carpinus betulus* (Senanayake et al. 2017a); *Pseudoplagiostoma dipterocarpicola* on the decaying wood of *Dipterocarpaceae* (Tang et al. 2022); species in *Gnomoniaceae* and *Sydowiellaceae* on woody bark (Senanayake et al. 2017a). Senanayake et al. (2017b) revised *Diaporthales* based on combined ITS, LSU, RPB2 and TEF1-a gene sequences, which revealed several new distinct clades, that were introduced as novel families.

History

Fries (1823) accommodated *Sphaeria* and its aligned taxa in the family *Sphaeriaceae*. Fuckel (1870) placed astromatic forms under subfamily *Ceratostomeae*, whereas stromatic forms were distributed among subfamilies *Dothideae*, *Melogrammeae*, *Melanconideae* and *Valseae*. *Sphaeriaceae* was divided into four subfamilies: *Bertieae* (*Linospora*, *Ceuthocarpon*), *Diaportheae* (*Diaporthe*, *Gnomonia*, *Hypospila*), *Melanconideae* (*Pseudovalsa*, *Melanconis*, *Hercospora*, *Cytospora*) and *Valseae* (*Valsa*) (Karsten 1873). Saccardo (1883c) used ascospore septation and pigmentation to classify diaporthoid taxa. Saccardo (1883c) divided *Sphaeriaceae* into several subfamilies, *viz*. having stromatic tissues in *Ceratostomeae*, *Clypeosphaerieae*, *Valseae*, *Melanconideae*, *Melogrammeae* and astromatic taxa in *Gnomonieae*. Lindau (1897a) resurrected *Sphaeriales* to accommodate *Clypeosphaeriaceae*, *Gnomoniaceae*, *Melanconidaceae* and *Melogrammataceae*, *Valsaceae* and some diaporthoid taxa placed in *Dothidiaceae* (*Dothideales*). von Höhnel (1917) included all diaporthoid taxa in *Diaporthaceae* and divided this family into two

subfamilies as Eu-Diaportheen for taxa with non-allantoid ascospores and Valseen for taxa with allantoid ascospores.

Nannfeldt (1932) introduced the order *Diaporthales* to accommodate Höhnel's Eu-Diaportheen and Valseen members, while excluding diatrypaceous taxa. Later, Luttrell (1951a) circumscribed *Diaporthales* with two families *Diaporthaceae* and *Melanosporaceae*. Chadefaud (1960) recognized three families in this order: *Diaporthaceae*, *Gnomoniaceae* and *Melanconidaceae*. Barr (1978) used the presence or absence of stromata, stromatic development and tissue types, the position of the ascomata and perithecial necks in the substrate and ascospore shape, to establish four families: *Gnomoniaceae*, *Melanconidaceae*, *Coryneaceae* and *Cytosporaceae*. Monod (1983) revised *Gnomoniaceae* and aligned taxa based on the characters of stromatic tissues, ascospores and asexual morphs. Eriksson (2001) recognized three families within *Diaporthales*: *Cytosporaceae*, *Melanconidaceae* and *Vialaeaceae*.

Castlebury et al. (2002) analyzed LSU sequence data of diaporthalean taxa for the first time. Consequently, they accepted *Cytosporaceae*, *Diaporthaceae*, *Gnomoniaceae* and *Melanconidaceae*. Castlebury et al. (2002) excluded *Vialaeaceae* from *Diaporthales* based on molecular data. Réblová et al. (2004) introduced *Togniniaceae* to *Diaporthales* based on SSU sequence data, and however Mostert et al. (2006) concluded that its placement was ambiguous based on LSU. *Togniniaceae* was excluded from *Diaporthales* and accommodated within *Togniniales* (Maharachchikumbura et al. 2015). Several families were introduced later: *Cryphonectriaceae* (Gryzenhout et al. 2006a), *Sydowiellaceae*, *Schizoparmaceae* (Rossman et al. 2007), *Harknessiaceae* (Crous et al. 2012c), *Pseudoplagiostomaceae* (Cheewangkoon et al. 2010), and *Macrohilaceae* (Crous et al. 2015b). Voglmayr & Jaklitsch (2014) resurrected *Stilbosporaceae*. Suetrong et al. (2015a) introduced *Tirisporellaceae* into *Diaporthales*, however Jones et al. (2015) later excluded this family from *Diaporthales*. Norphanphoun et al. (2016) introduced *Lamproconiaceae*. *Juglanconidaceae* was introduced by Voglmayr et al. (2017a). The families *Apiosporopsidaceae*, *Apoharknessiaceae*, *Asterosporiaceae*, *Auratiopycnidiellaceae*, *Erythrogloeaceae*, *Melanconiellaceae*, and *Prosopidicolaceae* were introduced based on molecular data and morphology (Senanayake et al. 2017b). Further additions to *Diaporthales* were: *Diaporthosporellaceae* (Yang et al. 2017b), *Diaporthostomataceae*, *Pseudomelanconidaceae*, *Synnemasporellaceae* (Fan et al. 2018) and *Tubakiaceae* (Braun et al. 2018). The most recently introduced families were: *Dwiroopaceae* (Xavier et al. 2019), *Foliocryphiaceae*, *Mastigosporellaceae* (Jiang et al. 2020b), *Neomelanconiellaceae* (Crous et al. 2018a) and *Pyrisporaceae* (Jiang et al. 2021b). Currently, there are 32 families accepted in *Diaporthales* (Hyde et al. 2024b).

General description

Species in *Diaporthales* form solitary or aggregated, immersed to erumpent, rarely superficial, orange, brown or black perithecial ascomata, with short or long necks, that are located in stromatic tissues or substrates, with a hamathecium lacking or with few paraphyses (Alexopoulus & Mims 1978, Barr 1978, Castlebury et al. 2002). Asci are unitunicate with a conspicuous refractive ring (Hawksworth et al. 1995, Rossman et al. 2007). Ascospores have diverse shapes, sizes and colors. The asexual morphs of *Diaporthales* are generally coelomycetous (Rossman et al. 2007), producing acervuli, pycnidial or synnematal conidiomata, with or without a well-developed stroma. Conidiogenesis is phialidic or rarely annellidic and conidia are usually unicellular or 1-septate (Rossman et al. 2007).

Sexual morph: *Pseudostromata* or *ascostromata* are well-developed, or poorly-developed, scattered, immersed or erumpent, solitary to aggregated, valsoid to diatrypoid, broadly elliptical, oval to circular from above, yellowish-orange, pale brown, dark brown to black, some species turning purple or umber in KOH. *Entostroma* normally limited to the region near the perithecial walls, prosenchymatous, pale-colored, and slightly differentiated from the surrounding bark tissue. *Ectostromatic* disc well- or poorly developed, subhyaline, yellowish-white, pale brown, rarely dark brown to black, pulvinate, flat or slightly convex, orbicular, circular or somewhat irregular, with or without black zone or a crust consisting of fungus tissue, sclerotioid, coriaceous. *Central column*

present or absent, if present beneath the disc more or less conical, comprising hyaline or pigmented hyphae mixed with a pigmented, cream, yellow, olive, brownish or grey, powdery amorphous substance. *Ascomata* are perithecial, scattered, solitary or aggregated, immersed to erumpent, rarely superficial, globose to subglobose, sometimes circinate, arranged in a valsoid to diatrypoid configuration or single, coriaceous, sometimes with plate-like ornamentation around the ostiole, black to brown, ostiolate, papillate. *Papilla* absent or if present, upright, long or short, one or more, central or eccentric, slanted to horizontal on host tissue, sometimes converging, with neck swollen at the tips, fuscous black to umber, ostiole with hyaline periphyses. *Peridium* is thin or thick, comprising outer, dark, thick-walled, cells of *textura angularis* and inner, mostly small, hyaline, thin-walled, flattened cells of *textura angularis*. *Hamathecium* aparaphysate or comprising few broad cellular, filiform to cylindrical, septate to aseptate, branched to unbranched, hyaline paraphyses and sometimes parenchymatous cells attached at the base and asci dissolving at maturity. *Asci* 2–32-spored, unitunicate, ellipsoid, cylindrical, fusiform, clavate, oblong-clavate, broadly fusoid to cylindrical-fusoid, short pedicellate, apex blunt, usually with distinct, J refractive ring. *Ascospores* overlapping uniseriate, biseriate, partially biseriate to fasciculately arranged, ovoid, ellipsoid, oblong, fusoid, cylindrical, filamentous or allantoid, aseptate to multi-septate, rarely distoseptate, constricted or not at the septa, hyaline, olivaceous to brown, smooth to sometimes ornamented walled, ends mostly rounded, rarely pointed, multi-guttulate, straight or curved, smooth- to sometimes ornamented walled to rarely ornamented, hyaline to dark brown. *Appendages* absent or present; if present, apical or basal, subulate, navicular or whip-shaped, smooth, hyaline. Asexual morph: coelomycetous. Stroma present or absent, immersed to superficial, opening by irregular rupture, globose, subglobose to irregular, solitary to gregarious, orange, brown to dark brown, sometimes loculate. *Conidiomata* are amphigenous, eustromatic, punctiform, pycnidial, synnematal or acervular, sometimes pyriform in section and divided into compartments by bending of peridium, subcuticular, peridermal or subepidermal, brown to black or orange with dark brown border, sometimes with a central, well-developed, pale brown, pseudoparenchymatous layer, becoming thinner or absent at the margin of the conidiomata, sometimes with pale colored, ectostromatic disc and central column or with radiate scutella. *Synnemata* are long, determinate, erumpent, pale brown, straight to curved, parallel. *Scutella* convex, membranous, brown, somewhat translucent, with a central hyaline or pale disc, giving rise to radiating hyphae, thick-walled cells radiating from a central point, rounded to pointed at the tips. *Conidiomatal wall* comprises pale to dark brown cells of *textura angularis* to *textura globulosa*. *Paraphyses* present or absent. If present, hyaline, cellular, subcylindrical, branched or not, with obtuse apex, septate, constricted at septa. *Conidiophores* reduced to conidiogenous cells or arising from the upper most cells of basal and parietal tissue or under the developing scutellum, densely aggregated or few, filiform, fusiform, cylindrical to globose, simple or branched, septate or aseptate, sometimes septate only at the base, smooth, hyaline or hyaline at the top, pale brown at the base, sometimes dimorphic. Alpha conidiophores tightly aggregated, subcylindrical, branched in mid region, consisting of few supporting cells, giving rise to septate, ampulliform, cylindrical to irregular conidiogenous cells or paraphyses, straight to sinuous, septate, cylindrical, hyaline to pale brown, branched only at the base, smooth, formed from the innermost layer cells of the conidiomatal wall, sometimes with terminal and lateral apex, with minute periclinal thickening and collarette. Beta conidiophores interspersed among alpha conidiophores, hyaline, subcylindrical, branched, septate. *Conidiogenous cells* lining the inner cavity of conidioma, enteroblastic to holoblastic, annellidic or phialidic, discrete or integrated, hyaline to olivaceous, smooth, lageniform, subcylindrical to ampulliform, with terminal truncate locus, simple or branched, proliferating several times percurrently near apex, with flaring collarettes or apex truncate, with minute periclinal thickening or terminal truncate locus. *Conidia* broadly ellipsoid, oval, obovoid, allantoid, fusoid to sigmoid, sinuate to slightly angular, hyaline to brown, hyaline when immature, becoming medium brown to dark brown at maturity, smooth-walled, guttulate, aseptate to euseptate or distoseptate, apex obtuse, base truncate with a visible scar or a flat protruding scar at the base. Sometimes the apical and basal cells are darker than other cells or with hyaline tip in apical cell, sometimes with or without a longitudinal

germ slit, sometimes with marginal frill or becoming golden brown at germination, with solitary, brown, wavy germ tubes (adapted from Senanayake et al. 2017b, 2018) (Figs. 210, 211).

Families included in *Diaporthales*

Apiosporopsidaceae Senan., Maharachch. & K.D. Hyde
Apoharknessiaceae Senan., Maharachch. & K.D. Hyde
Asterosporiaceae Senan., Maharachch. & K.D. Hyde
Aurantiopycnidiellaceae Senan., Maharachch. & K.D. Hyde
Coryneaceae Corda (=*Pseudovalsaceae* M.E. Barr)
Cryphonectriaceae Gryzenh. & M.J. Wingf.
Cytosporaceae Fr. (= *Valsaceae* Tul. & C. Tul.)
Diaporthaceae Höhn. ex Wehm.
Diaporthostomataceae X.L. Fan & C.M. Tian
Diaporthosporellaceae C.M. Tian & Q. Yang
Dwiroopaceae K.V. Xavier, A.N. KC, J.Z. Groenew., Vallad & Crous
Erythrogloeaceae Senan., Maharachch. & K.D. Hyde
Foliocryphiaceae C.M. Tian, N. Jiang & Crous
Gnomoniaceae G. Winter
Harknessiaceae Crous
Juglanconidaceae Voglmayr & Jaklitsch
Lamproconiaceae Norph., T.C. Wen & K.D. Hyde
Macrohilaceae Crous
Mastigosporellaceae C.M. Tian, N. Jiang & Crous
Melanconidaceae G. Winter
Melanconiellaceae Senan., Maharachch. & K.D. Hyde
Neomelanconiellaceae Crous
Phaeoappendicosporaceae Crous & M.J. Wingf.
Prosopidicolaceae Senan. & K.D. Hyde
Pseudomelanconidaceae C.M. Tian & X.L. Fan
Pseudoplagiostomataceae Cheew., M.J. Wingf. & Crous
Pyrisporaceae C.M. Tian & N. Jiang
Schizoparmaceae Rossman
Stilbosporaceae Link
Sydowiellaceae Lar.N. Vassiljeva
Synnemasporellaceae X.L. Fan & J.D.P. Bezerra
Tubakiaceae U. Braun, J.Z. Groenew. & Crous

Diaporthales family *incertae sedis*
Phaeochorellaceae Guterres, Galvão-Elias & Dianese

Diaporthales genera *incertae sedis*
Ceratoporthe Petr.
Cryptoleptosphaeria Petr.
Cryptonectriella (Höhn.) Weese
Cryptonectriopsis (Höhn.) Weese
Cytomelanconis Naumov
Diaporthella Petr.
Diatrypoidiella Manohar., Kunwar & D.K. Agarwa
Ditopellina J. Reid & C. Booth
Durispora K.D. Hyde
Exormatostoma Gray
Fremineavia Nieuwl.

Gibellia Sacc.
Gyrostroma Naumov
Hyalorostratum Raja & Shearer



Figure 210 – Morphology of asexual morph of taxa in *Diaporthales*. a–h, j, l, q Ascomata on substrate. i, k, m, n–p Cross section of ascomata. r–x Asci. y–z 20 Ascospores.

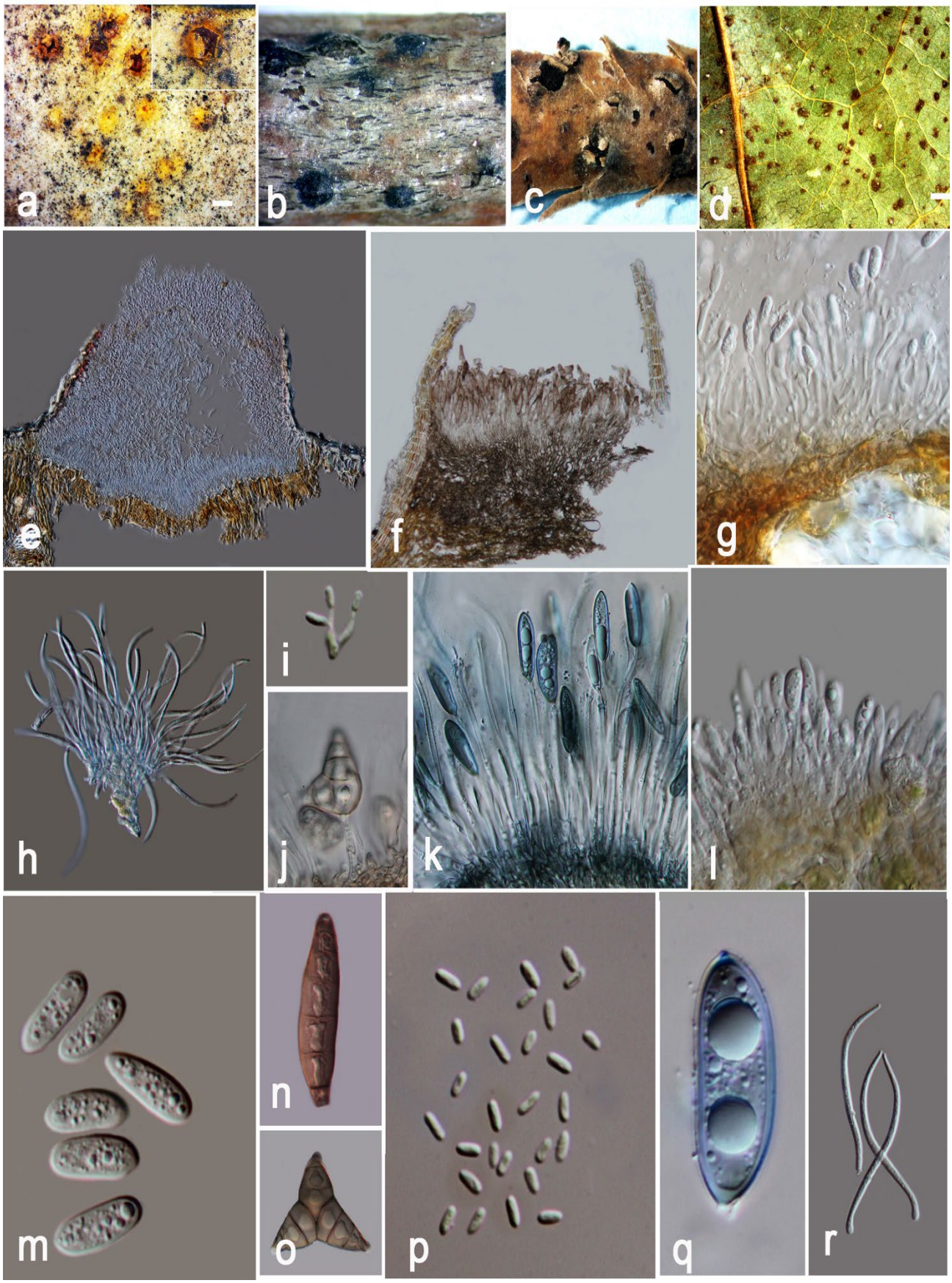


Figure 211 – Morphology of asexual morph of taxa in *Diaporthales*. a–d Conidiomata on substrate. e–g Cross section of conidiomata. h-l Conidiogenesis cells, conidiophores attached to conidia. m–r Conidia.

Hypophloeda K.D. Hyde & E.B.G. Jones
Hypospilina (Sacc) Traverso
Kapooria J. Reid & C. Booth
Keinstirschia J. Reid & C. Booth
Kensinjia J. Reid & C. Booth
Lollipopaia Inderb.
Macrodiaporthe Petr.
Melanamphora Lafl.
Phragmodiaporthe Wehm.
Phruensis Pinruan
Plagiophiale Petr.
Plagiostigme Syd.
Prostratus Sivan., W.H. Hsieh & Chi Y. Chen
Pseudocryptosporella J. Reid & C. Booth
Pseudothis Theiss. & Syd.
Pseudovalsella Höhn.
Savulescua Petr.
Skottsbergiella Petr.
Sphaerognomoniella Naumov & Kusnezowa
Stioclettia Dennis
Trematovalsa Jacobesco
Wehmeyera J. Reid & C. Booth

Evolution

Several research publications have suggested the combination of LSU, ITS, RPB2 and TEF1 sequence data provides the best resolution for *Diaporthales* (Senanayake et al. 2016, 2017a, b, 2018, 2023). However, in some cases, SSU, CALM, TUB2 and ACT have been used to resolve inter-generic taxonomic complications (Liu et al. 2015a, Maharachchikumbura et al. 2015, 2016, Hyde et al. 2016b, 2017b, 2020b, d, Li et al. 2016a, Norphanphoun et al. 2016, Tibpromma et al. 2017, Jayawardena et al. 2018, 2023, Wanasinghe et al. 2018, Phookamsak et al. 2019, Bundhun et al. 2021a, Manawasinghe et al. 2022, Norphanphoun et al. 2022). The divergence time for *Diaporthales* has been estimated as 180 MYA (Hyde et al. 2020b).

Justification of order and problems

Diaporthales is a well-established order, based on both morphology and molecular phylogeny. Two ambiguous families; *Togniniaceae* and *Tirisporellaceae*, have been excluded from *Diaporthales* and placed in their own orders (Jones et al. 2015, Maharachchikumbura et al. 2015).

Significance

Ecological and economic roles

Diaporthales is the type order of subclass *Diaporthomycetidae* (Senanayake et al. 2018). This is the most diverse order within this subclass. All members of *Diaporthales* are terrestrial, with their most common substrate being bark and twigs. Members of *Diaporthales* have a wide range of ecological habitats and modes of nutrition (Barr 1978). Generally, they are endophytes, phytopathogens or saprobes, although sometimes they occur as parasites or secondary invaders of injured plant tissues or those infected by other organisms (Castlebury et al. 2002, Rossman et al. 2007, Alvarez et al. 2016). There are no records of coprophilous, hypersaprobes or mycophylic species in *Diaporthales* (Senanayake et al. 2017b).

Phytopathogenic taxa are associated with fruits, leaves, stems and roots of a wide variety of hosts, including commercial crops. Some endophytes are opportunistic pathogens (Sieber 2007). Some severe pathogens annihilate large-scale plantations of economic crops, ornamental plants, timber monocultures and forests. *Cryphonectriaceae*, *Gnomoniaceae*, *Juglanconidaceae* and *Lamproconiaceae* usually comprise host-specific species. Udayanga et al. (2021) described some pathogenic taxa from strawberry plants. Multiple studies have revealed phytopathogenic species (Zhang & Blackwell 2001, Rossman et al. 2007, Yun & Rossman 2011, Crous et al. 2012b, c, Walker et al. 2012, Rossman et al. 2015a). Crop diseases caused by these fungi can lead to yield losses and reduce the quality of agricultural products, thereby negatively affecting the livelihoods of farmers and the food supply chain. Many species within *Diaporthales* are saprobes, which decompose dead organic matter. They play a vital role in nutrient cycling by breaking down complex organic compounds into simpler forms, making nutrients available for other organisms.

Some diaporthalean taxa can form symbiotic relationships with plants as endophytes. These fungi live within plant tissues without causing any harm to the host. They can help the plant by enhancing its resistance to disease, drought, and environmental stressors. Some species of *Diaporthales* have been investigated as potential biological control agents against invasive plant species (Billar de Almeida et al. 2020). If successfully implemented, this could provide an eco-friendly and cost-effective solution for the management of invasive plants. Fungi, including those within *Diaporthales*, are known to produce bioactive compounds with pharmaceutical potential. These compounds could support the development of new drugs and medical treatments (Nagarajan et al. 2021). Fungi, including *Diaporthales* species, play a significant role in biotechnological applications such as bioremediation. Additionally, some species inhabit soil and living animal and human tissues (Gryzenhout et al. 2006b, Senanayake et al. 2017b).

Chemical diversity

Fungal secondary metabolites include antibiotics, pheromones, pigments and toxins. Characteristic secondary metabolites have been used in the taxonomy of some fungal groups (Daranagama et al. 2018). If secondary metabolites are genetically inheritable traits, they may be phylogenetically and taxonomically informative (Zhang 2002). Therefore, *Diaporthales* have been extensively examined for secondary metabolites (Frisvad et al. 1998), including those produced by *Cryphonectriaceae*, *Cytosporaceae*, *Diaporthaceae* and *Gnomoniaceae* in culture media (Zhang 2002). However, the distribution of secondary metabolites between fungal species in *Diaporthales* and the role of metabolites is poorly understood. Hence, it is difficult to apply secondary metabolites to their systematics (Whalley & Edwards 1987, 1995, Rossman et al. 1999).

Other relevant data and future recommendations

Many families, genera and species were introduced to *Diaporthales* over the last decade. However, many taxonomic complications need to be resolved. Some earlier described taxa lack sequence data. This will affect their phylogenetic placement. The distribution of plant pathogenicity and chemical compounds produced by species in *Diaporthales* requires further research.

***Distoseptisporales* Z.L. Luo, K.D. Hyde & H.Y. Su, Fungal Diversity 99: 482 (2019)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

The monotypic order *Distoseptisporales* was introduced by Luo et al. (2019b) based on morphological characters and phylogenetic analysis. *Distoseptisporales* is placed in the class *Sordariomycetes*, subclass *Diaporthomycetidae* and comprises two families, namely *Aquapteridosporaceae* and *Distoseptisporaceae*, which can be separated based on multi-gene

phylogenetic analyses as well as morphological characters (Yang et al. 2015, Su et al. 2016a, Luo et al. 2019b, Hyde et al. 2021a).

History

During a north–south latitudinal survey of aquatic fungi on submerged wood and herbaceous material in streams and rivers in the Asian region, several hyphomycetous taxa were collected, including some sporidesmium-like taxa (Su et al. 2016a). Based on the morphological characters and phylogenetic evidence, a new family *Distoseptisporaceae,* with a single genus *Distoseptispora* was introduced (Su et al. 2016a). Luo et al. (2019b) raised *Distoseptisporaceae* to *Distoseptisporales* based on the morphology and phylogenetic analysis of combined LSU, SSU, RPB2 and TEF1 sequence data. *Aquapteridospora* is described by Yang et al. (2015) and placed as *Diaporthomycetidae* genera *incertae sedis*. Hyde et al. (2021a) introduced *Aquapteridosporaceae* to accommodate the single genus *Aquapteridospora* and placed this family in *Distoseptisporales*.

General description

Sexual morph: *Ascomata* solitary or gregarious, immersed to semi-immersed, perithecial, subglobose to ellipsoidal, ostiolate, with a short neck erumpent through host surface. *Ostiole* periphysate. *Ascomatal wall* coriaceous. *Paraphyses* sparse, persistent, septate, hyaline. *Asci* cylindrical, with a short pedicel, 8-spored. *Ascospores* overlapping, uniseriate, hyaline, smooth-walled, guttulate. Asexual morph: *Colonies* on the substrate effuse, hairy. *Mycelium* superficial or partly immersed, composed of branched, septate hyphae. *Conidiophores* macronematous, mononematous, cylindrical, single or in groups, unbranched, septate. *Conidiogenous cells* mono-polyblastic, terminal, integrated. *Conidia* vary significantly in their characteristics, especially in terms of shape and size (Fig. 212).

Families included in *Distoseptisporales*

Distoseptisporaceae K.D. Hyde & McKenzie
Aquapteridosporaceae K.D. Hyde & Hongsanan

Evolution

The divergence time for *Distoseptisporales* has been estimated as 102 MYA, which falls in the range of family status (Hyde et al. 2020d). Hyde et al. (2021a) re-estimated divergence time for *Distoseptisporales* as 158 MYA, which falls in the range of order status.

Justification of order and problems

Morphologically, *Distoseptisporaceae* share similar characters with *Sporidesmiaceae* (Su et al. 2016a), but the family can be distinguished from *Sporidesmiaceae* with strong molecular support (Su et al. 2016a, Luo et al. 2019b, Hyde et al. 2021a). Zhang et al. (2022b) reassessed both the generic and specific boundaries of *Distoseptispora* and provided a comprehensive summary of the species characteristics. Even though *Distoseptispora* species formed three distinct clades in phylogenetic analysis that received strong support, the morphological characters of these species only offer species-level differentiation and do not hold taxonomic significance for the broader categorization of *Distoseptispora* (Zhang et al. 2022b). This may need revision following further study based on more collections, especially if more sexual morphs of this genus are collected.

Significance

Ecological roles

Distoseptisporales are primarily saprobes found on woody substrates in freshwater habitats, and a few have been found in terrestrial habitats (, Yang et al. 2015, Su et al. 2016a, Luo et al. 2018, 2019b, Dong et al. 2020, Phukhamsakda et al. 2020, Shen et al. 2021). They play an important role in nutrient and carbon cycling, biological diversity and ecosystem functioning of freshwater ecosystems with their ability to decompose lignocellulose in woody litter, softening the wood and releasing nutrients (Hyde et al. 2016a).

Chemical diversity

No relevant studies are available for the chemical diversity of the members of *Distoseptisporales*.

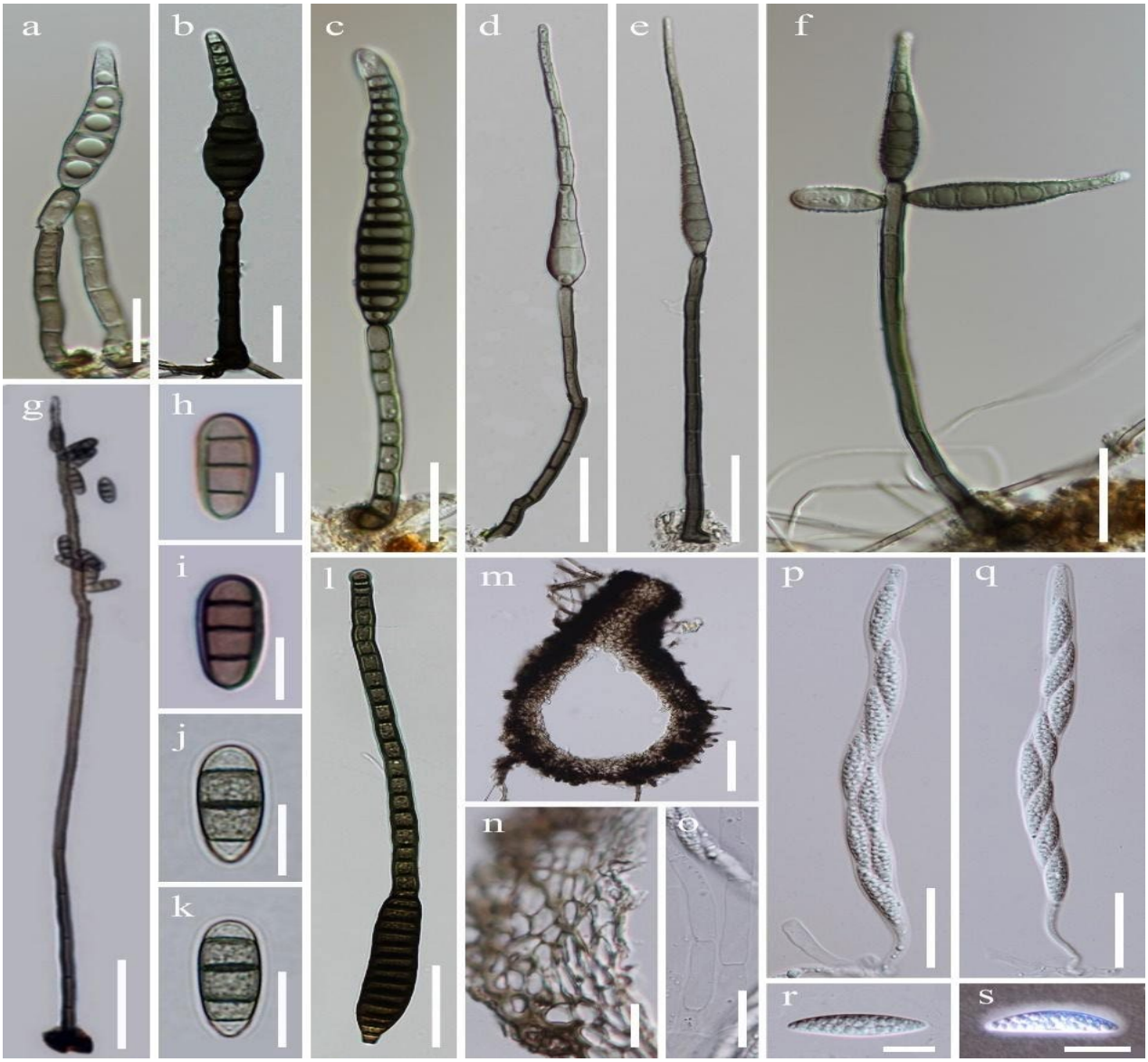


Figure 212 – Morphology of *Distoseptisporales.* a–f, l Asexual morph of *Distoseptispora* spp. g–k *Aquapteridospora* spp. m–s *Distoseptispora hyalina*. Scale bars: g = 60 µm, m = 50 µm, d, e, l = 35 µm, f, p, q = 30 µm, b, c = 25 µm, a = 15 µm, h–k, n, o, r, s = 10 µm.

Falcocladiales **R.H. Perera, Maharachch., Somrith., Suetrong & K.D. Hyde, Fungal Diversity 72: 218 (2015)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Hypocreomycetidae*

Introduction

Maharachchikumbura et al. (2015) introduced the monotypic order *Falcocladiales* to accommodate *Falcocladiaceae*. *Falcocladiaceae* comprises a single genus, *Falcocladium*.

History

Falcocladium was described by Crous et al. (1994) with *F. multivesiculatum* as the type species. Subsequently, six other species were added to the family (Crous et al. 1997, 2019e, 2021b, Somrithipol et al. 2007). *Falcocladiaceae* was introduced to accommodate *Falcocladium* by Jones et al. (2014) and maintained in the subclass *Hypocreomycetidae incertae sedis*. Based on multi-gene phylogenies, Maharachchikumbura et al. (2015) introduced the new order *Falcocladiales* to accommodate *Falcocladiaceae* within *Hypocreomycetidae*.

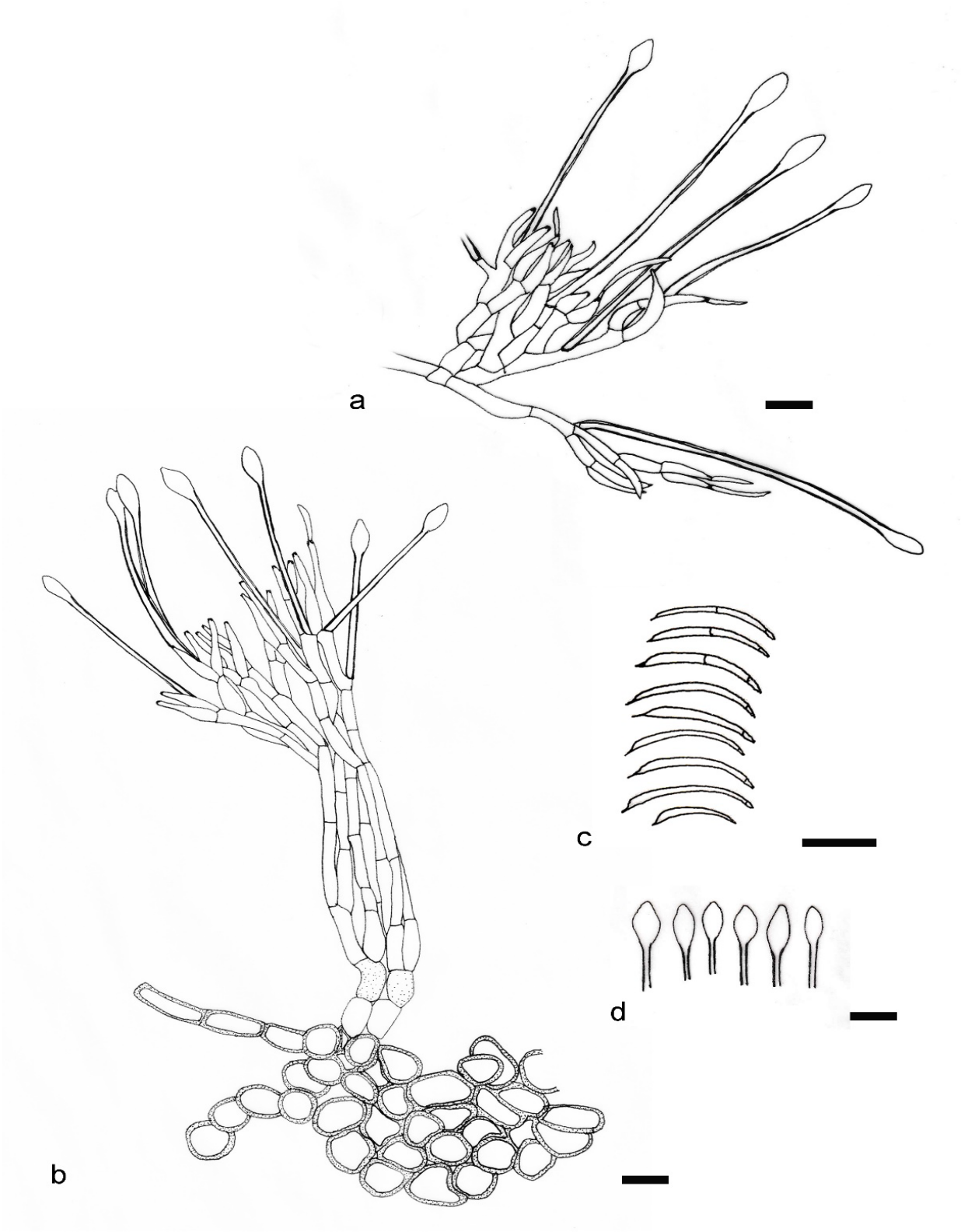


Figure 213 – Asexual morph of *Falcocladium multivesiculatum.* a Penicillate conidiophores arising from aerial mycelium. b Synnematal conidiomata arising from a stroma of chlamydospores. c Conidia. d Terminal vesicle of setae. Scale bars: a–d = 10 μm. (redrawn from Crous et al. 1994).

General description

Falcocladiales is characterized by hyphomycetous asexual morphs with sporodochial or synnematal or penicillate, setose conidiophores, ampulliform, phialidic, conidiogenous cells and 1-septate, hyaline, falcate conidia with short apical and basal appendages (Jones et al. 2014, Maharachchikumbura et al. 2016). Only the asexual morph is known for this order (Maharachchikumbura et al. 2015).

Sexual morph: Undetermined. Asexual morph: hyphomycetous, sporodochial or synnematal or penicillate, hyaline, intermixed with setae, arising from a stroma or microsclerotia or prostrate mycelium. *Setae* cylindrical, aseptate, hyaline, thick and smooth-walled, terminating in variedly-shaped vesicles. *Conidiophores* subcylindical, septate, hyaline, branched, forming up to three series of branches per conidioma (primary, secondary and tertiary). *Conidiogenous cells* phialidic, ampulliform, arranged in 2–6 whorls, with elongated necks and minute collarettes. *Conidia* 1-septate, falcate, guttulate, hyaline, smooth-walled, with short apical and basal appendages (adapted from Jones et al. 2014, Maharachchikumbura et al. 2016) (Fig. 213).

Families included in *Falcocladiales*

Falcocladiaceae Somrith., E.B.G. Jones & K.L. Pang

Evolution

The ordinal status of *Falcocladiales* was supported with divergence times of 171–241 MYA (Hongsanan et al. 2017a, Hyde et al. 2017a). Later, Hyde et al. (2020d) estimated as 192 MYA.

Significance

Ecological and economic roles

Species of *Falcocladium* are saprobic on leaf litter, including leaves of *Eucalyptus grandis* and *E. camaldulensis* in tropical and terrestrial habitats. However, there is no study reporting any pathogenicity in *Falcocladium*. Saprobic species decompose plant material, thereby playing an important role in nutrient and carbon cycling and ecosystem functioning (Hyde et al. 2016a).

Chemical diversity

No relevant studies are available for the chemical diversity of the members of *Falcocladiales*.

***Fuscosporellales* Jing Yang, Bhat & K.D. Hyde, Cryptogamie, Mycologie 37(4): 457 (2016)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Savoryellomycetidae*

Introduction

Based on analysis of combined LSU, SSU and RPB2 sequence data, the monotypic order *Fuscosporellales* in *Sordariomycetes* was introduced by Yang et al. (2016a) with *Fuscosporellaceae* as the type family. Six genera were assigned to *Fuscosporellaceae*, *viz*. *Bactrodesmiastrum*, *Fuscosporella* (as the type genus), *Mucispora*, *Parafuscosporella*, *Plagiascoma* and *Pseudoascotaiwania* (Yang et al. 2016a). At present, there are about 27 species of *Fuscosporellaceae*, they have a scattered distribution worldwide, i.e. Africa, Asia, Australia, Europe, North America, and South America (Hernández-Restrepo et al. 2015, Yang et al. 2016a, 2017a, 2023b, Boonyuen et al. 2021, Wijayawardene et al. 2021a).

History

Based on analyses of combined LSU, SSU and RPB2 data, Yang et al. (2016a) introduced *Fuscosporellaceae* as a novel family, and proposed the monotypic order *Fuscosporellales* to accommodate it. Taxonomic novelties originally introduced in *Fuscosporellaceae* were *Fuscosporella* (type genus), *Mucispora*, *Parafuscosporella* and *Pseudoascotaiwania* (Yang et al. 2016a).

Bactrodesmiastrum and *Plagiascoma* were originally placed in *Sordariomycetes* genera *incertae sedis* (Hernández-Restrepo et al. 2015, Réblová et al. 2016c). *Bactrodesmiastrum* was erected on the basis of *B. obscurum* (type species) (Holubová-Jechová 1984). The conidiophores and conidiogenous cells are dimorphic. The first morph is characterized by simple, semi-macronematous or macronematous, mononematous conidiophores, which are commonly reduced to conidiogenous cells arranged solitary or aggregated in groups, conidiogenous cells are brown to dark brown, smooth-walled, monoblastic, determinate, integrated, terminal, cylindrical to conical with truncate apex and swollen base. The second morph has conidiophores arising from pulvinate to subpustulate, scattered and black sporodochial conidiomata, simple or branched, pale brown to brown, smooth-walled conidiophores, and mostly moniliform, globose, subglobose or clavate, pale brown to brown conidiogenous cells. Conidia of *Bactrodesmiastrum* are solitary, acrogenous, septate, brown, clavate, obovoid, pyriform or navicular, obconic-truncate at the base (Holubová-Jechová 1984, Hernández-Restrepo et al. 2015). The monotypic genus *Plagiascoma* was established by Réblová et al. (2016c), with the type species *Plagiascoma frondosum*. This genus is characterized by perithecial, astromatic, immersed to semi-immersed ascomata with papilla or neck, periphysate ostioles, persistent and septate paraphyses, unitunicate, cylindrical to cylindrical-fusiform, stipitate asci with inamyloid apical rings, and fusiform, hyaline, transversely septate ascospores (Réblová et al. 2016c).

Multi-locus phylogenetic analysis of the LSU, SSU and RPB2 sequence data inferred *Bactrodesmiastrum* taxa clustered together with *Plagiascoma frondosum* and *Ascotaiwania persoonii*, and they nested in a strongly supported branch as *Sordariomycetes incertae sedis*, and were sister to *Pleurotheciales*, *Savoryellales*, and *Conioscyphales* (Hernández-Restrepo et al. 2015, Réblová et al. 2016c). Phylogenetic analyses (Réblová et al. 2016c, Yang et al. 2016a) indicated that *Ascotaiwania* is polyphyletic, and a distinct taxon *A. persoonii* clustered far away from the type species of *Ascotaiwania*. Thus, Yang et al. (2016a) established a new genus *Pseudoascotaiwania* to accommodate the new combination *P. persoonii* (synonymy: *Ascotaiwania persoonia*), and at the same time, a monotypic order *Fuscosporellales* and the family *Fuscosporellaceae* were established to accommodate *Bactrodesmiastrum*, *Plagiascoma* and *Pseudoascotaiwania* (Yang et al. 2016a).

General description

Species of *Fuscosporellales* are saprobic, and occur on twigs in terrestrial or aquatic habitats (Yang et al. 2016a). It has six genera, of which four (i.e. *Bactrodesmiastrum*, *Fuscosporella*, *Mucispora*, and *Parafuscosporella*) are asexual morphs, and *Plagiascoma* and *Pseudoascotaiwania* are sexual morphs. The sexual fruiting bodies produced by *Fuscosporellales* are typically perithecia, which are immersed to semi-immersed, dark brown to black, with papilla or necks (Fallah et al. 1999, Réblová et al. 2016c, Yang et al. 2016a). Ostioles are periphysate, some with beaked ostioles. The ascomatal walls consist of two or more layers, often fragile. The paraphyses of *Fuscosporellales* are abundant, septate, simple or branched. Asci are unitunicate, cylindrical, and apex with a inamyloid apical ring. Ascospores are cylindrical to fusoid, hyaline to light brown, and transversely septate (Yang et al. 2016a).

The asexual state of *Fuscosporellales* fungi is characterized by sporodochial conidiomata in blackish-brown to black. Their conidiophores are micronematous or macronematous, mononematous, simple or branched, hyaline or colorless to brown, and often reduced to conidiogenous cells arranged singly or aggregated in small groups. The conidiogenous cells are monoblastic, holoblastic, integrated, terminal, sometimes discrete, hyaline, pale brown, mid-brown to dark brown, obovate, globose to clavate. Their conidia are acrogenous, clavate, obovoid, pyriform,

obpyriform or navicular, septate, hyaline, dark brown to black (Hernández-Restrepo et al. 2015, Yang et al. 2016a).

Sexual morph: *Ascomata* perithecial, astromatic, immersed to semi-immersed, dark brown to black ascomata, with papillate or neck, periphysate ostiole, fragile ascomatal wall with several layers, septate paraphyses. *Asci* cylindrical to cylindricfusiform, stipitate, 8-spored, unitunicate asci, with inamyloid apical ring. *Ascospores* fusiform, uniseriate, hyaline or light brown, transversely septate ascospores. Asexual morph: sporodochial conidiomata. *Conidiophores* micronematous, macronematous, mononematous. *Conidiogenous cells* usually reduced to, blastic, hyaline, obovate to globose conidiogenous cells. *Conidia* brown, uniseptate, obovate to obpyriform conidia (adapted from Yang et al. 2016a) (Fig. 214).

Families included in *Fuscosporellales*

Fuscosporellaceae Jing Yang, Bhat & K.D. Hyde

Evolution

According to phylogenetic and molecular clock analyses of combined SSU, LSU, TEF1 and RPB2 data sets, the orders *Conioscyphales*, *Fuscosporellales*, *Pleurotheciales*, and *Savoryellales* cluster together as a robust branch in *Sordariomycetes*, with a stem age of 268 MYA (Hyde et al. 2017a). Divergence time estimates indicate that the monotypic order *Fuscosporellales* diverged from *Conioscyphales* + *Pleurotheciales* + *Savoryellales* at 218 MYA (Hongsanan et al. 2017a, Hyde et al. 2017a), and the divergence of *Fuscosporellaceae* crown group occurred at 126 (72–187) MYA (Dayarathne et al. 2019).

Justification of order and problems

In *Fuscosporellaceae* (*Fuscosporellales*), *Fuscosporella* and *Parafuscosporella* are phylogenetically distinct, but they have similar morphologies that are difficult to distinguish (Yang et al. 2016a). Therefore, the sporulating morphology on culture medium is recommended to complement the taxonomic characteristics of these two genera (Yang et al. 2016a). Since only sexual morphs have been reported in *Plagiascoma* and *Pseudoascotaiwania*, morphological comparisons with the other four asexual genera cannot be made. Moreover, the ecological and economic roles of *Fuscosporellales* taxa are limited. As a member of freshwater fungi, the future research work of *Fuscosporellales* should focus on the collection of samples and the excavation of morphological characteristics for taxonomy, and try to explore their application of secondary metabolites in ecological environments, especially in aquatic habitats.

Significance

Ecological and economic roles

Members of the order *Fuscosporellales* are saprobic on twigs in terrestrial or aquatic habitats (Yang et al. 2016a). Saprobes play an indispensable role in maintaining ecological balance and promoting ecosystem health. However, so far, the ecological and economic values of these taxa have not been deeply studied.

Chemical diversity

Relevant studies are not available for the chemical diversity of the members of *Fuscosporellales*.

Other relevant data and future recommendations

Further research is needed to explore the species diversity, ecology and distribution of *Fuscosporellales* taxa and closely related members. Taking this group as a case, it can discuss the differences between aquatic fungi and terrestrial fungi at the genome level by combining various methods, and understand their evolutionary process in adapting to different ecological environments. In the aspect of ecology, further research should also strengthen the understanding of this group in

influencing the dynamic balance of host plants in nature, and discuss its role in aquatic ecosystems and whether it has the function of monitoring and improving water quality.

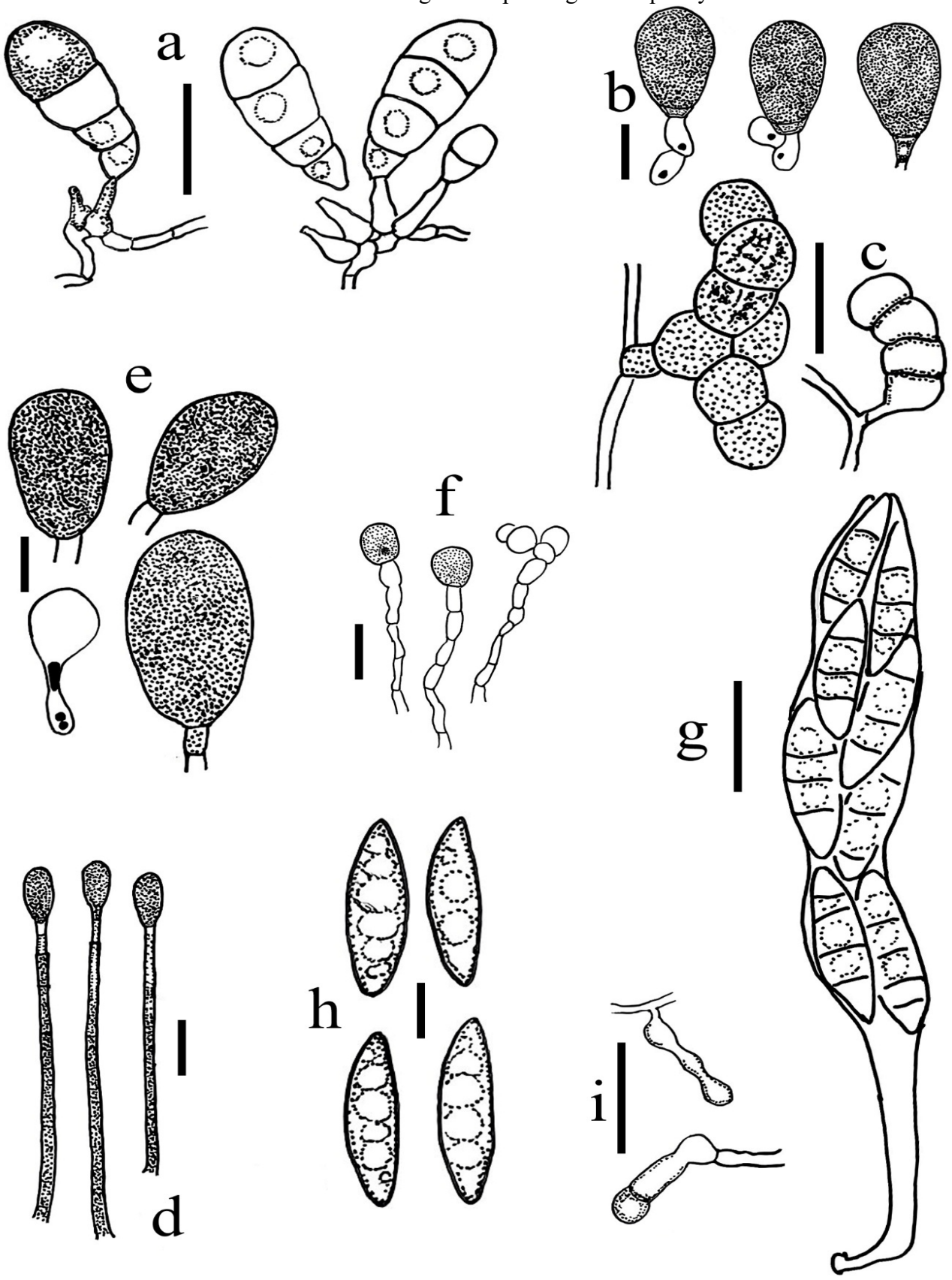


Figure 214 – Sexual and asexual morphs of *Fuscosporellales*. *Bactrodesmiastrum obscurum*: a Conidiophores, conidiogenous cells and conidia. *Fuscosporella pyriformis*: b Conidiogenous cells with conidia; c conidia and conidiogenous cells on PDA. *Mucispora phangngaensis*: d conidiophores

with conidia. *Parafuscosporella moniliformis*: e Conidiophores with conidia; f Conidia and conidiogenous cells on PDA; g–I *Plagiascoma frondosum*: g asci; h ascospores; i cells formed in vitro on vegetative hyphae on PCA. Scale bars: a, c, f, g, i = 20 μm, b, e, h = 10 μm, d = 50 μm.

Glomerellales **Chadef. ex Réblová, W. Gams & Seifert, Studies in Mycology 68: 170 (2011)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Hypocreomycetidae*

Introduction

Glomerellales was formally established by Réblová (2011), based on phylogenetic analyses of DNA sequence data. These analyses revealed a well-supported monophyletic lineage distinct from other orders within *Sordariomycetes*, providing strong evidence to establish it as a separate order. The production of either perithecia or acervuline fruiting bodies, unitunicate asci, one-celled ascospores, branched or verticillate conidiophores, and variable conidia characterises the members of this order. The hyphae are typically septate and can produce specialized structures like appressoria, while the colonies often show bright pigmentation ranging from orange, red, yellow, to pink (Cannon et al. 2012, O'Connell et al. 2012, Weir et al. 2012, Maharachchikumbura et al. 2016, Hyde et al. 2020d). Species in *Glomerellales* have a cosmopolitan distribution with various habitats such as soil, plant materials, crops and ornamental plants, grasslands and shrublands and plant residue (Okane et al. 2003, Réblová & Seifert 2008, Réblová et al. 2011, Jayawardena et al. 2021a, b). *Ascocodinaceae* consists of fungicolous taxa, adding more diversity in *Glomerellales* (Bao et al. 2023). *Glomerellales* comprises over 1000 species assigned to 20 genera and five families (Hyde et al. 2024b).

History

Early studies of *Glomerellales* go back to the 18th century. *Colletotrichum* was established by Corda (1831), while the sexual morph was established as *Glomerella* by Spaulding and von Schrenk (1917), with *Glomerella cingulata* as the type species. Initially, these taxa were placed in various other orders and genera based on their morphological similarities with other ascomycete groups (Cannon et al. 2012, Jayawardena et al. 2016, 2021a, b). Glomerella-like taxa were classified in the order *Phyllachorales* due to their perithecial and acervular fruiting bodies (Hawksworth et al. 1995). However, according to 'One name, One fungus' (1F=1N) adopted by the International Code of Nomenclature for algae, fungi and plants (McNeil et al. 2012), *Colletotrichum* took precedent over *Glomerella*, making it a synonym of *Colletotrichum* (Réblová et al. 2016b). The evolution of *Glomerellales* dates back to the early 1900s. The first discussion of the name *Glomerellales* came from Chadefaud (1960). He introduced the ordinal name *Glomerellales* and added *Glomerella*, *Phyllachora* and two other genera, but did not validly publish these introductions. The family name *Glomerellaceae* was published (invalid) by Locquin (1984b). Preliminary sequence-based studies and ontogenetic studies (Uecker 1994) confirmed that *Glomerella* and *Phyllachora* did not belong to the same fungal order. This is the first insight emerging from the taxonomic classification of *Glomerellales* using sequence-based studies. *Glomerellaceae* were included in the 9th edition of the Dictionary of the Fungi with an uncertain position within *Sordariomycetidae* (Kirk et al. 2001), and Zhang et al. (2006) validated the family *Glomerellaceae* with a Latin description and placed it within *Hypocreomycetidae*. Kirk et al. (2008b) placed this family in an uncertain position in the subclass *Hypocreomycetidae*.

Réblová et al. (2011) further explained the phylogenetic position of *Glomerellaceae* by analysing combined ITS, LSU, SSU and RPB2 sequence data. These analyses revealed a well-supported monophyletic lineage distinct from other orders within *Sordariomycetes* class and provided strong evidence for its establishment as a separate order. This was validly published with Latin diagnosis and two new families, *Australiascaceae* and *Reticulascaceae* which occupied a common clade with *Glomerellaceae* in *Glomerellales* (Réblová et al. 2011). *Glomerellaceae* is a monotypic family consisting of *Colletotrichum*, which comprises more than 300 species of different

life modes (Jayawardena et al. 2021a, b, Armand et al. 2023, Zhang et al. 2023d, Sui et al. 2024). The placement of *Glomerellales* was re-assessed by Maharachchikumbura et al. (2016). In that study, the authors conducted multi-locus phylogenetic analyses using nuclear ribosomal RNA genes (SSU, ITS, LSU) and protein-coding genes (RPB1, RPB2, TEF1) to investigate the evolutionary relationships and monophyly of the *Sordariomycetes* orders. Based on the phylogenetic evidence, the study formally established the order *Glomerellales* as a distinct lineage within *Sordariomycetes*. In that study, *Plectosphaerellaceae* which was introduced by Zare et al. (2007) was accepted in *Glomerellales*. Tibpromma et al. (2018) introduced *Malaysiascaceae* and Bao et al. (2023) introduced *Ascocodinaceae* to this order based on morphology and phylogeny. Chen et al. (2023b) identified *Glomerellales* to be the oldest order of *Hypocreomycetidae*, with a stem age of ~199 MYA.

General description

Glomerellales species produce both sexual and asexual reproductive structures. These structures allow a detailed understanding of their life cycle and their identification and classification. The sexual fruiting bodies produced by *Glomerellales* are typically perithecia, which are flask-shaped or globose structures with a prominent ostiole at the apex (Weir et al. 2012, Maharachchikumbura et al. 2016, Hyde et al. 2020d). The asci in *Glomerellales* are unitunicate, typically cylindrical or clavate. Ascospores produced in the asci are typically unicellular, hyaline, and have an ellipsoid to spindle-shaped appearance (Maharachchikumbura et al. 2016, Damm et al. 2019, Monkai et al. 2020, Bao et al. 2023). The asexual state of *Glomerellales* is produced on conidiophores, often surrounded by dark setae, which are often branched or verticillate (Tibpromma et al. 2018, Bao et al. 2023, Zhang et al. 2023d, e). The conidia can be unicellular or septate, and they exhibit a wide range of shapes (cylindrical, ovoid, oblong, fusiform, or irregular) and sizes (Jayawardena et al. 2016, 2021a, b, Maharachchikumbura et al. 2016, Tibpromma et al. 2018, Bao et al. 2023). Species of *Glomerellaceae* also produce asexual fruiting bodies known as acervuli, which are saucer-shaped or cushion-like conidiomata that emerge from the host tissue (Cannon et al. 2012, Jayawardena et al. 2021a, b). Some fungal genera in *Glomerellales* produce special infection structures called appressoria, which are melanized, dome-shaped structures that can penetrate host plant tissues during pathogenesis (adapted from O'Connell et al. 2012, Chethana et al. 2021a) (Figs. 215, 216).

Families included in *Glomerellales*

Ascocodinaceae D.F. Bao, K.D. Hyde & Z.L. Luo
Australiascaceae Réblová & W. Gams
Glomerellaceae Locq. ex Seifert & W. Gams
Malaysiascaceae Tibpromma & K.D. Hyde
Reticulascaceae Réblová & W. Gams

Glomerellales genus *incertae sedis*
Wenhsuisporus C.H. Kuo & Goh

Justification of order and problems

Glomerellales faces significant taxonomic issues and challenges. Hongsanan et al. (2017a) suggested that, based on the crown age, *Glomerellales* should be raised to a subclass. However, due to the instability of the placement, this was refrained. Several studies have highlighted the persistent problems with the taxonomy and species delimitation within this group, especially in *Glomerellaceae* (Jayawardena et al. 2021a, b, Aumentado et al. 2024). *Glomerellales* contains economically important genera i.e. *Colletotrichum*, and *Plectosphaerella* which exhibit high levels of morphological and genetic diversity (Konta et al. 2023, Peng et al. 2023), making accurate identification and differentiation of species challenging. *Colletotrichum* is considered as a cryptic genus which comprises 20 species complexes (Aumentado et al. 2024). There is ongoing debate and uncertainty about the exact species boundaries and delimitations within the order, especially in *Glomerellaceae*. New species continue to be described based on a single strain with minimal molecular data while classifying existing species into the order remains a challenge (Jayawardena et

al. 2021a, b). Solving the above problem requires a combination of extensive molecular phylogenetic analyses, a better understanding of cryptic diversity, and the development of more comprehensive taxonomic treatments for the order.

Significance

Ecological and economic roles

Glomerellales play a crucial role in the ecology of plant ecosystems, primarily as important plant pathogens that can have significant economic and agricultural impacts, but also potentially through their saprobic activities and contributions to overall microbial diversity. *Colletotrichum* and *Plectosphaerella* are common plant pathogens (Raimondo & Carlucci 2018, Jayawardena et al. 2021a, b). These pathogens can infect a wide range of agricultural and horticultural crops, including fruits, vegetables, cereals, and ornamental plants. *Glomerellales* species, particularly within the genus *Colletotrichum*, exhibit varying degrees of host-specificity, ranging from broad host range to highly specialized pathogens (Jayawardena et al. 2021a, b, Talhinhas & Baroncelli 2023).

Colletotrichum fructicola and *C. siamense* are known to have a broad host range, while *Colletotrichum kahawae* is only known from coffee berries in the African continent (Talhinhas & Baroncelli 2023). Another key factor in host-specificity is geographic variations. *Colletotrichum* species can exhibit different host preferences in different regions or ecological conditions. *Colletotrichum*, is responsible for significant crop losses in a variety of agricultural and horticultural crops worldwide. These plant pathogens can reduce yields, quality and profitability of farmers and have a direct impact on global food security, particularly in developing countries (Cannon et al. 2012, Jayawardena et al. 2021a, b). The development of fungicide resistance in certain *Glomerellales* species, such as *Colletotrichum* sp., complicates disease management and increases the cost of crop protection for farmers (Dowling et al. 2020). *Colletotrichum* spp. resistant to FRAC (QoI) fungicides have already been reported on multiple commercial temperate fruit crops in the United States including apple, strawberry, peach, and blueberry (Hu et al. 2015, Forcelini et al. 2018, Johnson 2018, Chechi et al. 2019). Species of *Glomerellales* can also be found as fungicolous (*Ascocodinaea*) saprobes (*Wenhsuisporus*) and endophytes, showing different ecological roles in nature.

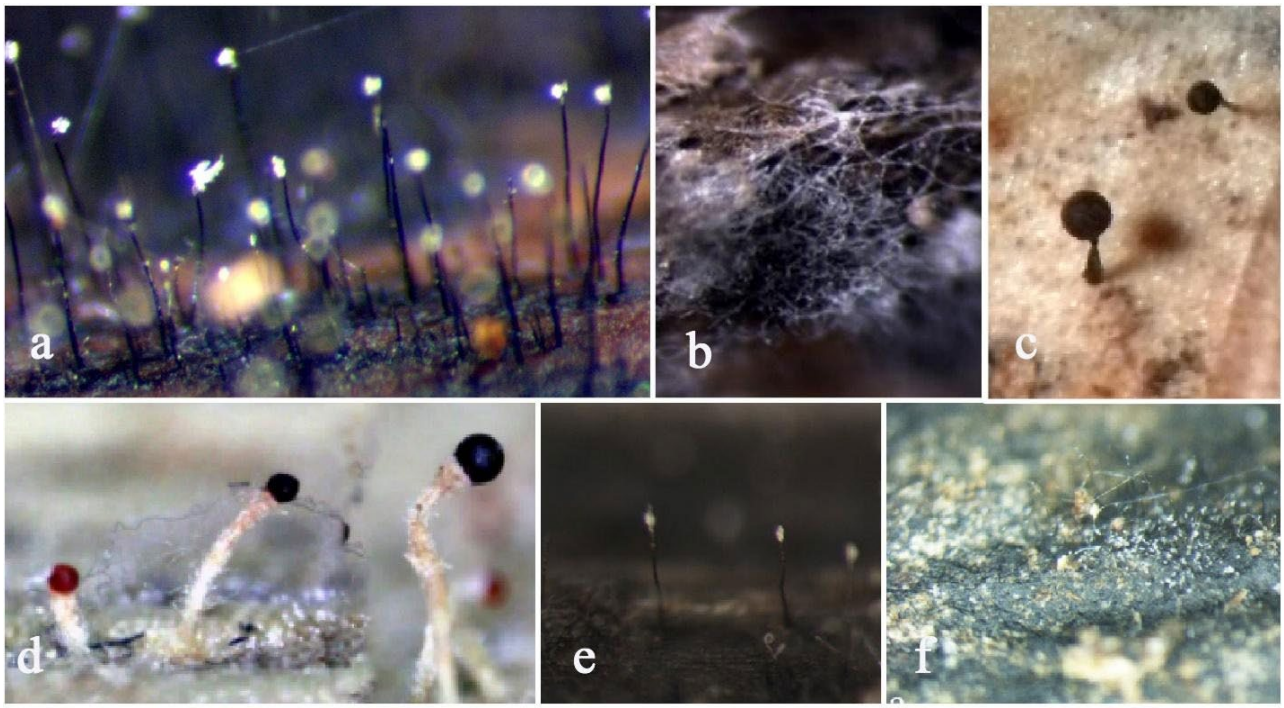


Figure 215 – Colony on substrate a *Australiascaceae* sp. b *Glomerellaceae* sp. c, d *Plectosphaerellaceae* sp. e, f *Reticulascaceae* sp.

Chemical diversity

Colletotrichum, are known to have a diverse range of secondary metabolites and chemical compounds, understanding their secondary metabolite production can provide insights into their pathogenicity, competition, and interactions with their host plants. *Colletotrichum* produces secondary metabolites such as colletotrichins, colletopyrones, colletotrins, melanin and colletodiol (Andi et al. 2001, Alkan et al. 2013). Some of the above secondary metabolites (Colletotrichin, Colletotrins A &B) exhibited potential phytotoxic effects such as inhibiting seed germination, root growth, and shoot development. Some species produce chemical compounds, such as Sterols (3b-Hydroxy-ergosta-5-ene, 3b-Ergosta-4,6,8(14),22-tetraen-3-one), Pyrones (Monocerin, Colletopyrone), Phenolics compound (Colletotrialide, 4-Methoxyphenol) and fatty acids (Oleic acid, Monopalmitolein) (Zhang et al. 2009a, Tianpanich et al. 2011, Artanti et al. 2014, Hsiao et al. 2016, Masi et al. 2017).

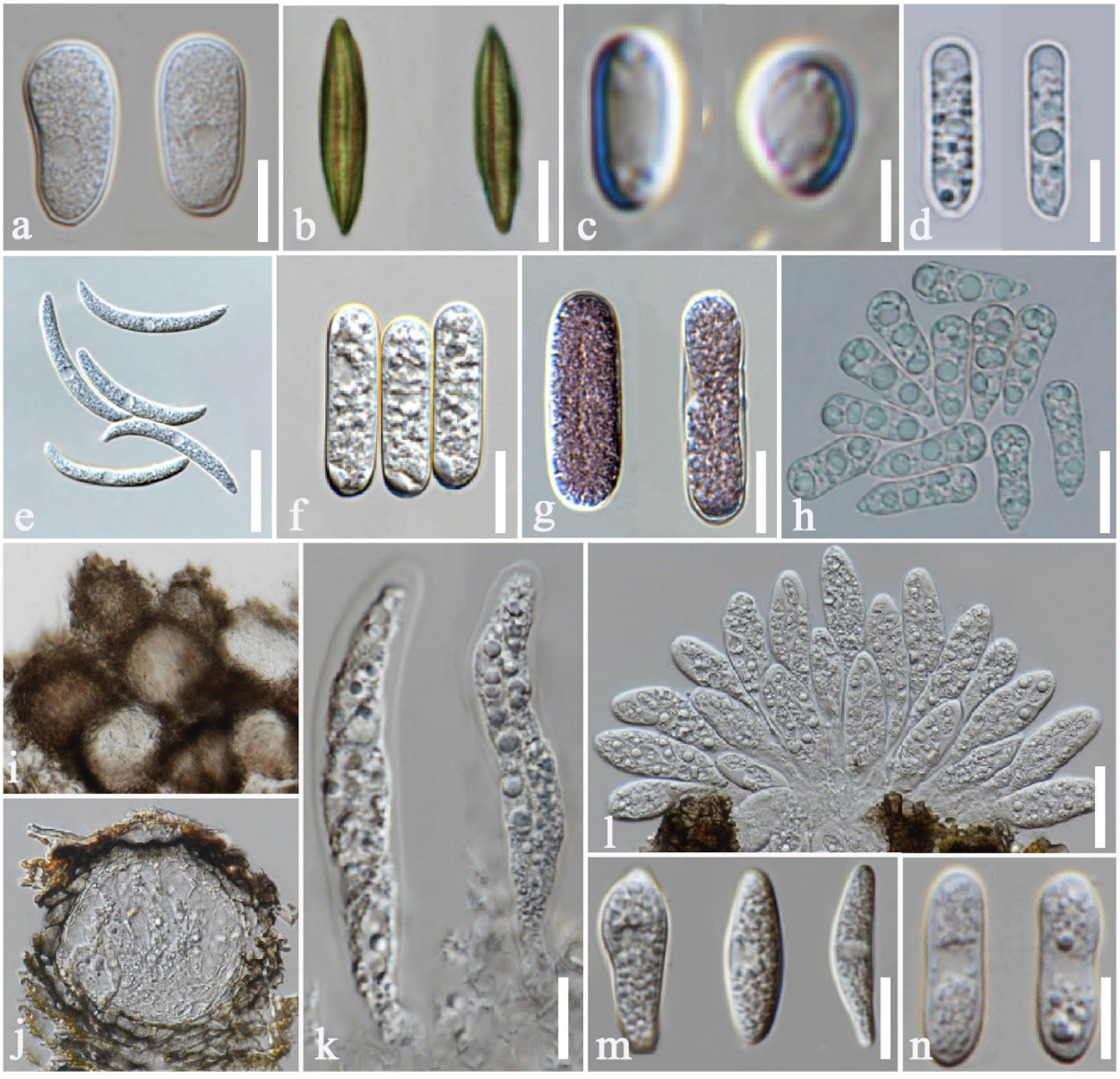


Figure 216 – Sexual and asexual morphs of *Glomerellales*. a *Australiascaceae* sp. b, c *Plectosphaerellaceae* spp. d, h *Reticulascaceae* spp. e–g, i–n *Glomerellaceae* spp. i Cross section through an ascomata of *Colletotrichum fructicola*. j Cross section through an ascoma of *Colletotrichum endophyticum*. k Ascospores of *C. fructicola*. l Ascospores of *C. endophyticum.* m Ascospore of *C. fructicola.* n Ascospore of *C. endophyticum.* Scale bars: i = 50 µm, a, c, d, f, k, m = 10 µm, b, n = 5 µm, e, g, h = 20 µm.

Several species also produce metabolites with biological activity such as anti-fungus activity, anti-bacterial activity, and cytotoxic activity. The metabolite 2-phenylethyl-1H-indol-3-yl acetate, 4-hydroxybenzamide, 2-(2-hydroxyphenyl) acetic acid has an antifungal effect on *Cladosporium cladosporioides* and *Cladosporium sphaerospermum* (Chapla et al. 2014). The metabolite 3b-Ergosta-5,7,9,22-tetraene has an antimicrobial effect on *E. coli* and *Bacillus megaterium* (bacteria), Colletotric acid has an antimicrobial effect on *Bacillus subtilis*, *Staphylococcus aureus* and *Sarcina lutea* (Zou et al. 2000, Zhang et al. 2009a). The metabolite alternariol 5-O-methyl ether showed cytotoxic activity on U2OS cells (Wang et al. 2014a), and demethylated monocerol showed cytotoxic activity on HepG2 cells (Tianpanich et al. 2011).

Other relevant data and future recommendations

Several recent studies have highlighted the ongoing difficulties in accurately delineating the species within this group. The genus *Colletotrichum*, an important representative of the *Glomerellales*, contains numerous species complexes that are morphologically closely related but are distinct species that are difficult to distinguish (Damm et al. 2019). The members have an enormous capacity to produce secondary metabolites, hence, further research is needed to uncover the full spectrum of bioactive compounds they can produce. The One Strain Many Compounds approach could lead to the discovery of new secondary metabolites with interesting biological activities.

Some of the phytotoxic secondary metabolites produced by *Glomerellales*, such as colletotrichins and liamocins, may have potential applications in the development of biopesticides or bioherbicides. Further research is needed to evaluate the feasibility and effectiveness of these compounds in controlling weeds and plant pathogens. In addition to their phytotoxic effects, the secondary metabolites of *Glomerellales* may possess antimicrobial, antifungal, and therapeutic properties that could be exploited for various applications, such as against a variety of microorganisms and for drug development.

***Hypocreales* Lindau, Die Natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten 1 (1): 343 (1897)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Hypocreomycetidae*

Introduction

Hypocreales, a prominent order in *Hypocreomycetidae*, is widely distributed in tropical and subtropical regions (Rogerson 1970, Põldmaa 2011, Huang et al. 2021a, Wei et al. 2023). This order contains 17 families, 309 genera, and over 4000 species. It is characterized by brightly colored, fleshy ascomata, 8-spored asci and various shapes of hyaline to light brown ascospores, and simple hypomycetous asexual morph (Kirk et al. 2008a, Maharachchikumbura et al. 2016, Wei et al. 2023). Secondary metabolites of some species were extracted for more extensive studies, like secondary metabolites of some entomogenous fungi can act as virulence factors and play multiple roles in insect pathogenicity by regulating various interactions between the producing fungi and their insect hosts (Zhang et al. 2020a). *Hypocreales* represents a fungal order of substantial ecological, economic, and applied significance. Understanding their taxonomy and conducting further research will enhance our ability to exploit the natural and biotechnological potential of these fungi.

History

The origins of *Hypocreales* can be traced back to the 18th century (Saccardo 1883a). Persoon (1794b) introduced the green powdery *Trichoderma viride*. Fries (1825) established the genus *Hypocrea*, typified by *H. rufa*, which features superficial, membranous, irregular ascomata. Later, De Notaris (1844) recognized it as the generic type of *Hypocreaceae*. However, Tulasne & Tulasne (1865) demonstrated that *T. viride* and *H. rufa* represent different stages of the same species, a finding further corroborated by Brefeld (1891). They showed that the conidial stage of *T. viride* could be

produced by inoculating *H. rufa* ascospores into pure culture. Based on nomenclature, *Hypocrea* is considered a synonym of *Trichoderma* (Rossman et al. 2013). Numerous hypocrealean fungi have been reported, primarily classified within the *Hypocreaceae* or *Clavicipitaceae* due to their fleshy ascomata (Miller 1949, Rogerson 1970). Engler & Prantl (1897) were the first to group six families (*Clavicipitaceae*, *Hypocreaceae*, *Hypomycetaceae*, *Hyponectriaceae*, *Melanosporaceae*, *Nectriaceae*), characterized by non-black, soft ascomata, thereby establishing the order *Hypocreales*. Rogerson (1970) provided a key to 104 genera within *Hypocreales*. This order comprises many pathogenic fungal strains found in a variety of ecosystems (Rossman 1996, Hjeljord et al. 1998, Rossman et al. 2013). In the early 21st century, the classification of *Hypocreales* was a subject of intense debate (Sung et al. 2007, Summerbell et al. 2011, Lombard et al. 2015). Rehner & Samuels (1995) conducted an LSU analysis of 40 species in *Hypocreales*, proposing a comprehensive classification that integrated morphological and phylogenetic analyses, including sexual and asexual morphs. Phylogenetic studies clarified that *Melanosporaceae* and *Hyponectriaceae* belong to *Melanosporales* and *Xylariales*, respectively (Hibbett et al. 2007). A modified classification of *Hypomycetaceae* to genus *Hypomyces*, and accommodated it in *Hypocreaceae* (Hibbett et al. 2007). Rossman (2000) noted that in some taxa, the asexual morph is nondescript, and both sexual and asexual morphs are often atypical for their respective genera, limiting the correlation between the sexual and asexual morphs and biological characteristics in some *Hypocreales* members. Seven families (*Bionectriaceae*, *Clavicipitaceae*, *Cordycipitaceae*, *Hypocreaceae*, *Nectriaceae*, *Niessliaceae*, *Ophiocordycipitaceae*) have been confirmed as belonging to *Hypocreales* through multi-gene analysis of a few representative strains (Schoch et al. 2007). The genera *Myrothecium*, *Peethambara* and *Stachybotrys* were classified as a monophyletic lineage in *Hypocreales* based on phylogenetic studies (Summerbell et al. 2011), leading Crous et al. (2014c) to establish the family *Stachybotriaceae* to encompass these three genera. Crous et al. (2015c) introduced *Flammocladiellaceae*, including the monotypic genus *Flammocladiella*, which is closely related to *Clavicipitaceae* and *Ophiocordycipitaceae* based on LSU analysis, despite lacking shared characteristics or ecologies. The synnematous genera *Psychronectria*, *Septofusidium* and *Tilachlidium* were placed in *Tilachlidiaceae* following multi-gene analysis (Lombard et al. 2015, Pawłowska et al. 2017). The fungicolous families *Calcarisporiaceae* and *Pseudodiploösporaceae* are recognized as monophyletic lineages in *Hypocreales*, each containing only one genus (Sun et al. 2017a, 2023). Zhuang & Zeng (2017) documented a hypocrealean fungi found on cocoons and established *Cocoonihabitaceae*. Crous et al. (2018a, b) introduced *Myrotheciomycetaceae*, which includes *Emericellopsis*, *Leucosphaerina*, *Myrotheciomyces*, and *Trichothecium*, while also establishing *Sarocladiacea*e for *Parasarocladium* and *Sarocladiumm* based on phylogenetic analysis. Xiao et al. (2023b) introduced the entomogenous family *Polycephalomycetaceae*. Darmostuk et al. (2024) described tropical lichen-inhabiting fungi and established *Paranectriaceae* through phylogenetic analysis. With the recent introduction of several new families, the order accommodates 29 families that are listed below.

General description

Initially, fungi of *Hypocreales* were identified as having fleshy ascomata, which led to confusion with certain members of *Xylariales* and *Melanosporales* (Hibbett et al. 2007). With the advancement of molecular analysis, the taxonomic units of various groups in *Hypocreales* were gradually clarified (Schoch et al. 2007, Summerbell et al. 2011, Xiao et al. 2023b, Wei et al. 2023, Darmostuk et al. 2024). Members of this order typically have brightly colored, membranaceous ascomata, often accompanied by appendages. They usually have 8-spored asci, produce hyaline or light brown ascospores and generally exhibit simple asexual morphs, such as Hyphomycetous *Lecanicillium* (Huang et al. 2018) and Coelomycetous *Eucasphaeria* (Crous et al. 2007).

Sexual morph: *Stroma* branched or unbranched. *Ascomata* perithecial or cleistothecial, solitary or gregarious, semi-immersed to superficial, sometimes sitting on a subiculum, globose to subglobose, yellow, orange, brown or black, membranaceous, tuberculate or smooth, glabrous or with setae or irregular appendages. *Peridium* composed of membranaceous, yellow or brown to

hyaline cells of *textura angularis* to *textura prismatica*. *Paraphyses* absent or filiform or cylindrical, septate, branched or unbranched. *Asci* 8-spored, unitunicate, cylindrical to clavate. *Ascospores* uni- or bi-seriate or overlapping, hyaline to brown, filiform or ellipsoidal, sometimes disarticulating into part-spores. Asexual morph: Hyphomycetous. *Mycelium* hyaline to light brown, superficial, effused. *Conidiophores* mononematous, macronematous, hyaline, unbranched, aseptate. *Conidia* oval to ellipsoidal, usually aseptate, hyaline, smooth-walled, guttulate. Coelomycetous. *Conidiomata* globose to subglobose, dark brown to black. *Conidiophores* hyaline, cylindrical to subcylindrical. *Conidia* oval to ellipsoidal, hyaline (adapted from Crous et al. 2007, Schoch et al. 2007, Huang et al. 2021a, Wei et al. 2023, Xiao et al. 2023b) (Figs. 217, 218, 219).

Families included in *Hypocreales*

Acremoniopsidaceae M. Li, M. Raza & L. Cai
Albomorchellophilaceae F.M. Yu, K.D. Hyde & Q. Zhao
Bionectriaceae Samuels & Rossman (= *Spicariaceae* Nann.)
Calcarisporiaceae Jing Z. Sun, X.Z. Liu & K.D. Hyde
Chrysonectriaceae L.W. Hou, L. Cai & Crous
Clavicipitaceae (Lindau) Earle ex Rogerson
Cocoonihabitaceae W.Y. Zhuang & Z.Q. Zeng
Cordycipitaceae Kreisel ex G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora
Cylindriaceae Crous & L. Lombard
Flammocladiellaceae Crous, L. Lombard & R.K. Schumach
Hypocreaceae De Not. (= *Trichodermataceae* Fr.)
Ijuhyaceae R.H. Perera, E.B.G. Jones, Maharachch. & K.D. Hyde
Myrotheciomycetaceae Crous
Nectriaceae Tul. & C. Tul. (= *Tubercul*ariaceae Fr.)
Neoacremoniaceae L.W. Hou, L. Cai & Crous
Niessliaceae Kirschst.
Nothoacremoniaceae L.W. Hou, L. Cai & Crous
Ophiocordycipitaceae G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora
Polycephalomycetaceae Y.P. Xiao, Y.B. Wang, T.C. Wen, H. Yu & K.D. Hyde
Pseudodiploosporaceae Jing Z. Sun, X.Z. Liu & H.W. Liu (= *Zelopaecilomyces* Jing Z. Sun, X.Z. Liu & H.W. Liu)
Pseudoniessliaceae L.W. Hou, L. Cai & Crous
Sarocladiaceae L. Lombard
Sedecimiellaceae M. Li, M. Raza & L. Cai
Stachybotryaceae L. Lombard & Crous
Stromatonectriaceae R.H. Perera, E.B.G. Jones, Maharachch. & K.D. Hyde
Tilachlidiaceae Lombard & Crous
Valsonectriaceae L.W. Hou, L. Cai & Crous
Xenoacrodontiaceae Crous
Xanthonectriaceae R.H. Perera, E.B.G. Jones, Maharachch. & K.D. Hyde

Hypocreales genera *incertae sedis*
Berkelella (Sacc.) Sacc.
Cephalosporiopsis Peyronel
Chondronectria Etayo, Flakus & Kukwa
Chlorocillium W. Gams & Zare
Cylindronectria Etayo
Endoantria Greiff & Döbbeler
Floraea Y.P. Tan, Vitelli & Steinrucken
Gynonectria Döbbeler
Haptospora G.L. Barron

Husseyia Y.P. Tan, Bishop-Hurley, R.G. Shivas & Marney
Illosporiopsis D. Hawksw.
Illosporium Mart.
Leptobarya Etayo
Lichenopenicillus Etayo
Metadothella Henn.
Munkia Speg.
Neomunkia Petr.
Neoniesslia Crous & Osieck
Paracosmospora Crous & Boers



Figure 217 – Thallus morphology of *Hypocreales*. a *Tolypocladium* sp. b *Metacordyceps kusanagiensis*. c *Keithomyces neogunnii*. d–e *Polycephalomyces* sp. f *Beauveria pseudobassiana*. g–h *Ophiocordyceps* sp. i *Ophiocordyceps nutans*. j *Paraisaria* sp. k *Samsoniella* sp. l *Stilbocrea* sp. m *Hypomyces armeniacus*. n *Metarhizium* sp. o *Valetoniella crucipila*. p *Pseudorhynchia polyrrhyncha*. q *Circinoniesslia nectriae*. r *Malmeomyces pulchellus*.

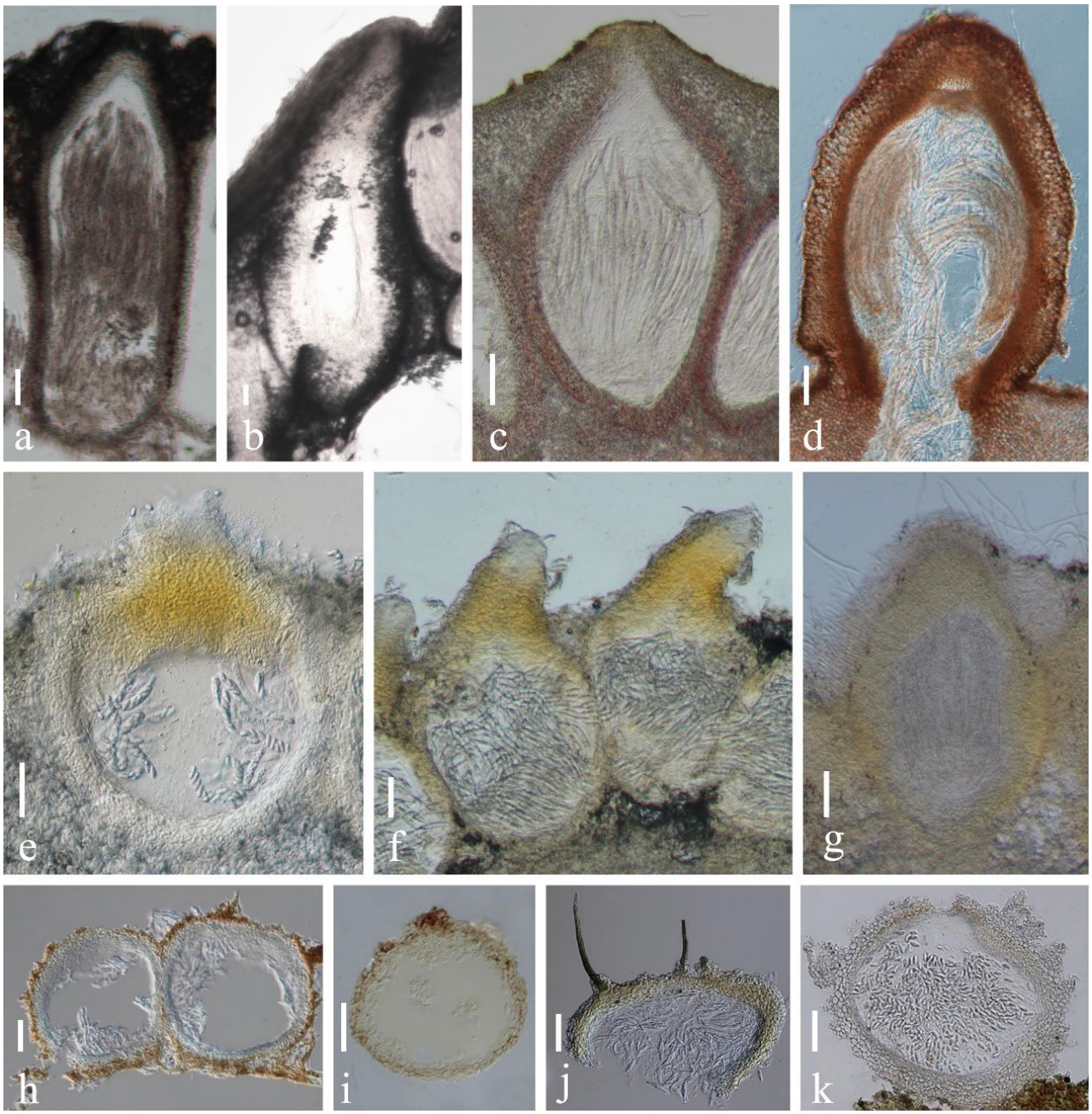


Figure 218 – Ascomata morphology of *Hypocreales*. a *Keithomyces neogunnii*. b–c *Ophiocordyceps* sp. d *Ophiocordyceps liangii*. e *Stilbocrea* sp. f *Hypomyces armeniacus*. g *Beauveria pseudobassiana*. h *Pseudorhynchia polyrrhyncha*. i *Valetoniella crucipila*. j *Malmeomyces pulchellus*. k *Circinoniesslia nectriae*. Scale bars: a–k = 50 µm.

Peloronectria Möller
Pseudomeliola Speg.
Rodentomyces Doveri, Pecchia, Sarrocco & Vannacci
Roselliniella Vain.
Saksenamyces A.N. Rai & P.N. Singh
Ticonectria Döbbeler
Tilakidium Vaidya, C.D. Naik & Rathod
Trichonectria Kirschst.

Evolution

The overall evolution of *Hypocreales* originated from the plant pathogenic fungal group *Nectriaceae*, and now is split into *Cordycipitaceae*, *Hypocreaceae*, and *Ophiocordycipitaceae*, forming the animal pathogenic fungi of the *Cordyceps* and ergot families (Lindau 1987). *Clavicipitaceae* is a plant symbiotic family and, was the last to differentiate, accompanied by a host change trend of "plant insect/fungus plant"(Zhang et al. 2015b). During the process of evolution, significant gene loss occurred in the genome, and the range of fungal parasitism continued to decrease (Zeng et al. 2019). Host specialization also became increasingly prominent, resulting in fungi with similar lifestyles in the *Hypocreales* exhibiting similar mechanisms of action to their hosts, even when differentiated into different branches.

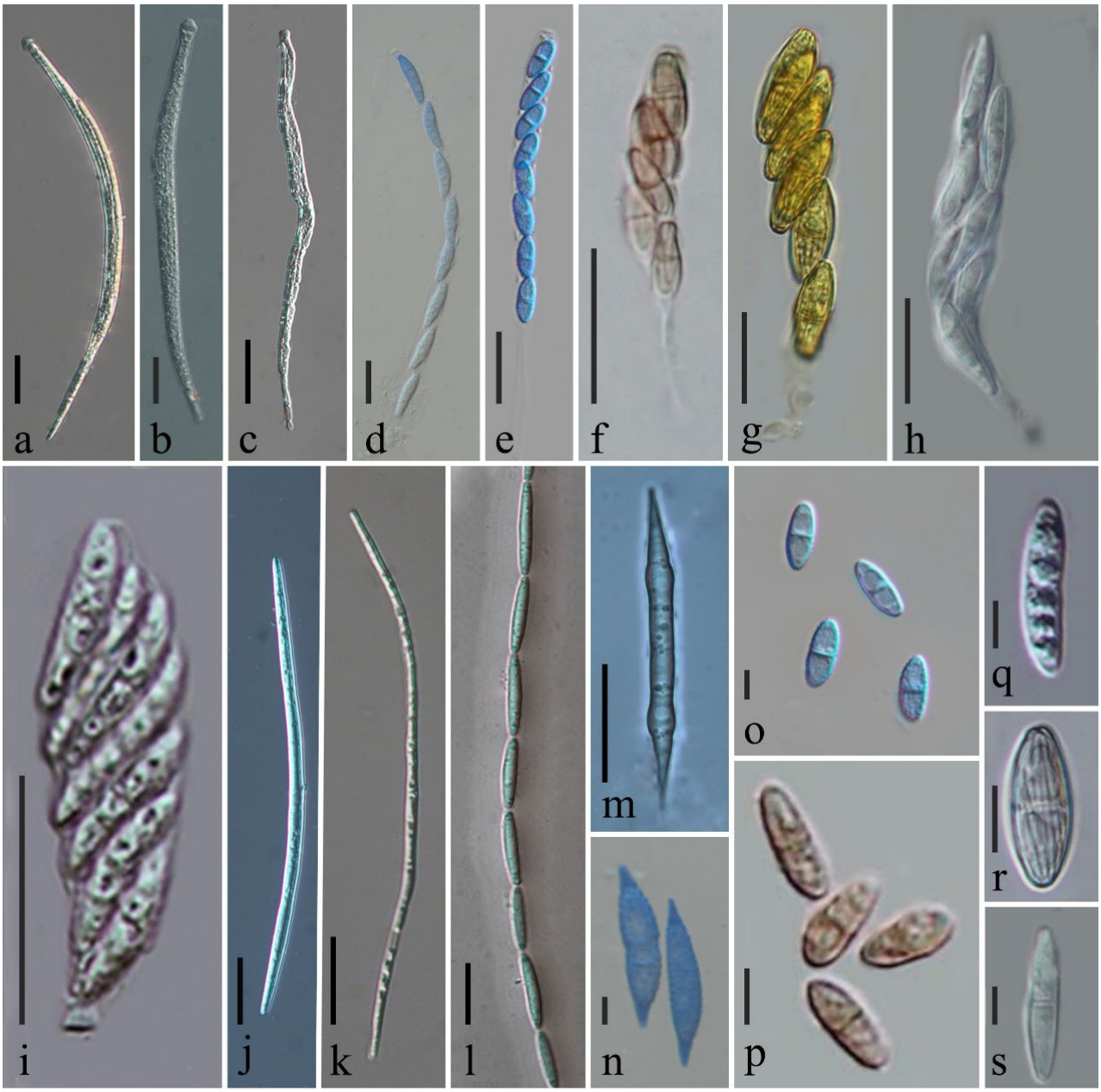


Figure 219 – Asci and ascospores morphology of *Hypocreales.* a, c, j, k, m *Ophiocordyceps* sp. b *Tolypocladium* sp. d, n *Hypomyces armeniacus.* e, o *Stilbocrea* sp. f, p *Valetoniella crucipila.* g, r *Circinoniesslia nectriae.* h, s *Pseudorhynchia polyrrhyncha.* i, q *Malmeomyces pulchellus.* l *Ophiocordyceps nutans*. Scale bars: a = 25 µm, b, d–f, h–k, m = 20 µm, c = 30 µm, g, l = 10 µm, n–s = 5 µm.

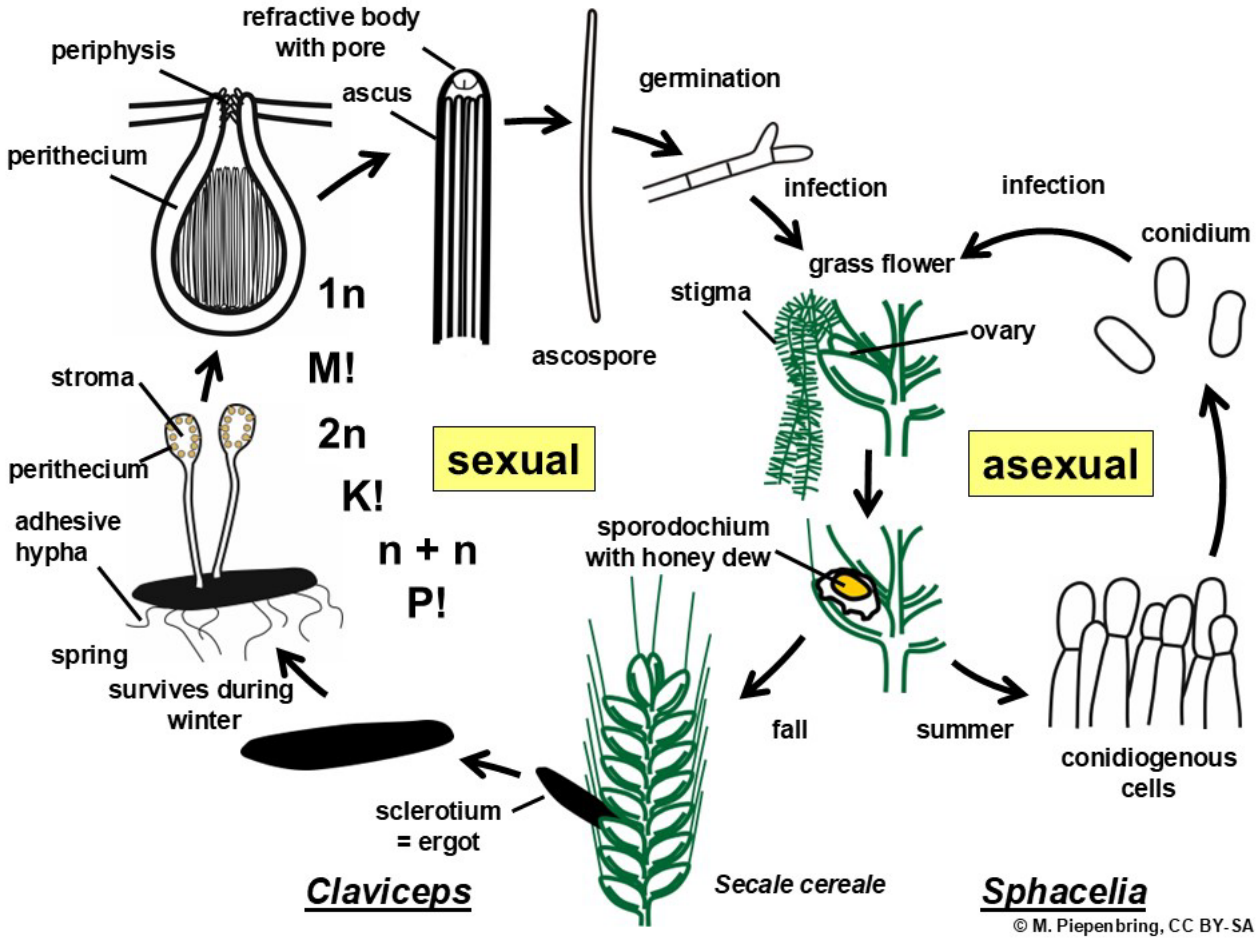


Figure 220 – Sexual and asexual life cycles of *Hypocreales* (From Mycological teaching diagrams by Meike Piepenbring (2023)). Abbreviations: 1n = haploid, 2n = diploid, P! = plasmogamy, K! = karyogamy, M! = meiosis. Black and white circles represent haploid nuclei of different mating types, circles of both colors represent diploid nuclei.

Hypocreales taxa are heavily influenced by their hosts during evolution, particularly in host-specific interactions. In symbiotic relationships with plants, especially monocotyledonous hosts, these fungi exhibit significant species co-evolution. The ecological habits of these fungi play a crucial role in insect parasitism, offering new insights into the mechanisms of fungal species formation and host transfer (Hyde et al. 2019). *Hypocreales* is one of the most diverse fungal orders in terms of lifestyle, encompassing plant parasitic, insect parasitic, and plant symbiotic fungi, which are significant in both agricultural and natural ecosystems (Zhang et al. 2015b, 2020b, Zeng et al. 2022b). *Cordyceps* and *Hypomyces* exhibit complex life cycles and specific host relationships. Studying the evolution of *Hypocreales* is of great significance for understanding its biological characteristics and its role in nature (Liu 2019, Zeng et al. 2022b, Wang et al. 2023a, Zhong et al. 2023).

Justification of order and problems

Hypocreales encompasses several critical areas, including systematic classification, ecological roles, evolutionary biology, and potential applications. Among these, *Cordyceps* has unique diversity (Kobayasi 1941, 1982, Mains 1957, 1958) and is characterized by the production of both submerged and surface asci on pedunculated and club-like to head-shaped stroma (Kobayasi & Shimizu 1960, Rogerson 1970). Host-specificity is primarily considered for the classification of *Cordyceps* (Kobayasi 1982), and they interact with ten orders of arthropods and the truffle-like genus *Cobras* as hosts. Most species are adapted to a single host or a closely related group. However, using host data for taxonomic classification is challenging due to difficulties in identifying immature hosts (such as larvae and pupae). Thus, phylogenetic analyses using ribosomal DNA (Artjariyasripong et al. 2001,

Sung et al. 2001, Stensrud et al. 2005), especially multiple independent loci, can provide a better understanding and classification of *Hypocreales* (Chen 2016b, 2019, Li 2019, Zou 2021, Zhao et al. 2022a).

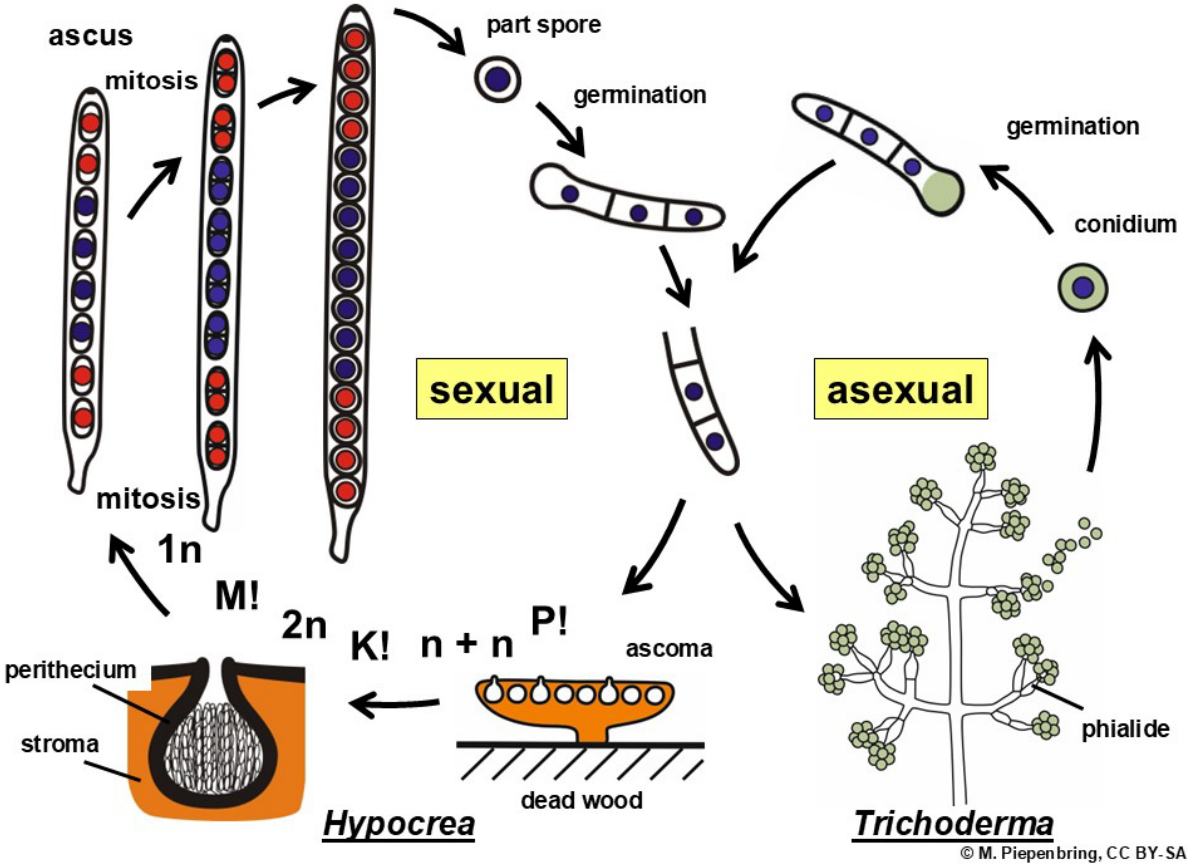


Figure 221 – Sexual and asexual life cycles of *Hypocreales* (From Mycological teaching diagrams by Meike Piepenbring (2023)). Abbreviations: 1n = haploid, 2n = diploid, P! = plasmogamy, K! = karyogamy, M! = meiosis. Black and white circles represent haploid nuclei of different mating types, circles of both colors represent diploid nuclei.

Cordyceps sinensis is a rare and precious traditional Chinese medicine, formed by the infection of bat moth larvae by *Cordyceps sinensis* in high-altitude grasslands found in the Qinghai-Tibet Plateau. The diverse climate and terrain of the Qinghai-Tibet Plateau, along with the rich species diversity of host insects, make *Cordyceps sinensis* an ideal subject for studying fungal evolution. Compared to other fungi, *Cordyceps* is notable for having the largest mitochondrial genome within the *Hypocreales* (Mains 1958, Kobayasi 1982, Hou 2016). Despite the significant value of studying *Hypocreales,* the species diversity and classification remain unclear. Morphological features were mainly used in the identification. However, most taxa exhibit substantial morphological variation. Due to insufficient ecological and biological data, many taxa in tropical and subtropical regions are not fully understood (Huang et al. 2021b, Wei et al. 2023). Compared to prokaryotes, predicting substrate selectivity in fungal adenosylation domains is less accurate, as current prediction algorithms are based on non-ribosomal peptide synthases from bacteria. Thus, establishing a mapping between protein sequences and product structures is essential for more precise functional predictions, necessitating more comprehensive databases and advanced analytical methods (Zou 2021).

Further research is needed to understand the ecological functions of *Hypocreales*. Despite advances in molecular systematics technology, genome and transcriptome data for many species remain insufficient, limiting the understanding of their evolutionary history and adaptation mechanisms. The genomes of *Hypocreales* may exhibit high complexity and variability. *Hypocreales*

have potential medicinal value; the extraction of their active ingredients and the study of their mechanisms of action are poorly explored (Huang et al. 2021b, Zou 2021). Some fungi with application potential, such as *Cordyceps*, face challenges in commercialization and sustainable production.

Significance

Ecological and economic roles

Members of *Hypocreales* are found in a variety of ecological environments, including soil, plants, insects, and other habitats. Many are saprophytes, symbionts, or parasites, playing essential roles in decomposing organic matter or parasitizing other organisms for nutrients. Some species produce distinctive odours due to biologically active volatile compounds; for example, *Trichoderma harzianum* releases a coconut-like aroma during solid-state fermentation (Sarhy-Bagnon et al. 1997). The parasitic members of *Hypocreales* can significantly impact agriculture and forestry. For instance, *Nectria* and *Fusarium* (*Nectriaceae*), major plant pathogens, infect over 700 vascular plant species, causing diseases like branch blight and fruit rot (Riffle 1986, Gaber et al. 2023). *Trichoderma*, a mycoparasitic genus in *Hypocreaceae*, is a common contaminant in edible fungi production (Zin & Badaluddin 2020). *Claviceps purpurea* (*Clavicipitaceae*), the grass ergot pathogen, reduces seed yields and produces toxic alkaloids (Pérez et al. 2013, Wyka et al. 2022). On the positive side, some species parasitize insects and serve as important biocontrol agents, such as *Purpureocillium lilacinum*, *Metarhizium anisopliae*, and *Beauveria bassiana*, which are used to manage agricultural and forestry pests, restore ecological balance, and promote human health (Zhuang 2020, Park et al. 2021). Additionally, some *Hypocreales* fungi, like *Ophiocordyceps sinensis* and *Cordyceps cicadae*, are valuable in traditional Chinese medicine (Zhuang 2020), while others, such as *Cordyceps militaris*, are emerging as novel nutritional resources (Chantawannakul et al. 2021).

Entomogenous fungi have played an outstanding role in controlling crop pests (Wang et al. 2022a). There are more than 170 fungal insecticides registered. Among them, 11 species are entomopathogenic fungi, of which more than 50% are *Beauveria bassiana* and *Metarhizium anisopliae* (Wang et al. 2010a). *Trichoderma* has evolved into a species-rich genus under the *Hypocreales*, mainly because of its economic and ecological significance (Zhao et al. 2024). They are efficient producers of enzymes and antibiotics and have been found as endophytes in plant tissues (Ahamed & Vermette 2008, Stracquadanio et al. 2020, Abdel-Mageed et al. 2022). They play a multifaceted role in plants, enhancing photosynthetic capacity, inducing defense mechanisms, and contributing to nutrient provision (Bae et al. 2011, Harman et al. 2021, Rees et al. 2022). *Trichoderma* also has biocontrol performance and its biocontrol mechanism is mainly reflected in the bactericidal effect of metabolites, bacteriolysis by extracellular enzymes, plant resistance induction and heavy parasitism. Recently, 70 pathogenic fungi from cultivated edible fungi belonging to the order *Hypocreales* were reported (Yu et al. 2024a).

The landmark drugs, cyclosporine and fingomod were also isolated from *Hypocreales* (Strader et al. 2011). Cyclosporin A isolated from *Tolypocladium inflatum* was discovered initially as an antifungal agent, and currently, it is a clinically important immunosuppressant (Dreyfuss et al. 1976, Kino et al. 1987). Natural product, ISP-I, is also isolated from *Isaria sinclairii* (Fujita et al. 1994). After structural modification, fingomod with stronger immune activity and lower toxicity was obtained (Kim et al. 2006, Brinkmann et al. 2010, Chun & Hartung 2010, Hyde et al. 2024a). *Samsoniella* is a cosmopolitan arthropod-pathogenic genus containing several species with significant economic and medicinal value (Wang et al. 2022a, 2023a). The world market has developed more than 260 healthcare products using *S. hepiali* as a raw material, generating an economic value of approximately RMB10 billion ($1.46 billion) annually (Wang et al. 2020c). According to Wang et al. (2022a), *Samsoniella* spp. have a wide distribution, and some species are considered potential biocontrol agents against pest insects. China developed the Bering capsule from the mycelium of *Hirsutella sinensis* and fermented the Jinshuibao capsule from the mycelium of *Ophiocordyceps sinensis*, which held a significant market share. *Cordyceps sinensis* can regulate the number of forest pests, maintain ecological balance and biodiversity (Fan et al. 2020a).

Chemical diversity

The interaction between *Trichoderma* and pathogenic fungi, as well as plants, is complex, with one of the crucial processes being the creation of active secondary metabolites (Song & Ji 2024). According to Song & Ji (2024), 445 new compounds have been isolated and identified from marine *Trichoderma* in the last 30 years, including terpenes, steroids, polyketides, peptides, alkaloids, and others, with more than half exhibiting anti-microalgal, zooplankton-toxic, antibacterial, antifungal, cytotoxic, anti-inflammatory, and other activities.

Besides cyclosporine and fingolimod, *Cordyceps sensu lato* also contains many active ingredients. *Cordyceps* contains over 200 bioactive metabolites, including nucleotides, polysaccharides, proteins, and fatty acids, with various pharmacological effects, including anti-microbial, anti-apoptotic, anti-cancer, and antioxidant properties (Liu et al. 2015b, Krishna et al. 2024). Xia et al. (2017) found that Cordycepin (COR) and anticancer drug Pentostatin (PTN) were synthesized simultaneously by the gene cluster in *Cordyceps militaris*, and the latter could also inhibit the degradation of cordycepin to 3'- deoxyinosine (3'-dI). *Samsoniella hepiali* is a well-known edible and medicinal fungus that is widely distributed in China and Argentina (Chen et al. 2021). Several studies have shown that *S. hepiali* possesses various pharmacological properties, including anti-cancer, analgesic, and proapoptotic activities (Dai et al. 1989, Jiang et al. 2010, Thakur et al. 2011, Wang et al. 2016b).

Other relevant data and future recommendations

The future development of *Hypocreales* covers diverse areas such as ecosystem services, biotechnology, conservation, and research. The entomopathogenic fungi, evolving from plant pathogens and saprobic fungi into insect pathogens, have developed sophisticated mechanisms for infecting and utilizing insects as a nutritional source (Wu & Chen 2024). While multi-gene phylogenetic analyses have revealed significant host transfers and lifestyle shifts, the evolutionary trends remain unclear. Hou (2016) provided insights into mitochondrial genomes of *Cordyceps sinensis*, offering a reference for studying mitochondrial genomes across strains.

The distribution and abundance of *Cordyceps* resources are influenced by geographical, climatic, and vegetative factors. Comprehensive investigations, classification, and phylogenetic studies of *Cordyceps sinensis* are needed, including multi-phase classification and germplasm resource libraries (Fan 2020). Zhuang & Zeng (2017) identified a potential new species, *Cocoonihabitus sinensis*, suggesting valuable insights for phylogenetic research. *Hypocreales* involved in wood decay play a crucial ecological role by breaking down complex organic substances. Future research should focus on understanding enzyme production for industrial applications and exploring the diversity and ecological adaptation. Gene editing techniques like CRISPR-Cas9 can elucidate the role of specific genes in fungal processes. *Hypocreales* taxa show promise in controlling plant diseases and promoting growth (Wu & Chen 2024). Continued interdisciplinary research and improved detection and cultivation techniques are vital for capturing variability and ecological roles in *Hypocreales*.

***Jobellisiales* M.J. D'souza & K.D. Hyde, Fungal Diversity 72: 219 (2015)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Jobellisiales was established by Maharachchikumbura et al. (2015) as a monotypic order to accommodate *Jobellisiaceae,* which was introduced by Réblová (2008). *Jobellisiaceae* comprises a single genus, *Jobellisia,* which consists of saprobic lignicolous species from terrestrial and freshwater habitats. *Jobellisia luteola* (Basionym: *Letendraea luteola* Ellis & Everh.) was introduced as the type species of *Jobellisia*. There are eight species of *Jobellisia* (Index Fungorum 2025, Species Fungorum

2025), but only three species (*Jobellisia* fraterna, *J. guangdongensis* and *J. luteola*) have DNA sequence data (Huhndorf et al. 1999, Réblová 2008, Liu et al. 2012a).

The taxonomic placement of *Jobellisiales* was determined based on multi-gene phylogenetic analyses and morphological characteristics (Maharachchikumbura et al. 2015). However, its phylogenetic placement was unstable because its taxa clustered with *Pleurostomataceae* (*Calosphaeriales*) (Hongsanan et al. 2017a). Therefore, the discovery and introduction of further *Jobellisiales* taxa are important to generate well-resolved and robust phylogenetic trees, thereby supporting their placement as a separate order. *Jobellisiales* taxa are characterized by large ascomata that typically appear superficial or semi-immersed on the host substrate, with a central ostiole (Maharachchikumbura et al. 2015, Huang et al. 2021b). The sexual morph is characterized by a thick peridium, cylindrical asci and melanized one-septate ascospores with a conspicuous germ pore (Maharachchikumbura et al. 2015). However, its asexual morph has not been documented so far (Huang et al. 2021b).

History

Initially, *Jobellisiales* was placed in the sub-class *Diaporthomycetidae* based on the multi-gene phylogenetic inferences of the combined LSU-SSU-RPB2-TEF1 sequence matrix (Maharachchikumbura et al. 2015, 2016). However, Wijayawardene et al. (2020) listed *Jobellisiales* under *Hypocreomycetidae. Jobellisiales* had an unstable phylogenetic placement. Hongsanan et al. (2017a) and Hyde et al. (2017a) found that *Jobellisiales* is phylogenetically related to *Calosphaeriales* and *Togniniales*. In Huang et al. (2021b), *Jobellisiales* clustered basal to *Calosphaeriales*, *Diaporthales*, *Tirisporellales* and *Togniniales*. *Jobellisiales* is distinguished from *Calosphaeriales* and *Togniniales* by clavate asci and hyaline allantoid ascospores. Furthermore, it differs from *Tirisporellales* by the presence of cylindrical asci and fusoid, falcate to lunate ascospores (Hyde et al. 2020d). Huang et al. (2021b) re-examined the type and authentic materials belonging to poorly studied genera, including *Jobellisia*. Based on their phylogenetic analyses of the concatenated LSU-SSU-RPB2-TEF1 sequence data, *Jobellisiales* is classified in *Diaporthomycetidae* instead of *Hypocreomycetidae*.

General description

Jobellisiales are found in both terrestrial and freshwater habitats. Morphologically, *Jobellisiales* resembles *Diaporthales* in having cylindrical or ellipsoidal asci and brown ascospores, but they are phylogenetically distinct (Hyde et al. 2020d, Huang et al. 2021b). *Jobellisiales* is morphologically distinct from their sister orders *Calosphaeriales*, *Togniniales* and *Tirisporellales* based on the different asci and ascospore shape (Hyde et al. 2020d).

Sexual morph: *Ascomata* semi-immersed or superficial, gregarious, perithecial, globose to subglobose, black to dark brown, ostiolate, exhibiting yellowish pigments externally. *Peridium* composed of three layers; inner layer composed of hyaline cells of *textura prismatica*; middle layer comprising brown to yellow cells of *textura angularis*; and outer layer consisting of brown or blue-green or orange cells of *textura angularis-globosa*. *Paraphyses* numerous, filiform, septate, unbranched. *Asci* unitunicate, cylindrical, with a long pedicel and a J- apical ring. *Ascospores* uni-seriate, ellipsoidal to subglobose, pale brown to dark brown, 0–1-septate, smooth-walled, guttulate, consisting of a conspicuous germ pore at the apex and/or base (Fig. 222). Asexual morph: Not observed.

Families included in *Jobellisiales*

Jobellisiaceae Réblová

Evolution

In the MCC tree of *Diaporthomycetidae*, *Jobellisiales* formed a sister clade to *Togniniales* with an estimated divergence time of 130–188 MYA (Hyde et al. 2017a). In the MCC tree by Hongsanan et al. (2017a), *Jobellisiales* diverged around 146 MYA, which falls within the ordinal range. However, its phylogenetic placement appeared unstable because it occasionally clustered with

Pleurostomataceae (*Calosphaeriales*). Consequently, *Jobellisiales* was reduced as a family within *Calosphaeriales* to maintain the monophyly of the group. A similar proposition was made by Wijayawardene et al. (2018), suggesting the reduction of *Jobellisiales* as a family within its sister order, *Calosphaeriales*. Despite being listed under *Hypocreomycetidae* by Hyde et al. (2020d) and Wijayawardene et al. (2020), *Jobellisiales* is accepted in *Diaporthomycetidae* based on its distinct phylogenetic clade (Huang et al. 2021b).

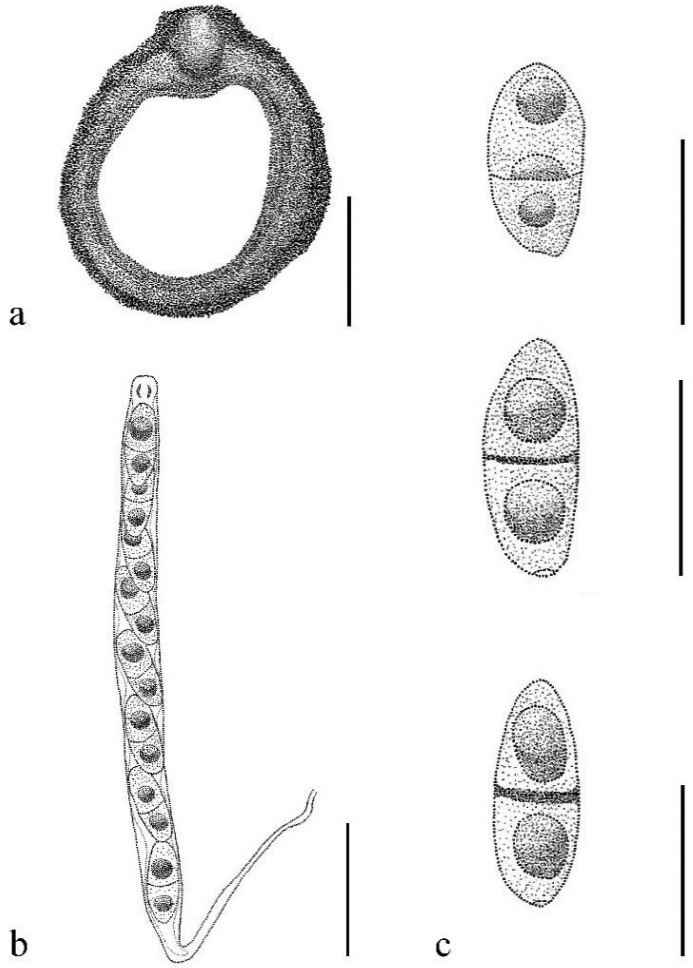


Figure 222 – Morphology of sexual morph characters of *Jobellisiales* (*Jobellisia luteola*) [(redrawn from Huang et al. (2021b)] a Ascomata. b Ascus. c Ascospores. Scale bars: a = 200 μm, b = 20 μm, c = 10 μm.

Justification of order and problems

Jobellisiales belongs to *Sordariomycetes* and many taxa within *Sordariomycetes* lack DNA sequence data, leading to unstable phylogenetic placements (Chen et al. 2023b). To date, *Jobellisiales* is represented by a single genus. Expanding the number of *Jobellisiales* or sister taxa in the phylogenetic analyses can provide a precise understanding of their taxonomy through an examination of their evolutionary relationships. The inclusion of more taxa in the analysis provides a greater number of data points for comparison, thereby enhancing the accuracy of the resulting phylogenetic tree. The discovery of additional *Jobellisiales* taxa with DNA sequence data for multiple gene regions will contribute to a more comprehensive representation of fungal diversity. This can lead to the development of accurate and robust phylogenetic trees, thereby validating the placement of *Jobellisiales* as a separate order. Adding to that, obtaining *Jobellisiales* taxa in the asexual morph is important to understand their life cycles, ecology and evolution. Since asexual morphs can differ greatly from sexual morphs, documenting both is crucial for accurate identification and classification.

Significance

Ecological and economic roles

Jobellisiales consists of saprobic lignicolous taxa from terrestrial and freshwater habitats (Huang et al. 2021b). Saprobic organisms play a crucial role in ecosystem functioning, as they contribute to the maintenance of biodiversity, nutrient recycling, soil health, and overall ecosystem resilience (Niego et al. 2023a, b). To date, *Jobellisia luteola* has been reported from temperate regions, including Ohio (Ellis & Everhart 1895), as well as in Iowa, Michigan, North Carolina and New York (Barr 1993b, Huhndorf et al. 1999, Huang et al. 2021b). Further research is necessary to explore the diversity, ecology and distribution of *Jobellisiales* taxa and closely related members. Novel species and genera may be discovered in the future, enhancing our understanding of this group.

Chemical diversity

Relevant studies are not available for the chemical diversity of *Jobellisiales*.

Other relevant data and future recommendations

Future studies should prioritize the collection of more samples of *Jobellisiales* taxa, reporting them in both the sexual and asexual morphs. Field surveys in diverse ecological habitats with a broadened geographic sampling should be conducted. Season and weather conditions that harbours the development of asexual morph features should be considered. DNA sequence data for multiple gene regions should be obtained for an accurate classification of taxa in this order.

Koralionastetales Kohlm., Volkm.-Kohlm., J. Campb. & Inderb., Mycological Research 113(3): 377 (2009)

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Lulworthiomycetidae*

Introduction

Koralionastetales was established by Campbell et al. (2009) to accommodate *Koralionastetaceae* and the genera *Pontogeneia* and *Koralionastes* within *Sordariomycetes* based on morphological characterization, along with phylogenetic analyses conducted based on SSU and LSU sequence data.

History

Koralionastetaceae was established by Kohlmeyer & Volkmann-Kohlmeyer (1987a) for a newly established genus *Koralionastes* with three new species (*Koralionastes angustus, K. ellipticus* and *K. ovalis*) based on their distinct morphology and ecology, which was accepted under *Ascomycota* genera *incertae sedis* (Eriksson 2006).

Koralionastetaceae was distinguished by having ascomata that are attached to coralline-covered corals and are often enclosed by crustose sponges with thick-walled ascospores and germinate into hyphae bearing phialidic antheridia with enteroblastic spermatia. The family was also reported as the first filamentous ascomycetes that formed a close association with corals and marine sponges (Kohlmeyer & Volkmann-Kohlmeyer 1987a). *Pontogeneia* was introduced to accommodate five species that parasitized marine Phaeophyta (Kohlmeyer 1975) and was placed in *Sordariomycetes incertea sedis*. The genus presently comprises eight species with *Pontogeneia padinae* as the type. *Pontogeneia* also shows distinct ecology and morphology like *Koralionastes* by having one-layered ascospore walls that are filamentous or ellipsoidal ascospores and occur in algicolous habitats. Both genera share similar morphology in having germ tubes forming antheridia but differ in ascospores morphology and habitat.

Campbell et al. (2009) initially obtained the sequence data for *Koralionastes* and *Pontogeneia* and found that both genera formed a monophyletic clade basal to *Lulworthiales*. Both genera differ from *Lulworthiales* in having septate paraphyses in the hamathecium, presence of periphyses, ascospores without apical structures and occur on coral rock and algae whereas *Lulworthiales*

(represented by *Lulworthia*/*Lindra*) lack paraphyses in hamathecium but centrum initially filled with a pseudoparenchymatous tissue, lack of periphyses and ascospores with mucus-containing apical chambers but not found in the genus *Lindra*. They are mostly found on wood but also reported on Spartina, Thalassia, Zostera, algae and coral rock. Based on morphological and phylogenetic evidence, *Koralionastetales* was established. The close phylogenetic association between *Lulworthiales* and *Koralionastetales* was also found in later studies (Réblová et al. 2010, 2015a, Maharachchikumbura et al. 2015, Hyde et al. 2020d). Maharachchikumbura et al. (2015) established a new subclass *Lulworthiomycetidae* to accommodate *Lulworthiales* and *Koralionastetales* based on morphological and phylogenetic support. The subclass recovered in the basal lineage of *Sordariomycetes* in the phylogenetic analysis that was conducted based on LSU, SSU, TEF, and RPB2 sequence data.

General description

The members of *Koralionastetales* are distinguished by having centrum containing paraphyses and periphyses with ascospores that are ellipsoidal, fusiform to filiform, thick or thin-walled, without any apical structures and especially have the formation of antheridia on germ tubes. The asexual morphs are unknown. However, spermatia are enteroblastic and subglobose and originate in bisipetal succession (Kohlmeyer & Volkmann-Kohlmeyer 1987a).

Sexual morph: *Ascomata* black, subglobose, ovoid or ellipsoidal, superficial, ostiolate, papillate or epapillate, periphysate, subiculate, or without subiculum. *Paraphyses* simple, septate. *Asc*i 8-spored, unitunicate, clavate to ellipsoidal or fusiform, pedicellate, deliquescent. *Ascospores* overlapping, hyaline, ellipsoidal to fusiform, multi-septate near the apices, or filiform and evenly multi-septate, thick or thin walled, germinating apically, lacking appendages. Asexual morph: Spermatia enteroblastic, subglobose (Fig. 233).

Families included in *Koralionastetales*

Koralionastetaceae Kohlm. & Volkm.-Kohlm.

Evolution

Hyde et al. (2020d) estimated the divergence time for *Koralionastetales* as 210.5 MYA. The marine order also shows a close phylogenetic association with marine orders *Luworthailes* and *Spathulosporales* (Hyde et al. 2020d). However, due to the polyphyletic nature of *Lulworthiales*, the delineation of these marine orders is challenging.

Justification of order and problems

Koralionastetales accommodates 13 species (eight species from *Pontogeneia* and five species from *Koralionastes*). However, the phylogenetic placement of the order has been established based on sequence data obtained from two species (one species from each genus). In addition, the phylogenetic placement of the type species of both genera is unknown, and most species are rarely collected with one collection (Campbell et al. 2009). Thus, extant fresh collections and more sequence data can provide better phylogenetic resolution with members of other marine orders. Hyde et al. (2020d), mistakenly reported *Pontogeneia rostrata* as a marine fungus. However, this is not a fungal species but a gammarid amphipod (Momota & Nakaoka 2017) and is a homonym of Animalia (*Pontogeneia* Speg., 1975 [Fungi] non *Pontogeneia* Boeck, 1871 [Animalia]).

Significance

Ecological and economic roles

Pontogeneia species inhabit marine algae, including Chlorophyta and Phaeophyta from California, Caribbean, Cuba, Mexico, Queensland (Australia) and Spain (Campbell et al. 2009). *Koralionastes* species are found on dead coral rubble among different species of crustose sponges from Belize, Central America and Queensland (Australia) (Kohlmeyer & Volkmann-Kohlmeyer 1987a, 1990).

Chemical diversity

No relevant studies are available for the members of *Koralionastetales*.

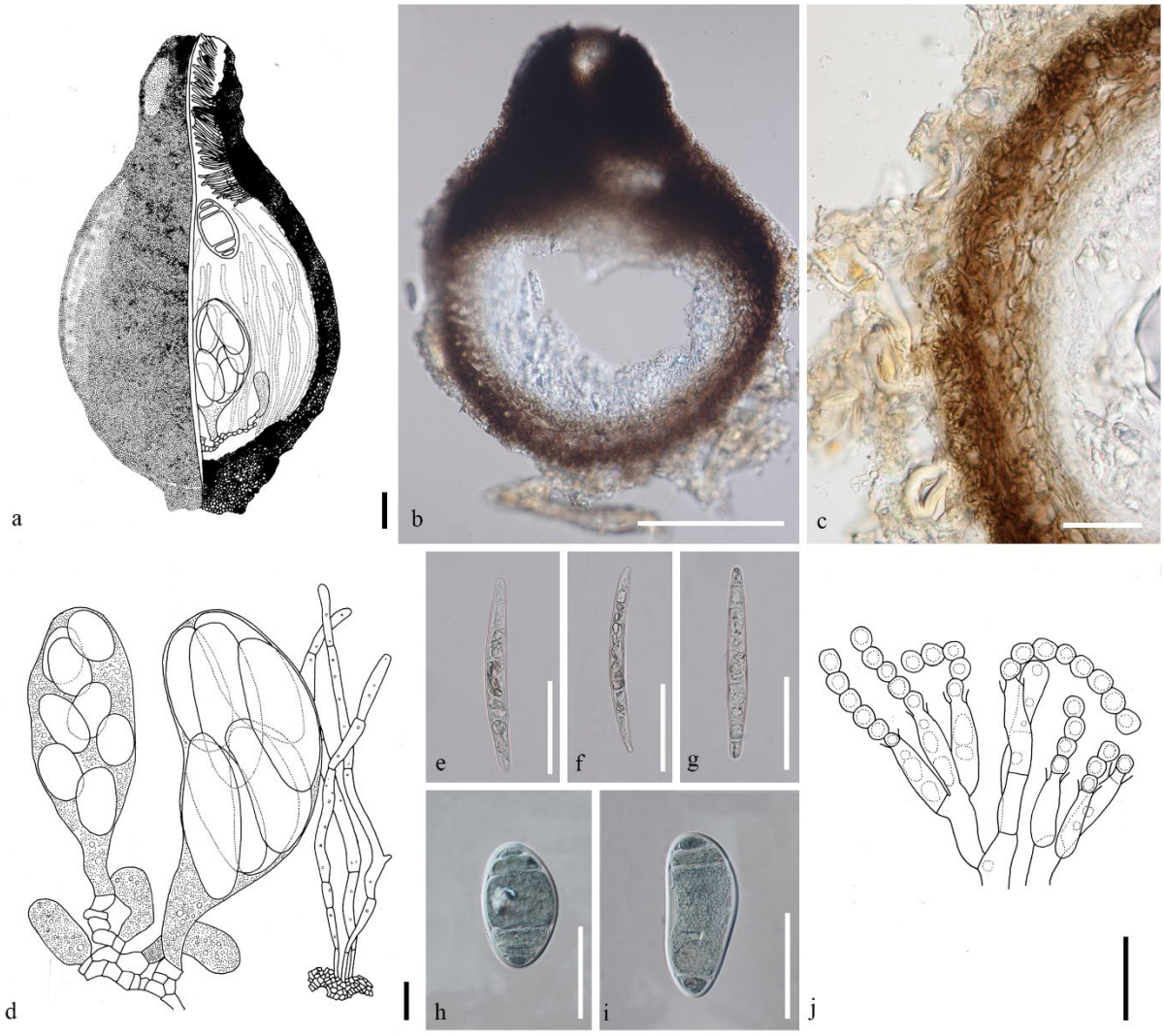


Figure 223 – Morphology of *Koralionastetales*. a Ascomata (a *Koralionastes ovalis*, b *Pontogeneia padinae*). c Peridium (*P. padinae*). d Asci in different developmental stages and paraphyses (*K. ovalis*). e–i Ascospores (e–g *P. padinae*, h, i *K. ovalis*). j Phialidic antheridia producing enteroblastic spermatia (*K. angustus*) (drawn from Kohlmeyer & Volkmann-Kohlmeyer 1987a). Scale bars: a, h, i = 50 µm, b = 100 µm, c, e–g = 20 µm, d = 25 µm, j = 10 µm.

Lulworthiales **Kohlm., Spatafora & Volkm.-Kohlm., Mycologia 92(3): 456 (2000)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Lulworthiomycetidae*

Introduction

Kohlmeyer et al. (2000) introduced the order based on a phylogenetic study and morphological observations and showed that the genera *Lulworthia* and *Lindra* did not group in *Halosphaeriales* but formed a separate clade. Subsequently, other genera have been included in the order (see Jones et al. 2019 for a complete list). Two families, *Lulworthiaceae* and *Koralionastetaceae*, were included in the order, the latter referred to a new order *Koralionastetales* (Campbell et al. 2009). *Lulworthiales* is unique in that all taxa are known only from the marine environment. One exception is a *Lulworthia* sp. isolated from a lake in Yunnan (Cai et al. 2002), but there have been no subsequent collections.

History

The *Lulworthiales* is based on the genus *Lulworthia* introduced by Sutherland (1915) from material collected at Lulworth Cove, Dorset, UK, on the brown alga *Fucus vesiculosus*. Barghoorn & Linder (1944), unaware of the Sutherland paper, described the genus *Halophiobolus*, later synonymised by Kohlmeyer et al. (2000). Initially, the genera *Lulworthia* and *Lindra* were included in the family *Halosphaeriaceae* (*Halosphaeriales*) by Muller & von Arx (1962). Molecular studies by Kohlmeyer et al. (2000) demonstrated two lineages within *Halosphaeriales* and the genera *Lulworthia* and *Lindra* were assigned to the family *Lulworthiaceae* (*Lulworthiales*). Subsequently, other genera were assigned to the order based further molecular and morphological studies, including *Orbimyces* (Barghoorn & Linder 1944, Jones et al. 2008), *Zalerion* (Moore & Meyers 1962), *Cumulospora* (Schmidt 1985, Abdel-Wahab et al. 2010), *Kohlmeyeriella* (Jones et al. 1983a, Campbell et al. 2005), *Spathulospora* (Inderbitzin et al. 2004), *Haloguignardia* (Harvey 2004), *Lulwoana* (Campbell et al. 2005), *Lulwoidea* (Campbell et al. 2005), *Rostrupiella* (Koch et al. 2007), *Halazoon* (Abdel-Wahab et al. 2010), *Hydea* (Abdel-Wahab et al. 2010), *Matsusporium* (Abdel-Wahab et al. 2010), *Moleospora* (Abdel-Wahab et al. 2010), *Moromyces* (Abdel-Wahab et al. 2010), *Sammeyersia* (Abdel-Wahab et al. 2017), *Paralulworthia* (Poli et al. 2020) and *Rambellisea* (Braconcini et al. 2024). Dayarathne et al. (2025) introduced the genus *Lindriella* for three *Lindra* species that did not group within the *Lindra* clade. Currently, the *Lulworthiales* includes 21 genera and 68 species, with eight new species (*Hydea mangrovei*, *Lulworthia norwegica*, *Matsusporium japonica*, *Moromyces mangrovis*, *Paralulworthia lignicola*, *Rostrupiella longispora*, *Sammeyersia yanbuensis*, *S. thailandica*) introduced by Dayarathne et al. (2025).

Maharachchikumbura et al. (2015) introduced this new subclass *Lulworthiomycetidae* for the orders *Lulworthiales* and *Koralionastetales*, and this was accepted by Hyde et al. (2017a) and Hongsanan et al. (2017a). Molecular data (Dayarathne et al. 2025) supports the inclusion of *Koralionastes* and *Pontogenia* in the family *Koralionastetaceae* (*Koralionastetales*) as proposed by Campbell et al. (2009). However, the inclusion of the genus *Spathulospora* within the *Lulworthiales* is questionable as proposed by Inderbitzin et al. (2004), although it groups within the *Lulworthiales* in Dayarathne et al. (2025). Inclusion of *Koralionastes*, *Pontogenia* and *Spathulospora* in the *Lulworthiales* is further discussed in the section on Evolution.

General description

Lulworthiales comprises genera with both sexual and asexual morphs, with some asexual morphs not linked to their sexual stage, while none have been reported for the genus *Rambellisea* (Braconcini et al. 2024) (Figs. 224, 225).

Sexual morph: *Ascomata* superficial or deeply immersed, immersed or partly immersed in wood usually with a long neck that are vertically or horizontally laying on the substrates, globose to subglobose, cylindrical or ellipsoid, ostiolate, with a papilla or with a cylindrical, straight or irregular long neck, carbonaceous or coriaceous, and dark brown, black or purple (*Halazoon purpurea* = *Lulworthia purpurea*) (Alongi et al. 1999, Kohlmeyer et al. 2000, Jones et al. 2015). *Spathulospora* species have bottle-shaped or subglobose ascomata seated on a thin stroma (subiculum) with sterile hairs, particularly elaborate in *S. adelpha* and *S. phycophila* (Kohlmeyer 1973, Kohlmeyer & Volkmann-Kohlmeyer 1987a, 2003, Kohlmeyer et al. 2000, Campbell et al. 2005, Azevedo et al. 2017). *Asci* 8-spored, often clavate to fusiform, unitunicate, thin-walled, usually without apical apparatus or deliquescing early; and with or without a short stalk (Kohlmeyer 1973, Kohlmeyer & Volkmann-Kohlmeyer 1989, Campbell et al. 2005, Azevedo et al. 2017). In *Rostrupiella* species asci are cylindrical with tips rounded which become pointed (Koch et al. 2007), while in *Spathulospora* they are arranged in a hymenium, but without paraphyses (Inderbitzin et al. 2004). *Ascospore* ellipsoid, fusiform to filiform with or without septa. *Lulworthia* species have ascospores and end chambers are filled with mucus released as a drop when in water (adapted from Jones et al. 2009, Abdel-Wahab et al. 2010). Asexual morph: hyphomycetes, variously-shaped helicoid conidia (Abdel-Wahab et al. 2010), while *Orbimyces* is significantly different by having conidia with a large black basal cell and a crown of 4–5 radiating arms (1 polar and 4 lateral) (Barghoorn & Linder 1944,

Jones et al. 2008). Other taxa have chlamydospore-producing "asexual" morphs e.g., *Paralulworthia* (Poli et al. 2020, 2021) and *Rambellisea* (Braconcini et al. 2024).

Families included in *Lulworthiales*

Lulworthiaceae Kohlm., Spatafora & Volkm.-Kohlm.
Lulworthiales genera *incertae sedis*
Hiogispora Abdel-Wahab & Nagahama
Paramoleospora M. Li & L. Cai

Evolution

Hyde et al. (2017a) and Hongsanan et al. (2017a) recognised the orders *Lulworthiales* and *Koralionastetales* in the well-supported MCC tree in the subclass *Lulworthiomycetidae*. They postulated a stem age of 289 MYA for these taxa, suggesting an evolutionary scenario where *Koralionastetales* diverged from *Lulworthiales*. Subsequently, Bao et al. (2023) examined the evolution of the freshwater *Hypocreomycetidae* while also revisiting the origins of certain marine fungi. In their study, *Lulworthiales* received a stem age of 158.53 MYA for *Hydea pygmea* and 62.32 MYA for *Cumulospora marina* and *Lindra thalassiae* (= *Linderilella thalssiae*). However, in this latest review, the *Koralionastetales* was not included. The relationship between *Pisorisporiales* and the previously mentioned orders is robustly substantiated by the MCC tree analysis conducted by Hyde et al. (2017a) and Hongsanan et al. (2017a). However, the stem age of *Pisorisporiales*, ca. 266 MYA (Hyde et al. 2017a), coincides with the divergence times indicative of a separate subclass.

The current understanding of these relationships is based on available evidence, which hints at the possibility of future taxonomic reclassifications. Given the divergence times observed, it would not be surprising if *Lulworthiales* and *Koralionastetales* were eventually recognized as distinct subclasses, pending further evidence. The presence of numerous missing lineages within these groups contributes to the unstable phylogenetic positions of some genera, such as *Pontogeneia*. Despite more than 21 genera and 68 species being recognized within the *Lulworthiales* and *Koralionastetales* (Species Fungorum 2025, Dayarathne et al. 2025), comprehensive DNA data remains limited for many of these species. To date, only species within the genera *Paralulworthia* and *Sammeyersia* have been sequenced for protein-coding genes, such as RPB2 and TEF1-α (Dayarathne et al. 2025). Beyond these, orders like *Spathulosporales* also suffer from a lack of sufficient sequence data, with a notable absence of protein sequence information, rendering their taxonomic placement unstable. To enhance our understanding of the evolutionary relationships within these marine fungi, it is imperative to acquire fresh specimens from underrepresented genera, extract DNA from these and existing cultures and focus on sequencing more informative genetic regions. This approach will enable the construction of a more robust MCC tree, offering a clearer and more precise view of the evolutionary dynamics within these fungal groups.

Justification of order and problems

Kohlmeyer et al. (2000) established the *Lulworthiales* in a well-supported lineage and distinct from taxa assigned to the *Halosphaeriaceae*, with distinct features of long filiform hyaline ascospores with unique end chambers filled with mucilage and released as drops for their attachment to surfaces (Jones 1994). Although many genera are hyphomycetes, they have been linked to sexual morphs with long filiform ascospores with end chambers, e.g., *Cumulospora* and *Halazoon*. However, the systematics of the *Lulworthiales* is not free from problems for several reasons and has been problematic for several reasons: 1. Many genera have been rarely collected and are difficult to culture, which has hindered their phylogenetic study, e.g., *Haloguignardia* and *Spathulospora*. 2. There have been few studies of genera on macroalgae, coral, tunicates and marine animals, although metabarcoding studies have revealed diverse lineage of fungi associated with these substrates (Pang et al. 2021). 3. The genus *Lindra* has been shown to be polyphyletic but lack of material for sequencing of the type species *Lindra inflata* has hampered resolution (Pang et al. 2021). 4. The acceptance of the name *Lulwoana* over the more common asexual morph *Zalerion maritimum* requires resolution. 5. Morphology of ascomata of the taxa in the *Lulworthiales* has been overlooked

and was only used as a secondary character to delineate the taxa. 6. Lack of sequences for protein-coding genes, such as RPB2 and TEF1-α, except for the genera *Paralulworthia* and *Sammeyersia*. 7. Problems with the sequencing and characterization of the genus *Paralulworthia*.

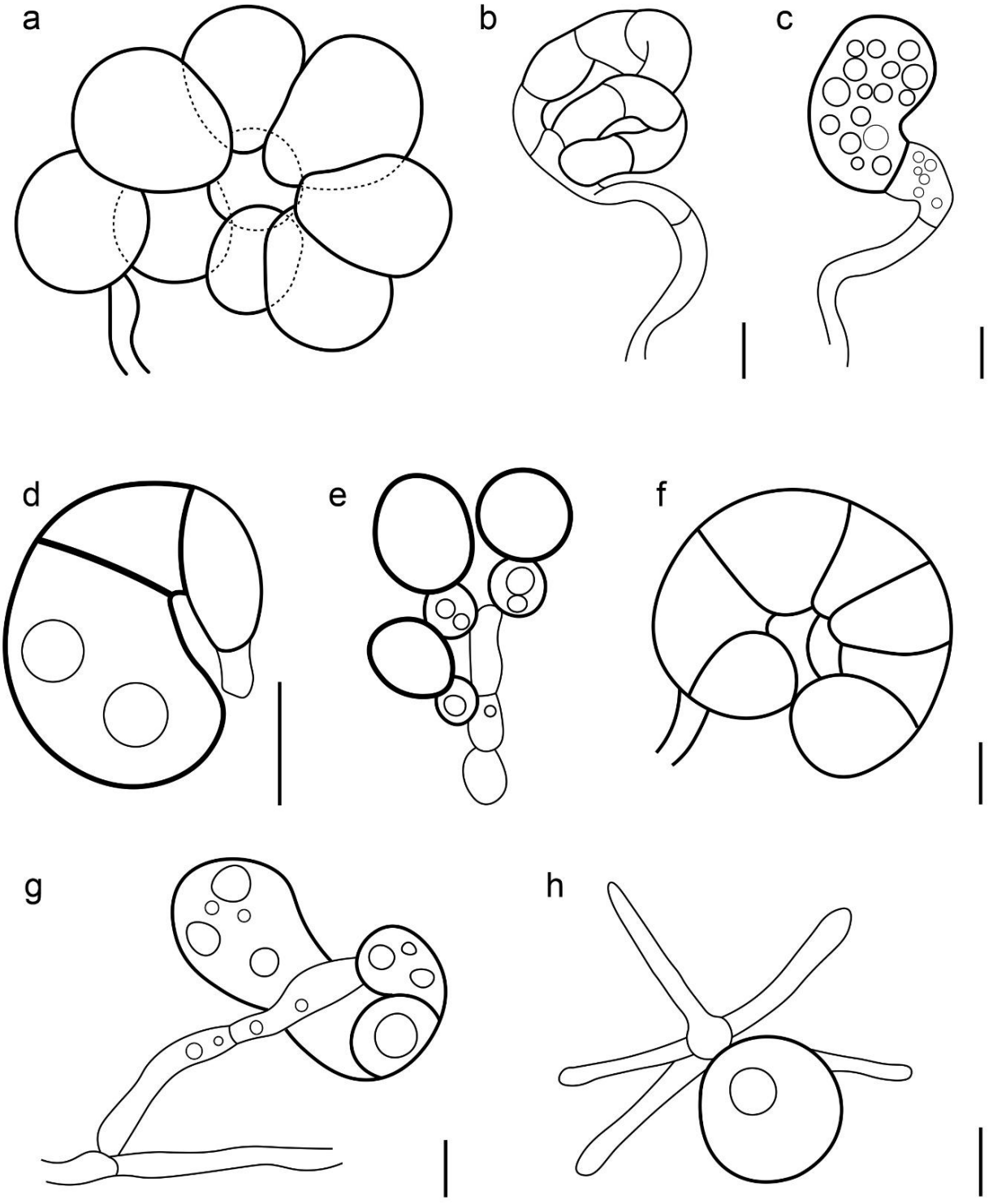


Figure 224 – Asexual morphs of selected genera in the *Lulworthiales*. a *Cumulospora marina*. b *Halazoon melhae*. c *Halazoon fuscus*. d *Hydea pygmea*. e *Hydea mangrovei*. f *Matsusporium japonica.* g *Matsusporium tropicale.* h *Orbimyces spectabilis*. Scale bars: a–h = 10 µm.



Figure 225 – Sexual morphs of selected genera in the *Lulworthiales* (a *Kohlmeyeriella tubulata* ascospore with polar spines and a released drop of mucilage. *K tubulata* SEM of ascospore and polar spines. c *Halazoon purpurea* apical chamber with released mucilage drop (SEM). d *Lindra* inflata *ascospore* with globose apical appendages. e *Halazoon purpurea* spore attachment (SEM)).

Significance

Ecological and economic roles

Ecologically, members of the *Lulworthiales* are early colonizers of wood exposed in marine habitats (Meyers 1953, 1954, Jones 1963, Byrne & Jones 1974, Grasso et al. 1990, Hyde 1991). Jones (1963) exposed test panels of beech and Scots pine at rafts in UK coastal waters: Langstone Harbour, Portsmouth, Sutton Harbour, Plymouth and Menai Straits, North Wales and retrieved at 6-week intervals up to 72 weeks and noted that *Halazoon purpurea* and *Lulworthia floridana* were present on beech panels at 12 weeks along with *Lulwoana uniseptata* (as the asexual morph *Zalerion maritimum*). Byrne & Jones (1974) exposed Scots pine (*Pinus sylvestris*) and beech (*Fagus sylvatica*) test panels at three locations in the United Kingdom (UK): Langstone Harbour, Port Erin and Newton Ferrers for up to one year with the most frequently occurring species were *Lulworthia* sp. (76% incidence of occurrence), *Lulwoana uniseptata* (=*Zalerion maritimum* 67%) and *Ceriosporopsis halima* (36%). At tropical locations, members of the *Lulworthiales* appear later in the colonization of wood block as observed in Mandai mangrove, Singapore (Leong et al. 1991) when the early colonisers (6–18 weeks) were *Verruculina enalia*, *Lignincola laevis* and *Payosphaeria minuta*.

Members of the *Lulworthiales* have been reported from a wide range of timbers including: basswood and sycamore panels (Gold 1959); *Autranella congolensis*, *Bailloella toxisperme*, *Dicorynia quianensis*, *Letestus durissima*, *Lophira alata*, *Sarcocephalus diderrichii*, *Tieghemella africana*, *T. heckelii*, *Vouacapoua americana* (very durable) and *Eucalyptus marginata* (durable) (Furtado & Jones 1980); *Betula alleghaniensis*, *Pinus strobus* and *Picea glauca*; and mangrove timbers *Bruguiera cylindrica* and *Rhizophora apiculata* (Leong et al. 1991); *Rh. apiculata* and *Xylocarpus granatum* poles (Hyde 1991), and many others. Widely reported from salt marsh plants:

Spartina spp. (Jones 1963, Barata 2002, Calabon et al. 2021b), seagrasses: *Posidonia oceanica* (Poli et al. 2022), seaweeds (Sutherland 1915); tunicates (Braconcini et al. 2024), polyurethane panels (Jones & Le Campion-Alsumard 1970).

Many taxa in the *Lulworthiales* have been shown to be active in the decay of wood, particularly the genus *Lulworthia* (Barghoorn & Linder 1944, Meyers & Reynolds 1959a, b). Various aspects of wood decay have been researched: cellulolytic activity (Meyers & Reynolds 1959a, b), microscopic observations (Mouzouras 1986, 1989b), scanning and transmission microscopy (Leightley 1980), weight loss (Mouzouras 1986, 1989b) enzyme activity (Schaumann et al. 1986). *Lulworthia* and *Lulwoana* species cause soft decay with distinctive cavities in the secondary cell wall, resulting in weight losses of selected wood samples. *Lindriella thalassiae* (= *Lindra thalassiae*) has been reported to degrade turtle grass an ecologically important marine flowering plant (Orpurt et al. 1964), while *Haloguignardia* sp. and *Lulworthia kniepii* were reported as parasites on red and brown algae (Kohlmeyer 1973, Alongi et al. 1999). Gall formation in species of the brown algae *Cystoseira* and *Sargassum* was generally caused by *Haloguignardia* spp. (Apt 1988, Alongi et al. 1999). *Lulwoana uniseptata* has been reported in extreme environments, such as saline soils (Hujslova et al. 2010), while Torta et al. (2015) believe that a *Lulwoana* sp. in *Posidonia oceanica* roots helped the host to capture mineral nutrients, through lytic activity by living as an endophyte. *Matsusporium tropicalis* commonly occurs on a variety of substrata, such as, calcareous animal shells, 'chicken bone', endoskeleton of *Seibia* and feathers (Nambiar & Raveendran 2015). Likewise, *Paralulworthia* species have been reported as endophytes of the seagrass *Posidonia oceanica*, from seawater contaminated by oil spills and on submerged wood (Poli et al. 2021).

Chemical diversity

Worldwide production of antibiotics is immense, especially of penicillins (100,000 tons), tetracyclines (5,500 tons) and cephalosporins (2,500 tons) (Jenssen et al. 2021), mostly derived from terrestrial fungi. However, despite the great diversity of marine fungi and the many hundreds of bioactive compounds reported, few have reached commercial production. Indeed, few secondary metabolites has been reported for members of the *Lulworthiales*. One example is the compound lulworthinone (Jenssen et al. 2021), which shows antibacterial activity against reference strains of *Staphylococcus aureus* and *Streptococcus agalactiae*, as well as several clinical MRSA isolates with MICs in the 1.56–6.25 μg/ml range. The compound also had antiproliferative activity against human melanoma, hepatocellular carcinoma, and non-malignant lung fibroblast cell lines, with IC 50 values of 15.5, 27, and 32 μg/ml, respectively. Inhibition of bacterial biofilm formation was observed, but no eradication of established biofilm could be detected. No antifungal activity was observed against *Candida albicans*.

While *Lulworthiales* species have not been widely tested for the production of secondary metabolites, their ability to yield other compounds of commercial interest, such as, lipids, has proven to be more successful (Alves et al. 2020). Abraúl et al. (2023) studied the fatty acid profile of the fungi *Emericellopsis cladophorae* and *Zalerion maritimum* to assess their anti-inflammatory, antioxidant, and antibacterial potential of their lipid extracts. *Zalerion maritimum* was shown to possess high contents of polyunsaturated fatty acids e.g., 34%, including the omega-3 fatty acid 18:3 n-3, and lipid extracts with anti-inflammatory activity of 88% of inhibition at 200 μg lipid mL−1. This lipid did not have any antibacterial properties at the concentrations tested.

The degradation of lignocellulose by members of the *Lulworthiales* is well-documented as exemplified by the studies of Meyers & Reynolds (1959 a, b), and Mouzouras (1986, 1989b). Specific enzymes produced by member of the *Lulworthiales* include: cellulase, xylanase (*Hydeia varia*, *Sammeyersia grandispora*, *Lulworthia* spp.) and illustrates how little has been accomplished. Schaumann et al. (1986) studied exoenzyme production by 37 different *Lulworthia* isolates, concluding that cellulase and gelatinase were produced by all strains, but lacked alginase and chitinase. Some strains yielded peroxidase (95%), amylase (84%), caseinase (76%), and laminarinase (71%).

Magnaporthales **Thongk., Vijaykr. & K.D. Hyde, Fungal Diversity 34: 168 (2009)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Sordariomycetidae*

Introduction

Magnaporthales is an order of *Sordariomycetes*, *Ascomycota*, comprising five families, 36 genera and over 200 species (Zhang et al. 2016b). The accepted families of *Magnaporthales* are *Ceratosphaeriaceae*, *Magnaporthaceae*, *Pseudohalonectriaceae*, *Pyriculariaceae* and *Ophioceraceae* (Hyde et al. 2020d, 2024b). Multi-gene phylogenetic analyses and phylogenomics indicate that these five families form a monophyletic clade with sufficient support (Jiang et al. 2021a). About half of *Magnaporthales* species are devastating pathogens of cereals and other monocotyledonous plants, causing a serious loss in the yield of annual crops in temperate regions (Khemmuk 2017). Additionally, some members of *Magnaporthales* are saprobes and endophytes in the natural environment. *Ceratosphaeriaceae* is a monotypic family containing only *Ceratosphaeria* which is characterized by perithecial, immersed to erumpent ascomata, clavate asci, transversely septate, fusoid, slightly curved ascospores and a harpophora-like anamorph (Crous et al. 2020b). Species of *Ceratosphaeriaceae* live as saprobes on decaying wood or twigs or leaves and are distributed in terrestrial and aquatic habitats (Perera et al. 2016a, Luo et al. 2019b, Manawasinghe et al. 2022, Yang et al. 2023b). *Magnaporthaceae* is the largest family in *Magnaporthales*, comprising 27 genera (Hyde et al. 2024b). *Magnaporthaceae* is characterized by perithecial ascomata with cylindrical, black neck, subcylindrical, short-pedicellate asci with apical ring and filiform or fusoid, hyaline to olivaceous, curved to sigmoid ascospores. Magnaporthaceous species produce hyphomycetous asexual morph which is characterized by branched or unbranched conidiophores, pigmented, phialidic conidiogenous cells and hyaline to pale brown conidia with various shapes (Hyde et al. 2020d). *Pseudohalonectriaceae* contain a single genus *Pseudohalonectria* which is characterized by erumpent to immersed ascomata with conical neck, cylindrical to clavate asci with a thimble-shaped, refractive apical ring, and hyaline to pale brown, cylindrical or ellipsoidal ascospores (Hyde et al. 2020d). *Pyriculariaceae* consists of 11 genera and most members of this family are pathogens to *Poaceae*. The pathogenic species produce an appressorium to penetrate shoots of rice, maize, wheat, bluegrass, and *Digitaria* (Zhang et al. 2016b). *Ophioceraceae* comprises *Ceratosphaerella* and *Ophioceras* (Wijayawardene et al. 2022a).

History

Magnaporthaceae was proposed by Cannon (1994) to accommodate its type genus *Magnaporthe* and five related genera, *Buergenerula*, *Clasterosphaeria*, *Gaeumannomyces*, *Herbampulla* and *Omnidemptus*. *Magnaporthe salvinii*, the type of *Magnaporthe* was originally considered as a member of *Diaporthaceae* in *Diaporthales* (Krause & Webster 1972). Later *Magnaporthe* was rejected in favor of its anamorphic genus *Nakataea* as the latter name was used prior to the former one (Luo & Zhang 2013). Most magnaporthaceous species have necrotrophic or hemibiotrophic nutritional modes, infecting shoot or root system of *Poaceae* and *Cyperaceae* plants through appressoria or hyphopodia (Luo & Zhang 2013). Recent molecular studies revealed that this family has versatile lifestyles containing endophytic and saprobic genera (Luo & Zhang 2013). Thongkantha et al. (2009) introduced a new order *Magnaporthales,* to accommodate a single family *Magnaporthaceae,* on the basis of SSU-LSU rDNA sequences. Klaubauf et al. (2014) introduced two new families into *Magnaporthales*, *Pyriculariaceae* and *Ophioceraceae,* based on the phylogenetic result inferred from a combined LSU/RPB1 alignment. Hongsanan et al. (2017a) introduced *Pseudohalonectriaceae* to accommodate *Pseudohalonectria*, based on the molecular clock analysis of LSU, SSU, TEF1α, and RPB2 sequences. Luo et al. (2019b) separated *Ceratosphaeriaceae* from *Magnaporthaceae* based on phylogenetic analysis of LSU and TEF1α sequences.

General description

Generally, *Magnaporthaceae* species with a parasitic nature tend to develop hyphopodia that serve for attachment and for the absorption of nutrition from the host plant. The hyphopodia are brown, simple or lobed, and these morphologic characteristics are of taxonomic significance in species delimitation (Hernandez-Restrepo et al. 2016). Ascospores of *Magnaporthaceae* are highly diverse. Generally, genera with filiform ascospores commonly came up with simple, pigmented conidiophores with flared collarettes, and curved, aseptate conidia (harpophora-like). Genera with fusiform ascospores tend to produce pigmented median cells, simple, pigmented conidiophores, septate, pyriform to obclavate, pigmented conidia (Hernandez-Restrepo et al. 2016). Most species of *Pyriculariaceae* are established based on their asexual morphs that are characterized by pyriform 2-septate conidia and rhexolytic secession. *Ceratosphaeriaceae*, *Ophioceraceae* and *Pseudohalonectriaceae* often occur as saprobes on decaying wood in aquatic or terrestrial habitats and are characterized by black ascomata with long neck protruding substrate (Klaubauf et al. 2014).

Sexual morph: *Ascomata* perithecial, with short or long necks, ostiolate, yellow, brown or black, often staining substrate, immersed or superficial. *Peridium* consisting of a conspicuous outer layer of brown, thick-walled, angular cells and a distinguishable inner layer of hyaline, thin-walled, flatten cells. *Paraphyses* cylindrical, cellular, septate, wide at the base and gradually tapering toward the apex. *Asci* cylindrical, 8-spored, unitunicate, with a refractive apical. *Ascospores* septate, fusoid to clavate, often filiform, hyaline to yellow-brown, guttulate or eguttulate, smooth-walled, without appendage or gelatinous sheath. Asexual morph: *Mycelium* comprises smooth, branched, septate hyaline to pale brown hyphae. *Conidiophores* macronematous, hyaline to pale pigmented, thick-walled, solitary or loosely aggregated, branched or unbranched, cylindrical, erect. *Conidiogenous cells* monoblastic or polyblastic, integrated, producing holoblastic conidia sequentially from denticulate loci. *Conidia* hyaline to yellow-brown, typically unicellular to 2–3-septate, obpyriform, obclavate, or fusoid, with a distinct truncate basal scar (Figs. 226, 227).

Families included in *Magnaporthales*

Ceratosphaeriaceae Z.L. Luo, H.Y. Su & K.D. Hyde
Magnaporthaceae P.F. Cannon
Ophioceraceae Klaubauf, E.G., LeBrun & Crous
Pseudohalonectriaceae Hongsanan & K.D. Hyde
Pyriculariaceae Klaubauf, E.G., LeBrun & Crous

Evolution

Terrestrial habits and a saprotrophic lifestyle are speculated as the plesiomorphies of the *Sordariomycetes* fungi according to recent phylogenetic analysis (Vijaykrishna et al. 2006, Zhang et al. 2006, Schoch et al. 2009a). *Magnaporthales* diverged from other *Sordariomycetes* ca. 31 MYA and shifted from a terrestrial to an aquatic environment but maintained the ancestral saprotrophic lifestyle (Luo et al. 2015b, Zhang et al. 2018c). Meta-analysis has revealed that *Magnaporthales* species have geographical, host, and tissue specificities. *Magnaporthales* species were mainly reported from middle and low latitudes, while almost none of them can be found in high altitudes (Feng et al. 2021). *Gaeumannomyces*, *Magnaporthiopsis*, and *Pyricularia* are the best studied and widespread genera, thus, the global geographic information map of them was made to show the distribution of different species in each genus. This research resulted in the finding that the three genera have characteristics of host-specificity, indicating that their geographical distribution depends on their host distribution. The evolutionary history of nutrition and infection mode has been inferred from phylogenomic analysis of 82,715 amino acid positions derived from 226 genes, which has revealed three main lineages in *Magnaporthales*, which correspond to *Magnaporthaceae*, *Pyriculariaceae* and *Ophioceraceae* (Luo et al. 2015b). *Ophioceraceae* is the earliest-diverging clade in *Magnaporthales*. *Ophioceraceae* mainly contains saprobic species that are associated with submerged wood in freshwater habitats and this family split from the assemblages of *Magnaporthaceae* and *Pyriculariaceae* at ca. 24 MYA (Zhang et al. 2018c).

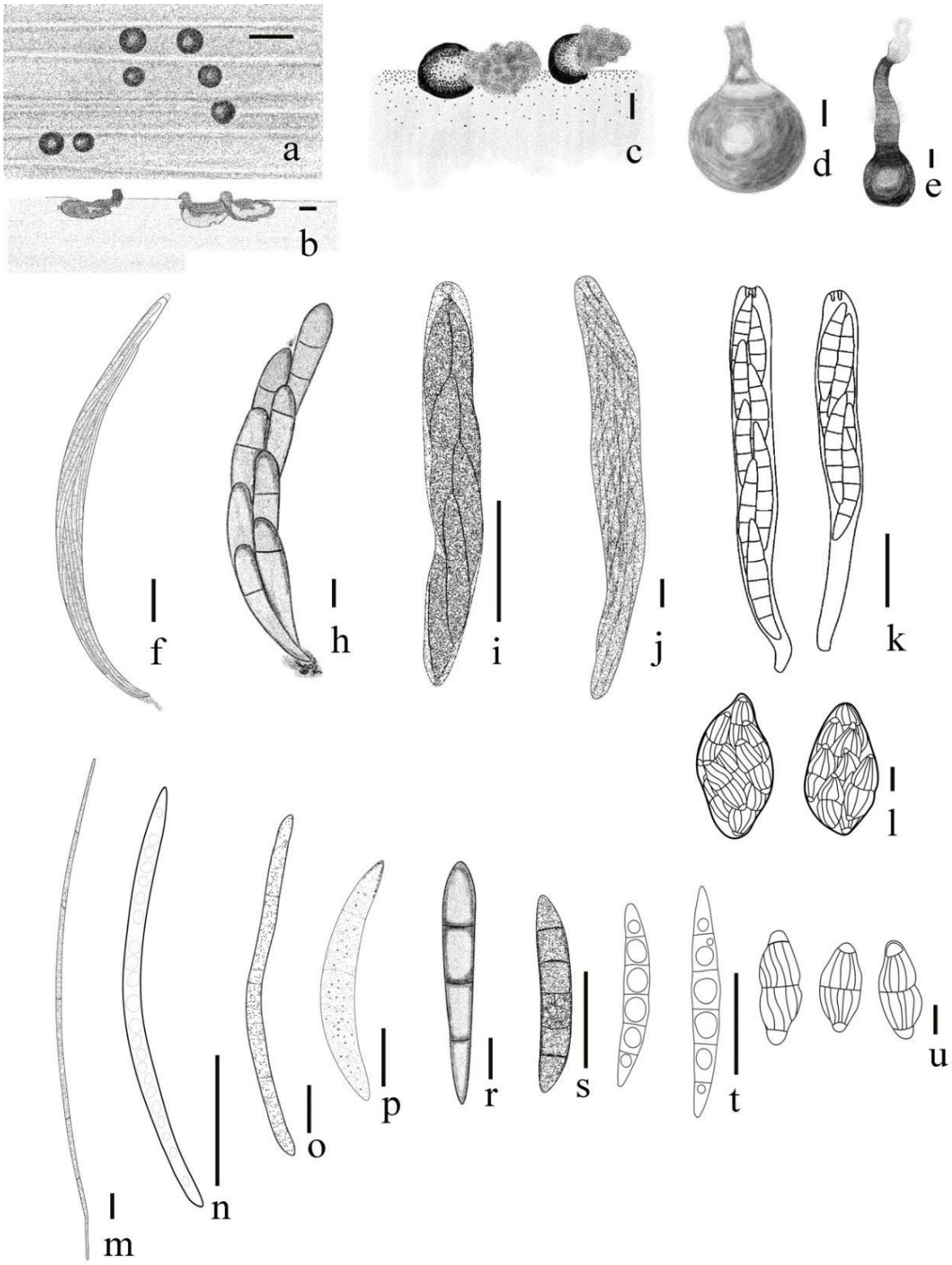


Figure 226 – Sexual morph of *Magnaporthales*. a Sclerotia. b Vertical section of immersed perithecia c–e Ascomata. f–l Asci. m–o Ascospores (a, p *Nakataea oryzae.* b *Plagiosphaera immerse.* c, l, u *Budhanggurabania cynodonticola.* d *Gaeumannomyces oryzicola.* e *Magnaporthiopsis poae.* f, m *Kohlmeyeriopsis medullaris.* h, r *Buergenerula spartinae.* i *Pseudohalonectria lutea.* j, o *Plagiosphaera immersa*. k, t *Herbampulla crassirostris.* n *Aquafiliformis lignicola*). (redrawn from Yao et al. 1992, Scheuer & Nograsek 1993, Luo & Zhang 2013, 2022, Klaubauf et al. 2014, Crous et al. 2015d, Wong et al. 2015, Hernández-Restrepo et al. 2016, Luo et al. 2019b, Song et al. 2019). Scale bars: a = 200 µm, b, c = 100 µm, d = 50 µm, g = 40 µm, f, k, n, p = 20 µm, e, h, j, o, r, l, u = 10 µm.

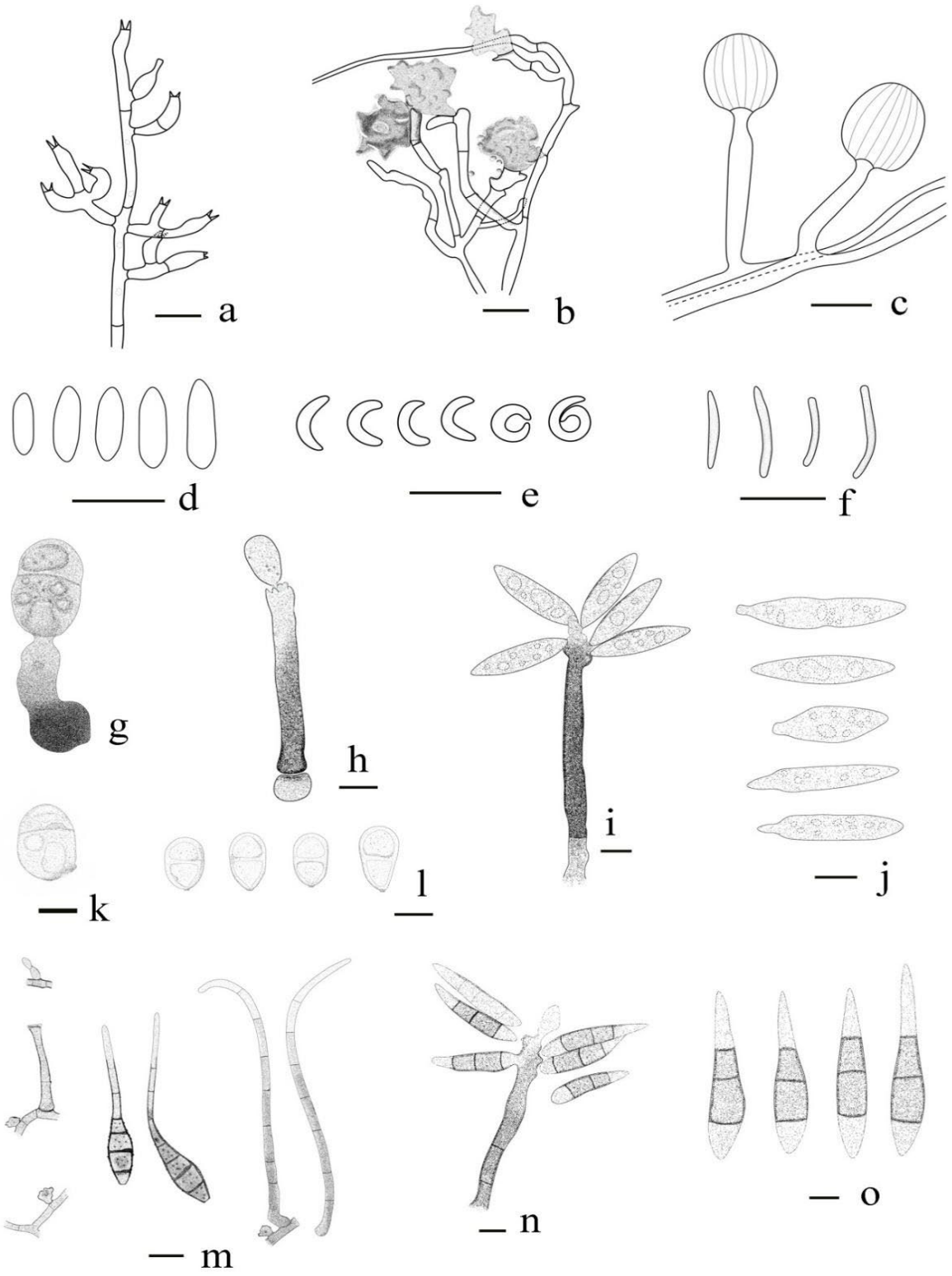


Figure 227 – Asexual morph of *Magnaporthales*. a, c, h–i, m, n Conidiophores. b Appressorium. d e, f, k, l, j, o Conidia (a *Gaeumannomyces arxii.* b *Gaeumannomyces glycinicola.* c, f *Ceratosphaeria lampadophora.* d, e *Gaeumannomyces walkeri.* g, k *Deightoniella roumeguerei.* h, l *Neocordana musae.* i, j *Macgarvieomyces juncicola.* m *Clasterosphaeria cyperi.* n, o *Pyriculariopsis parasitica*). (redrawn from Sivanesan 1984, Klaubauf et al. 2014, Hernández-Restrepo et al. 2015, Luo & Zhang 2022). Scale bars: m = 25 μm, a–l, n, o = 10 μm.

Pyriculariaceae cause blast diseases on aerial tissue of *Poaceae* and other monocot plants using an appressorium and produce pyricularia-like asexual morphs. *Magnaporthaceae* generally produce phialophora-like asexual state and infect the plant root. The split between *Pyriculariaceae* and *Magnaporthaceae* occurred about 21 MYA (Luo et al. 2015a, Zhang et al. 2018c).

Justification of order and problems

Species with harpophora-like conidiophores were originally accommodated to *Harpophora* based on phenotypic traits (Gams 2000). However, phylogenetic analysis showed that species with harpophora-like conidiophores are polyphyletic in *Magnaporthales*, thus, a combination of characters, including teleomorph, host range, pathogenicity, conidial morphology, as well as molecular evidence, is deserved to differentiate genera in *Magnaporthales*. Additionally, some genera of *Magnaporthales* are lacking sufficient molecular data to clarify their affinity with other genera. Such a case can be seen in *Pseudohalonectria* (Perera et al. 2016b). Therefore, more under-sampled taxa are needed for future phylogenetic analysis to better understand their evolution and to re-evaluate the current taxonomy.

Significance

Ecological and economic roles

Nutritional modes of *Magnaporthaceae* species are diverse, ranging from pathogens, saprobes, to endophytes and are distributed in both terrestrial and aquatic habitats. Members of this family have been found on all parts of the host plant, including leaf, stem and root (Huhndorf et al. 2008, Yuan et al. 2010, Luo & Zhang 2013, Klaubauf et al. 2014, Hernández-Restrepo et al 2016). *Magnaporthales* species have various ecological niches that are phylogenetically informative. A phylogenetic study of *Magnaporthales* based on combined ACT/ITS/RPB1 sequences has revealed clearly distinguished clades that correspond well corresponding to their ecological characters. *Magnaporthaceae* and *Pyriculariaceae* are the two major families that contain many pathogenic species. *Gaeumannomyces graminis* is a notorious pathogenic species in *Magnaporthaceae*. It is well-known as the causal agents of take-all disease on cereal crops and grasses (Hernandez-Restrepo et al. 2016).

Magnaporthales is a well-known, economically important order that contains many destructive phytopathogens. *Pyricularia oryzae* (syn. *Magnaporthe oryzae*, *Magnaporthe grisea*) is a model organism for studying the interaction between a pathogenic fungus and host plant (Tan et al. 2023). Rice infected by *Pyricularia oryzae* initially presents white to grey-green lesions or spots with darker borders. Older lesions are elliptical or spindle-shaped and whitish to grey with necrotic borders, and in the end, lesions may enlarge and coalesce to kill the entire leaf (Rodrigues et al. 2017). This pathogen causes rice blast, preventing maturation of the actual grain and thus reducing the yield of crops, which could feed over 60 million people worldwide (Scardaci et al. 2003). *Gaeumannomyces graminis* is a causal agent of take-all disease on various hosts, including wheat, barley, rye as well as grass such as Bromegrass, Quackgrass, and Bentgrass (Hernandez-Restrepo et al. 2016). The infected plants show the symptoms of yellowing, stunting, reduced tillers and bleached seed heads in the initial stage. Later, the plant can easily be pulled out from the soil as the root system has been destroyed because of the blackening of the crown and stem base (Kwak & Weller 2013). Summer patch is a turfgrass disease caused by *Magnaporthiopsis poae* (Wong et al. 2022). A lawn infected with summer patch will appear as irregular patches, rings, and crescents. The pathogen attacks the roots of grass before the symptoms can be observed. Large patches will often appear suddenly with no indication of previous disease activity (Wong et al. 2022). *Pyriculariaceae* cause blast diseases on aerial tissue of *Poaceae* and other monocot plants using an appressorium and produce pyricularia-like asexual morphs (Luo et al. 2015a, Zhang et al. 2018c).

Chemical diversity

Filamentous fungi are active producers of a variety of secondary metabolites, including mycotoxins, antibiotics, and other pharmaceutically useful small molecules (Enespa & Chandra 2019). It is not exceptional for taxa of *Magnaporthales*. Secondary metabolites of *Pyricularia* spp.

may be involved in rice infection (Motoyama et al. 2021). The rice blast fungus, *Pyricularia oryzae* has been reported to produce Tenuazonic acid (TeA) that is toxic to mammals, posing a threat to the food safety in human (Yun et al. 2017). In addition, terrestric acid is another phytotoxic metabolites isolated from *Pyricularia oryzae*, which has an adverse influence on growth of root and chlorophyl synthesis (Nukina 1988). Pyrichalasin H is a phytotoxic metabolite derived from *Pyricularia grisea* that has strong inhibitory activity to the growth of rice seedlings (Nukina 1987).

***Meliolales* Gäum. ex D. Hawksw. & O.E. Erikss., Systema Ascomycetum 5(1): 180 (1986)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Sordariomycetidae*

Introduction

Meliolales, the largest order of epifoliar fungi, primarily consists of biotrophic and obligate parasitic fungi found in tropical and subtropical regions (Bermúdez-Cova et al. 2022). This order comprises two families (*Armatellaceae* and *Meliolaceae*) and eight genera (Zeng et al. 2020). They occur on the surface of leaves, petioles, and twigs, and occasionally appear on fruits as well. The globally recorded species of *Meliolales* are approximately 3,064 (Piepenbring et al. 2011, Hongsanan et al. 2015b, Zeng et al. 2017, Bermúdez-Cova et al. 2022). These fungi are also known as "black mildews" or "dark mildew," manifest as colonies of black, densely constructed, branched superficial hyphae (Rodriguez Justavino et al. 2015). These species are characterized by branched, dark brown superficial mycelium with two-celled hyphopodia, globular to subglobose dark brown perithecia, and dark brown septate ascospores (Zeng et al. 2020).

History

Hawksworth & Eriksson (1986) initially introduced *Meliolales* to encompass *Meliolaceae*, and later on, Hosagoudar (2003) expanded this to include the *Armatellaceae*. Lumbsch & Huhndorf (2010), supported by Hongsanan et al. (2015b, 2017a) and Maharachchikumbura et al. (2016), positioned *Meliolales* within *Sordariomycetes*. Hongsanan et al. (2015b) thoroughly examined the genera in *Meliolales*, while Zeng et al. (2017) compiled a checklist for identifying various species of *Meliolales* based on the host information. Zeng et al. (2018) also devised a proficient DNA protocol to extract DNA from *Meliolaceae* species. In a recent phylogenetic analysis by Zeng et al. (2020), based on LSU, SSU, and ITS data, it was demonstrated that *Meliolales* could be divided into four distinct clades at the generic level (*Meliola*, *Irenopsis*, *Asteridiella*, and meliola-like), despite exhibiting similar appearances that sometimes overlap.

General description

Members of *Meliolales* are usually characterized by a biotrophic habitat, superficial or rarely immersed dark hyphae with lateral hyphopodia and/or phialides. Many genera of *Meliolales* have superficial, globose to subglobose or flattened ascomata that develop on the black, web-like colonies, bearing a dark peridium and ascomatal appendages, with the exception of *Amazonia* possessing flattened thyriothecia. Asci are unitunicate, usually 2–4-spored, with brown, 3–4-septate ascospores (Mibey & Hawksworth 1997, Hosagoudar & Riju 2013). The asexual morph of *Meliolaceae* species has been reported as phialides on hyphae, however, they are morphologically and phylogenetically poorly studied.

Colonies epiphyllous or hypophyllous. *Hyphae* superficial, brown, straight to flexuous, septate, branched, reticulate, with hyphopodia and phialides. *Hyphopodia* alternate to unilateral or opposite, 2-celled, brown. *Setae* straight to hooked, dark brown, forming on hyphae or ascomata. Sexual morph: *Ascomata* superficial, membranaceous or carbonaceous globose to subglobose with 1 to multi-loculate, or as flattened thyriothecia in *Amazonia*. *Peridium* comprising hyaline inner stratum, and dark brown outer stratum of *textura angularis*. *Paraphyses* evanescent. *Asci* 2–4-spored, unitunicate, asci wall attenuated or broken when mature, without a fixed shape. *Ascospores*

ellipsoidal to oblong, aseptate or 3–4-septate, constricted at the septum, hyaline or becoming brown when mature. Asexual morph: *Phialides* ampulliform or flask-shaped on hyphae. *Conidiogenous cells* formed directly from vegetative hyphae. *Conidia* unicellular, small and hyaline (Figs. 228, 229).

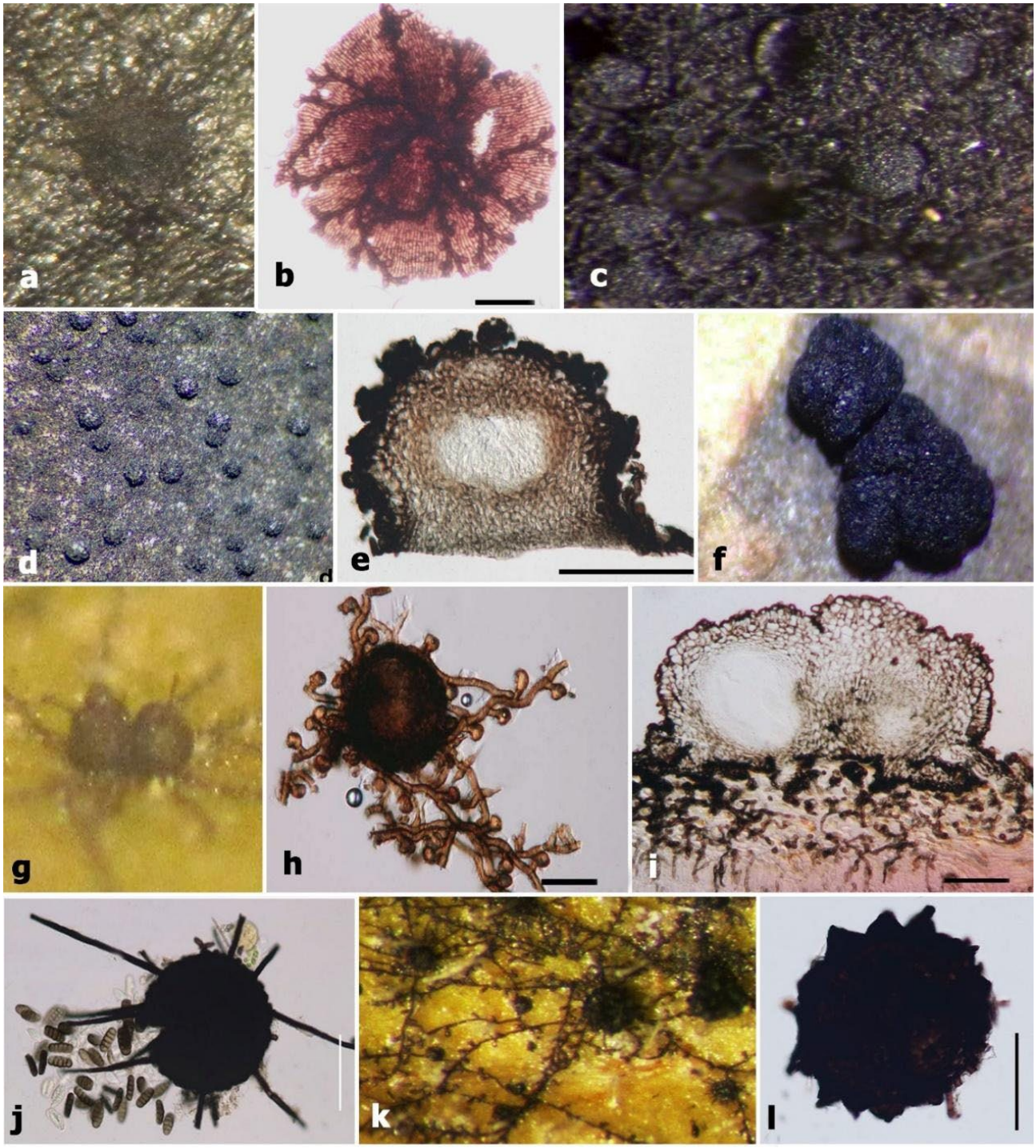


Figure 228 – Ascomatal morphology of *Meliolales*. a, b *Amazonia* sp. c *Cryptomeliola* sp. d, e *Armatella* sp. f, i *Endomeliola* sp. g, h *Irenopsis* sp. j *Meliola* sp. k, l *Asteridiella* sp. (adapted from Hongsanan et al. (2015b) and Marasinghe et al. (2020)). Scale bars: b = 50 µm, h, j, l = 100 µm.

Families included in *Meliolales*

Armatellaceae Hosag.

Meliolaceae G.W. Martin ex Hansf.

Evolution

Hongsanan et al. (2016b) estimated the crown age of *Meliolales* as 135 MYA and Hyde et al. (2020d) estimated it as 219 MYA. There are 14 *Meliolinites* species recorded from different paleomycological studies. These fossils are common during the Eocene to Miocene, where Samarakoon et al. (2019) re-described *Meliolinites* species with line drawings and estimated the minimum age for *Meliola* as 54 MYA. Bera et al. (2022) reported a complete morphology of *Meliolinites bhutanensis* dated back to the late Miocene Pliocene.

Justification of order and problems

The taxonomy of *Meliolales* becomes complicated due to the scattered taxonomic descriptions with insufficient data and a lack of sequence data (Bermúdez-Cova et al. 2022). Consequently, taxonomic placements of certain genera and species remain uncertain within *Meliolales* (Bermúdez-Cova et al. 2022). Historical identification of meliolaceous taxa mainly depended on host-based interpretation of taxa might inadvertently lead to the repetitive re-establishment of the same taxa. Due to their biotrophic nature, it is difficult to obtain molecular data by cultivating them on artificial media, and direct DNA extraction is commonly used by mycologists. Some genera within this order are yet to undergo sequencing, necessitating fresh collections of their prototype species to obtain molecular data.

Significance

Ecological and economic roles

The occurrence of *Meliolales* is more frequent during the cooler seasons in scrublands or open park areas situated in tropical and subtropical regions with annual dry periods (Hansford 1961, Goos & Andersons 1974, Hongsanan et al. 2015b). Species of this order can be readily distinguished by the blackened layer of mycelium appearing on the leaf surface. They are biotrophic and develop hyphopodia that penetrate the leaf surface, enabling them to extract nutrients from the host plants. However, this process does not result in significant harm to the host except for the reduction in essential components such as chlorophyll, starch, sugars, proteins, and amino acids (Hosagoudar et al. 1997a, Old et al. 2003). Furthermore, the darkened mycelium covering the host leaf surfaces can reduce the efficiency of photosynthesis and increase the temperature of the leaf surfaces (Hosagoudar et al. 1997a, Hosagoudar & Raju 2013, Hongsanan et al. 2015b). The extensive growth of these species also exerts notable impacts on agricultural crops, leading to decreased yield and reducing the marketable price of fruits (Wellman 1972).

Chemical diversity

No relevant studies are available for the chemical diversity of *Meliolales*.

Other relevant data and future recommendations

Species of *Meliolales* are widely distributed all over the world, but mostly lack molecular data. Some genera (*Amazonia*, *Armatella*, *Cryptomeliola* and *Endomeliola)* have never been sequenced yet and are accommodated in uncertain placements in *Meliolales*. Therefore, it is vital to recollect representative species of these genera and obtain molecular data to confirm their placements in *Meliolales*. Studies regarding the ecological and pathogenic aspects of meliolaceous fungi are inadequate. Host-specificity of this order has not been confirmed, and future studies are needed to confirm the validity of the host-based nomenclatural approach for identifying species of *Meliolales*. Extensive sampling from different habitats and hosts is needed to increase the understanding of these fungi, as well as the sexual and asexual connections.

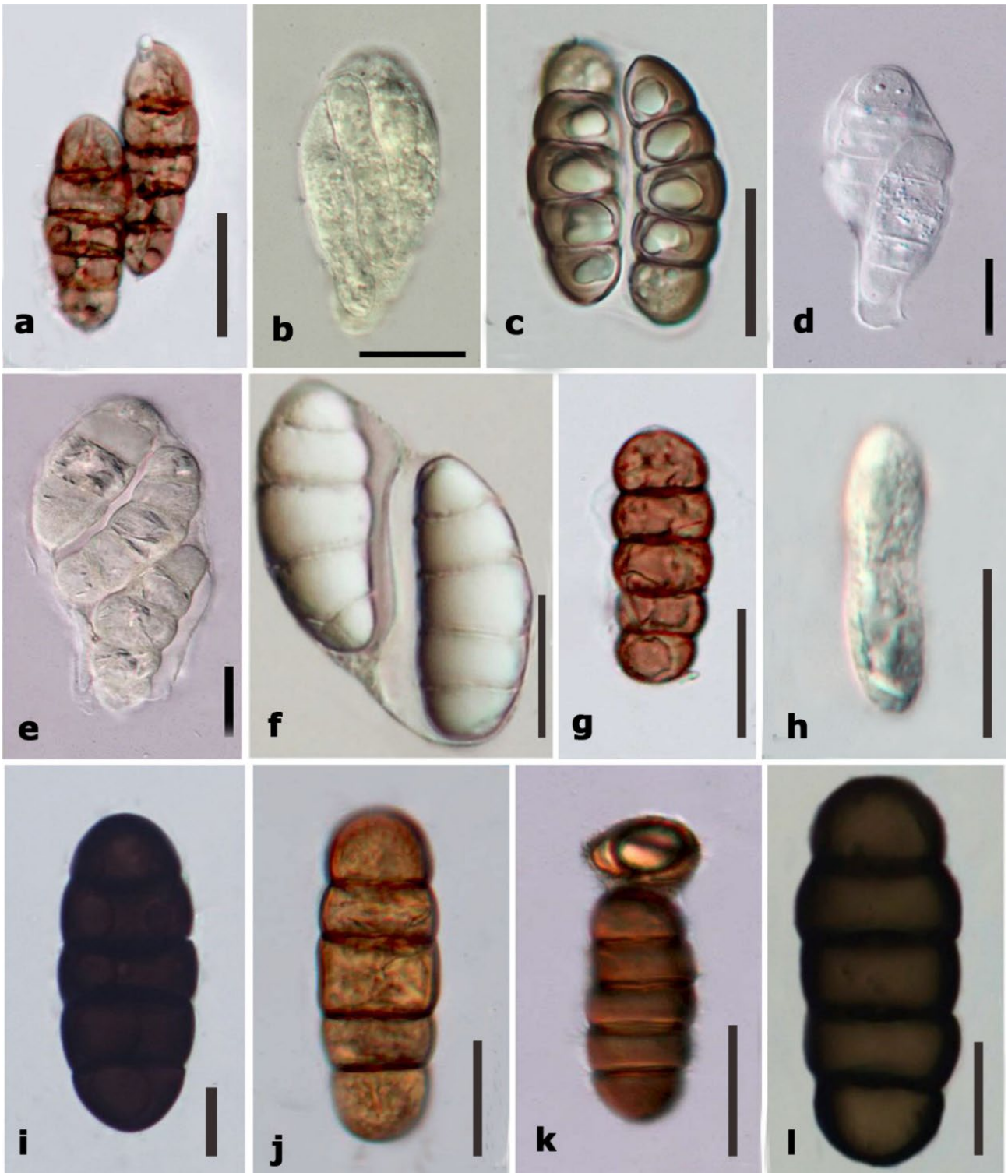


Figure 229 – Asci and ascospores morphology of *Meliolales*. a, g *Amazonia* sp. b, h *Armatella* sp. c, i *Asteridiella* sp. d, k *Irenopsis* sp. e, g *Endomeliola* sp. f, l *Meliola* sp. j *Cryptomeliola* sp. (adapted from Hongsanan et al. (2015b)). Scale bars: a–f = 20 µm, g–l = 10 µm, i–k, n = 10 µm.

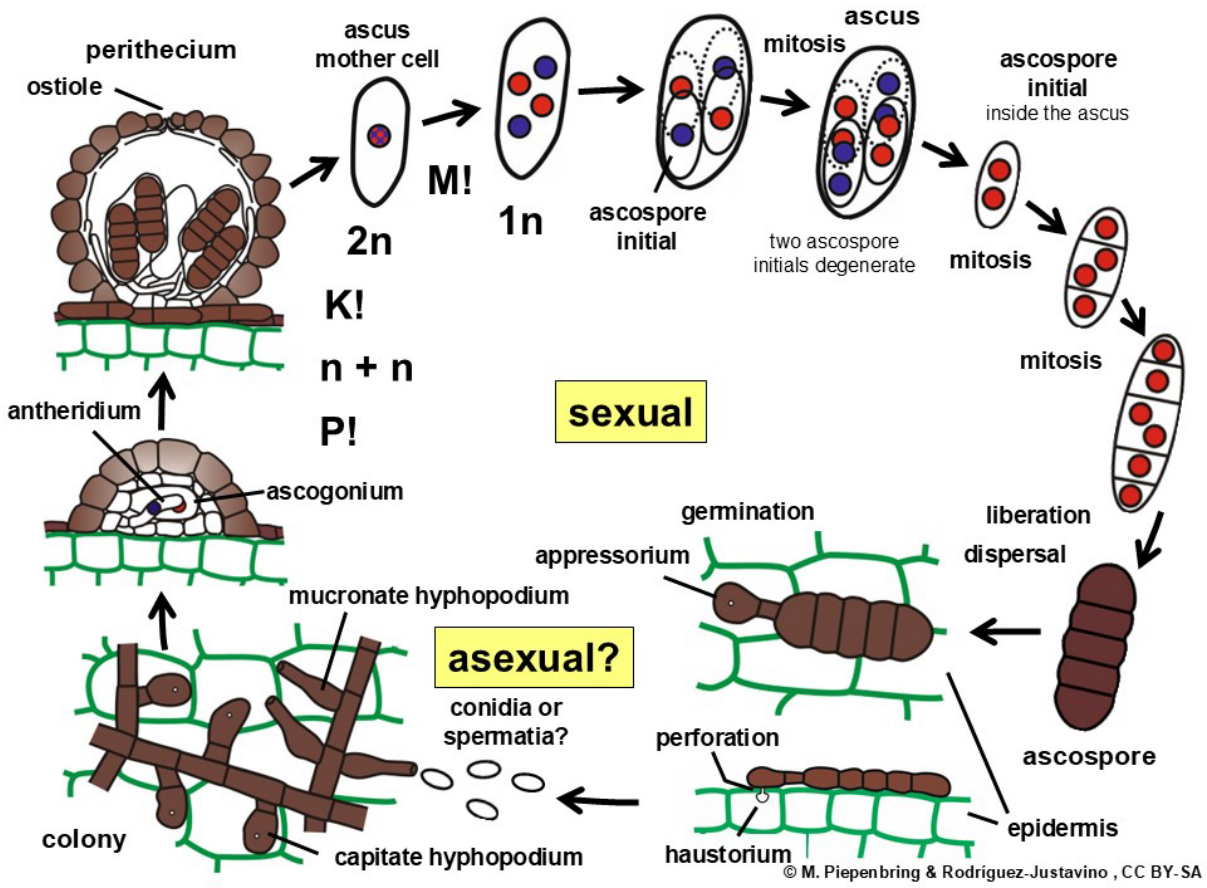


Figure 230 – Sexual and asexual life cycles of *Meliolales* (From Mycological teaching diagrams by Meike Piepenbring (2023)). Abbreviations: 1n = haploid, 2n = diploid, P! = plasmogamy, K! = karyogamy, M! = meiosis. Black and white circles represent haploid nuclei of different mating types, circles of both colors represent diploid nuclei.

Microascales **Luttr. ex Benny & R.K. Benj., Mycotaxon 12(1): 40 (1980)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Hypocreomycetidae*

Introduction

Microascales, an order within the subclass *Hypocreomycetidae* and class *Sordariomycetes*, represents a diverse and ecologically significant group of fungi. First described by Benny & Kimbrough (1980), this order has since been expanded to include nine families, *viz*. *Ceratocystidaceae*, *Chadefaudiellaceae*, *Cornuvesicaceae*, *Gondwanamycetaceae*, *Graphiaceae*, *Halosphaeriaceae*, *Microascaceae*, *Synnematotriadelphiaceae* and *Triadelphiaceae*. According to recent studies, *Microascales* is classified into 127 genera (Wijayawardene et al. 2022a, Bao et al. 2023, Mapook et al. 2023). *Microascales* predominantly consists of saprobic fungi and they exhibit a remarkable adaptability to a range of habitats, including plant and wood surfaces, algae, mammal dung, compost, polluted water and soil (Bao et al. 2023, Mapook et al. 2023). One of the interesting aspects of *Microascales* is their pathogenic and parasitic capabilities. Some species within this order exhibit pathogenic tendencies towards insects, animals, plants and even humans. Notably, research by de Hoog et al. (2011a), Sandoval-Denis et al. (2013, 2016a, c), Lackner et al. (2014), and Kylle et al. (2020) has revealed species that parasitize beetles and flies, demonstrating a complex interaction with other organisms. Morphologically, most *Microascales* species are characterized by the absence of stroma and the presence of perithecial ascomata, which may or may not have an ostiole. A distinctive feature of their reproductive strategy is the production of percurrently proliferating

conidiogenous cells, known as annellides. Additionally, some families within this order exhibit chlamydospore-like or aleurioconidial synanamorphs, as noted by Abbott et al. (1998). The study of *Microascales* is crucial for understanding fungal biodiversity and ecology, which has significant implications, such as agriculture and environmental management, given their diverse roles and interactions within various ecosystems.

History

Eriksson (2006) demonstrated that *Hypocreomycetidae* forms a monophyletic clade within *Sordariomycetes*, comprising four orders, *viz*. *Coronophorales*, *Halosphaeriales*, *Hypocreales* and *Microascales*. *Halosphaeriales* was initially placed under *Microascales*, making *Microascales* paraphyletic (Hibbett et al. 2007). However, Hyde et al. (2020d) presented evidence that *Microascales* is a monophyletic clade based on their multi-gene phylogenetic analysis. This finding is in agreement with studies by Maharachchikumbura et al. (2015, 2016) and Hongsanan et al. (2017a). In the outline of *Ascomycota*, Wijayawardene et al. (2022a) recognized 111 genera within *Microascales*. Bao et al. (2023) introduced a new family, *Cornuvesicaceae*, to accommodate the genus *Cornuvesica* within *Microascales*. Additionally, Mapook et al. (2023) validated *Graphiaceae* as a separate family within the order *Microascales*, accommodating the genus *Graphium* and providing a registration identifier, along with corrected type citations and reference to the original descriptions. Chuaseeharonnachai et al. (2020) established that the genus *Synnematotriadelphia* forms a basal taxon to *Triadelphia* and is positioned in the family *Triadelphiaceae*. In a recent phylogenetic analysis, Mapook et al. (2023) used ITS, LSU, SSU and RPB2 data to introduce *Synnematotriadelphiaceae* as a distinct family within *Microascales*, placing it in a clade comprising *Triadelphiaceae* and *Graphiaceae*. Currently, *Triadelphiaceae* consists of *Triadelphia* and *Synnematotriadelphiaceae* includes *Synnematotriadelphia* (Mapook et al. 2023).

General description

Microascales is characterized by the absence of stroma and the presence of black perithecial ascomata with long necks, or, more rarely, cleistothecial ascomata that lack paraphyses. The asci are roughly spherical and short-lived, developing either singly or in chains. The aseptate or aseptate, colorless ascospores often feature ornamenting ridges or wings. In the family *Microascaceae*, the anamorphs produce percurrently proliferating conidiogenous cells.

Sexual morph: *Ascomata* perithecial to elongate, immersed to semi-immersed, becoming superficial, aggregated to scattered, globose, subglobose to obpyriform or ovoid, carbonaceous, light brown or dark brown to black. Clothed with spines or digitate or stellate appendages, ornamented or unornamented or within undifferentiated ornamental hyphae, the upper part formed from anastomosing setae. *Ostioles* lacking or papillate to long cylindrical, ostiolar canal with periphyses or pseudoparenchyma. *Peridium* psedoparenchymatous, thick- or thin-walled cells, composed of *textura angularis* embedded in the substrate and with an aerial "capillitium". *Paraphyses* lacking. *Asci* 8-spored, unitunicate, smooth-walled, fusiform, clavate or rarely subglobose to globose with or without apical structures. *Ascospores* overlapping, aseptate, hyaline to pale brown, cylindrical to ellipsoidal or fusiform, appendages or gelatinous sheaths or both. Asexual morph: *Hyphomycetous*, forming arthrospores. *Hyphae* hyaline or brown, superficially or immersed, septate, branched. *Conidiophores* mononematous, macronematous or sporodochial to synnematous, single or aggregated in sporodochia or synnematous, smooth-walled, septate, hyaline or mid to dark brown, tapering towards apex, unbranched or branched. *Conidiogenous cells* phialidic, with annellidic extensions, borne terminally or laterally on vegetative hyphae, short simple or little branched, oblong cylindrical to flask-shaped gradually tapering to the apex, hyaline or pale brown. *Conidia* aseptate, smooth-walled, in chains, varied in shape, cylindrical to oblong or allantoid, globose to subglobose, rectangular, obocate or clave, hyaline or pale yellow to dark brown (adapted from Sandoval-Denis et al. 2016c, Cho et al. 2020). (Figs. 231, 232, 233).

Families included in *Microascales*

Ceratocystidaceae Locq. ex Réblová, W. Gams & Seifert

Chadefaudiellaceae Faurel & Schotter ex Benny & Kimbr.
Cornuvesicaceae D.F. Bao, K.D. Hyde & Z.L. Luo
Gondwanamycetaceae Réblová, W. Gams & Seifert
Graphiaceae De Beer
Halosphaeriaceae E. Müll & Arx ex Kohlm.
Microascaceae Luttr. ex Malloch
Synnematotriadelphiaceae Mapook & K.D. Hyde
Triadelphiaceae Y.Z. Lu, J.K. Liu, Z.L. Luo & K.D. Hyde

Microascales genera *incertae sedis*
Bisporostilbella Brandsb. & E.F. Morris
Cephalotrichiella Crous
Gabarnaudia Samson & W. Gams
Nautosphaeria E.B.G. Jones
Parasporendocladia W.P. Wu & Y.Z. Diao
Sporendocladia G. Arnaud ex Nag Raj & W.B. Kendr.
Tubakiella Sakay., K.L. Pang & E.B.G. Jones

Evolution

The evolutionary status of *Microascales* has been substantiated by divergence times estimated to be between 171–241 MYA, as supported by Hongsanan et al. (2017a). There is robust support for the classifications of *Hypocreales*, *Torpedosporales* and *Microascales* within the Maximum Clade Credibility (MCC) tree. Most families within the subclass *Hypocreomycetidae* are well-supported and align with the recommended divergence times. However, the placement of *Graphiaceae* within *Microascales* necessitates further investigation due to its stem age of 166 MYA and its well-supported placement in both phylogenetic and MCC trees. Hyde et al. (2020d) have estimated the divergence time for *Microascales* at approximately 216 MYA. *Microascales* species are found in both terrestrial and aquatic habitats.

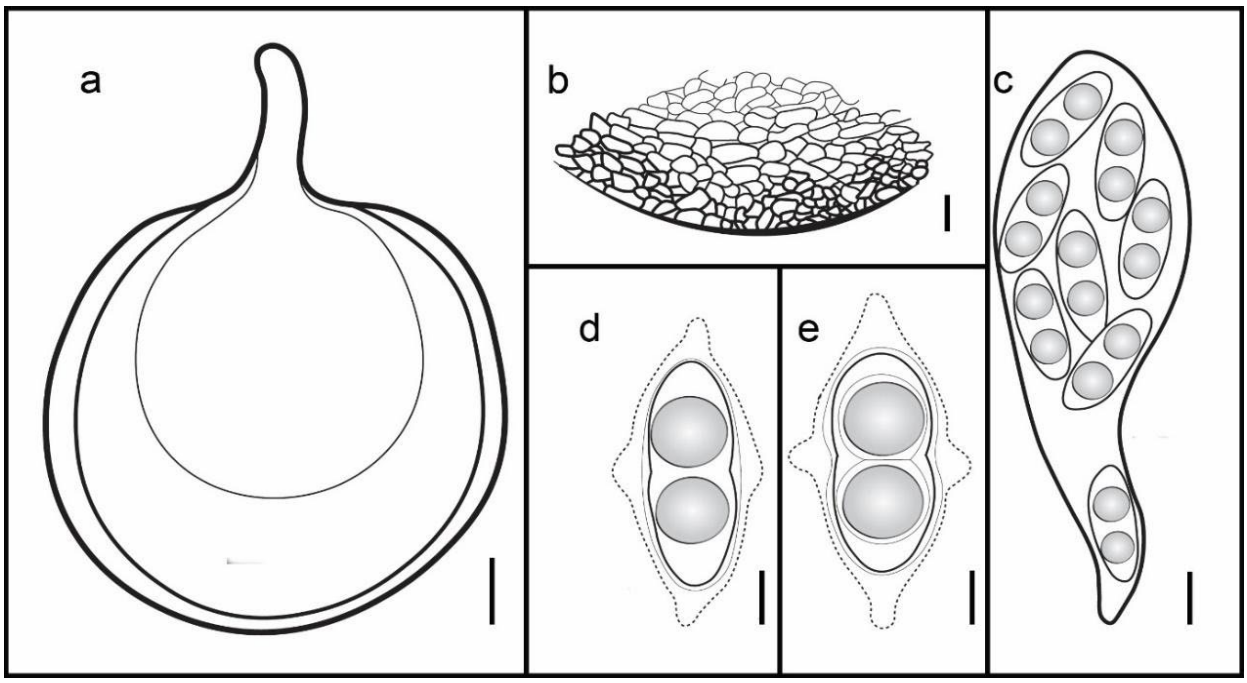


Figure 231 – Sexual morph of *Microascales*. a Ascoma. b Thick, two-layered peridium. c Ascus. d, e Ascospores (a–e *Ebullia octonae*) (drawn from Chu et al. 2015). Scale bars: a = 100 μm, b = 20 μm, c = 10 μm, d, e = 5 μm.

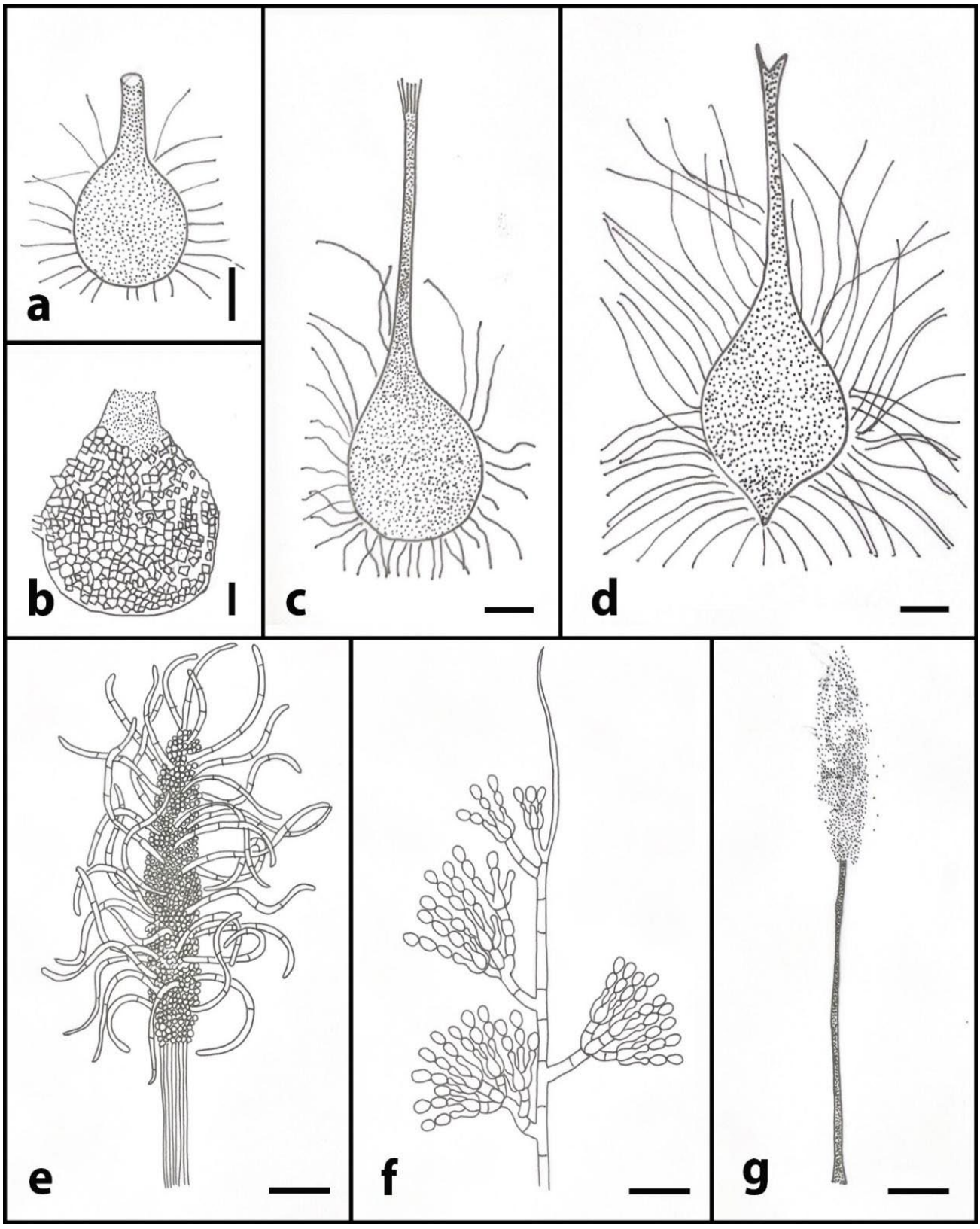


Figure 232 – Asexual and sexual morphs of *Microascales*. a, b Conidioma of *Huntiella chinaeucensis*. c Conidioma with a neck with a thickened base of *Ceratocystis quercicola.* d Ascoma densely covered with dark, fertile hyphae of *Ceratocystis quercicola*. e. Young synnema showing setae of *Trichurus gorgonifer*. f Hyphae and penicillate conidiophores of *Trichurus gorgonifer*. g Synnemata of *Cephalotrichum asperulum* (drawn or redrawn from Sandoval-Denis et al. 2016a, Cho et al. 2020). Scale bars: a–d = 100 µm, e–g = 200 µm.

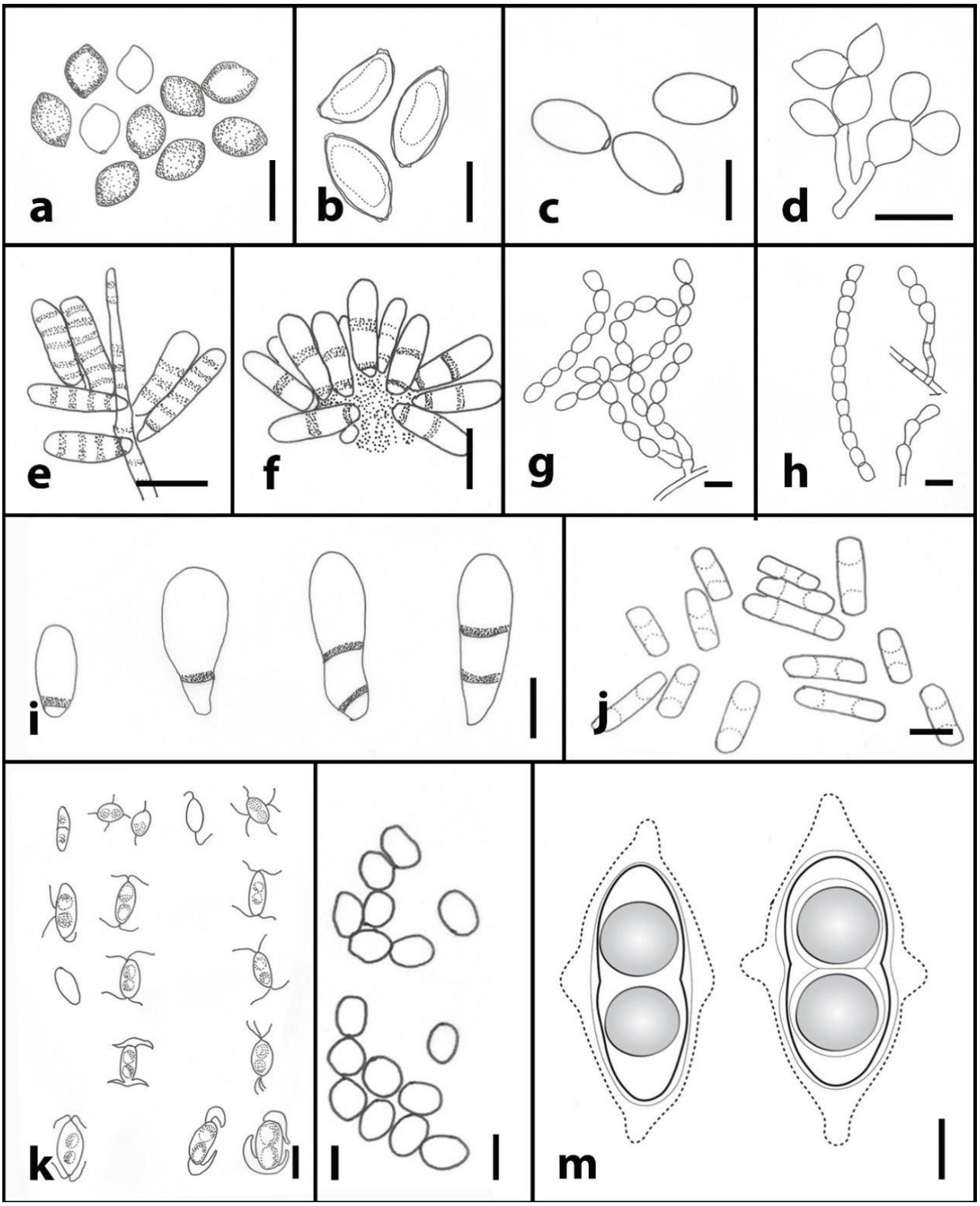


Figure 233 – Spores morphology in *Microascales*. a, b Conidia of *Cephalotrichum microsporum*. c Conidia of *Acaulium caviariforme*. d Polyblastic conidiogenous cells and conidia of *Cephalotrichum hinnuleum*. e A cluster of chlamydospores and phialides of *Berkeleyomyces basicola*. f Conidiophores with conidia of *Triadelphia hexaformispora*. g. Conidia of *Cephalotrichum brevistipitatum*. h Chain of barrel-shaped conidia and Aleuriospores showing basauxic generation of *Ceratocystis quercicola*. i. Conidial types of *Triadelphia mukdahanensis*. j Endoconidia of *Berkeleyomyces rouxiae*. k Type of conidia of *Remispora* spp. l Ascospores of *Ceratocystis quercicola.* m Ascospores with a sheath of *Ebullia octonae* (drawn or redrawn from Chu et al. 2015,

Sandoval-Denis et al. 2016a, Nel et al. 2018, Cho et al. 2020, Chuaseeharonnachai et al. 2020, Mapook et al. 2023). Scale bars: a–c, i = 5 μm, d–h, j–m = 10 μm.

In terrestrial habitats, most species produce asexual morphs with hyphomycetes and coelomycetes, which facilitates the widespread dispersion of their reproductive structures as a survival mechanism. This is supported by the work of de Beer et al. (2014), Sandoval-Denis et al. (2016a, c), Nela et al. (2018) and Cho et al. (2020). Conversely, most species in aquatic habitats produce sexual morphs, thereby protecting their reproductive structures. Additionally, they produce spores with appendages, which serve as a mechanism to spread their spores effectively (Shearer & Miller 1977, Sakayaroj et al. 2005b, Chu et al. 2015, Li et al. 2016b).

Justification of order and problems

The taxonomy of *Microascales* is challenging due to scattered taxonomic descriptions that often lack sufficient data and are missing sequence data (Li et al. 2016b). As a result, the taxonomic placement of certain genera and species within *Microascales* remains uncertain, which is supported by findings from both Li et al. (2016b) and Hongsanan et al. (2017a). There are very few species within *Microascales* for which sequence data are available, leaving their host-specificity unresolved. Depending on interpretations of taxa based on their hosts could unintentionally result in the same taxa being classified multiple times. Additionally, there are some genera within this order for which sequencing has not been conducted. This underscores the need for new collections of their type species to secure molecular data for a more definitive taxonomic resolution.

Significance

Ecological and economic roles

Most species within the *Microascales* are saprobic, thriving on plants, woody substrates, bark, leaves and other cellulosic plant remains, as well as on algae, mammal dung, compost, polluted water and soil (Jones & Hyde 1988, Hyde & Lee 1998, Jones & Pang 2012, Cho et al. 2020, Mapook et al. 2023). The saprobic taxa of *Microascales* possess the ability to break down lignocellulosic materials in the woody litter (Yuen et al. 1998, Bucher et al. 2004a). Some *Microascales* species are pathogenic, affecting terrestrial and aquatic plants, tree bark, the gut of weevils, and even humans (Al-Hedaithy 2001, Bucher et al. 2004a, Edathodu et al. 2013, Crous et al. 2015f). They are destructive plant pathogens, causing severe diseases in various economically important crops, trees, and ornamental plants, including coffee, cacao, eucalyptus, and giant taro, with global distribution (Roux et al. 2004, van Wyk et al. 2010, Li et al. 2016b, Mbenoun et al. 2016). For instance, *Ceratocystis fimbriata* is notorious for causing wilt and die-back disease in *Eucalyptus* clones in the Republic of Congo (Roux et al. 2000) and a severe leaf blight disease on *Alocasia macrorrhiza* in Yunnan, China (Li et al. 2016b). Additionally, certain *Microascales* species are pathogenic, often affecting the infructescences of *Protea* species and parasitizing bark beetles like *Cossonus* (Wingfield et al. 1988, Marais et al. 1998, van der Linde et al. 2012). *Knoxdaviesia* was initially discovered in the infructescences of *Protea* spp. infested by insects (Wingfield et al. 1988, Marais et al. 1998), and subsequent species of *Knoxdaviesia* have been associated with *Scolytidae* (bark beetles) (Bright & Torres 2006, Kolařík & Hulcr 2009). *Knoxdaviesia cecropiae* and *K. scolytodis* have been isolated from the bodies and galleries of *Scolytidae unipunctatus* in *Curcuma angustifolia*, respectively and *Knoxdaviesia serotectus* from discolored plant material of the same host in Costa Rica (Kolařík & Hulcr 2009). These species also act as vectors for mites associated with insects that infest *Euphorbia* species (van der Linde et al. 2012). *Gondwanamyces* species have been reported to cause lesions on healthy succulent branches of *Euphorbia* spp., leading to population declines in South Africa (van der Linde et al. 2012). Species of the *Gondwanamycetaceae* have shown the ability to grow on all monosaccharides present in *Protea* nectar (Aylward 2017).

Chemical diversity

Sordarin-type compounds have been reported in certain species of *Microascales* (Vicente et al. 2009). However, there is limited information regarding the overall chemical diversity within this

fungal order. According to studies by El-Elimat et al. (2021), numerous freshwater fungi have undergone chemical investigations, leading to the isolation of 283 secondary metabolites exhibiting a huge chemical diversity and biological activities. Given that *Microascales* includes many freshwater ascomycetes, there is significant potential for discovering diverse secondary metabolites within this group, provided they are thoroughly studied.

Other relevant data and future recommendations

The species within the *Microascales* order are globally distributed, yet many lack molecular data. Several genera, such as *Anisostagma*, *Appendichordella*, *Ascosacculus*, *Bathyascus*, *Carbosphaerella* and *Chadefaudia* have yet to be sequenced and are currently placed with uncertainty within *Microascales*. To solidify their taxonomic positions, it is crucial to recollect representative species from these genera and obtain molecular data for verification. The host-specificity of species within the *Microascales* order has not been adequately confirmed through molecular studies. Future research should aim to establish the reliability of a host-based nomenclatural approach for the *Microascales*. Comprehensive sampling across various habitats and hosts is essential to enhance our understanding of these fungi.

***Myrmecridiales* Crous, Persoonia 34: 219 (2015)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

The genus *Myrmecridium* has been raised to accommodate ramichloridium-like taxa with hyaline mycelium and pale to unpigmented, pimple-like denticles by Arzanlou et al. (2007). In the following years, several additional species have been described in this genus, and it remained as a distinct and undefined clade in the *Sordariomycetes* (Crous et al. 2011b, 2013b, Jie et al. 2013). Subsequently, *Myrmecridiales* and *Myrmecridiaceae* have been established by Crous et al. (2015d) to accommodate *Myrmecridium*, based on LSU sequence data analyses with *Myrmecridiaceae* as the type family in *Sordariomycetes*. *Myrmecridiales* has been placed under *Diaporthomycetidae* by Hongsanan et al. (2017a), who have shown this family to have phylogenetically a closer relationship with *Distoseptisporaceae* and *Magnaporthales* in addition to *Annulatascales* and *Thyridiaceae* based on LSU, SSU, TEF1 and RPB2 analyses. There are 21 species and two varieties that have been included so far in *Myrmecridium*. Another family *Xenodactylariaceae* was established within the order *Myrmecridiales* by Crous et al. (2018a) based on the monotypic genus *Xenodactylaria*. This genus produces hyaline conidiophores, conidiogenous cells and conidia with the latter occurring in short chains. The members belonging to the order *Myrmecridiales* have been reported from soil (Arzanlou et al. 2007, Jie et al. 2013, Peinter et al. 2016), on plant tissues as saprobes (Crous et al. 2012c, 2018a) and on submerged wood in freshwater environments (Réblová et al. 2016a, Tibpromma et al. 2017, Luo et al. 2019b).

History

Myrmecridium schulzeri has been described under different genera over time, including *Psilobotrys*, *Chloridium*, *Rhinocladiella*, *Ramichloridium*, *Acroheca*, *Pleurophragmium* and *Rhinotrichum*. *Myrmecridium schulzeri* was described in detail as *Acrotheca acuta* by Hughes (1951a). Hoog (1977) has discussed the reasons for non-suitability of any of the above genera. *Myrmecridium* has been introduced by Arzanlou et al. (2007) to accommodate ramichloridium-like taxa having hyaline mycelium, and pale to unpigmented conidiophores with pimple-like conidiogenous denticles at their apices and producing obovoid or fusiform conidia, tapering towards a narrowly truncate base. *Ramichloridium schulzeri* and its varieties are placed in the new genus *Myrmecridium* by Arzanlou et al. (2007). Initially, this genus has been placed under *Sordariomycetes* genera *incertae sedis*. Later the genus was placed under *Hypocreomycetidae*, genera *incertae sedis*

(Crous et al. 2015c, Maharachchikumbura et al. 2016). A new order *Myrmecridiales* has been introduced by Crous et al. (2015d) based on the family *Myrmecridiaceae* to accommodate the species belonging to *Myrmecridium*. Another genus *Neomyrmecridium* was subsequently added in the order with a strongly supported clade in molecular analysis (Crous et al. 2018a), which has also been confirmed by Hyde et al. (2020b).

Presently, there are two families and three genera in the order *Myrmecridiales*. *Myrmecridium* has 23 species and two varieties (Index Fungorum 2025), including the recently reported species (Crous et al. 2021d, 2022b, c, Yang et al. 2023b, Tan & Steinrucken 2024, Tian et al. 2024).

General description

The only species with sexual morph known so far among different species of *Myrmecridium* is *M. montsegurinum*. The family *Myrmecridiaceae* is characterized by vertically arising conidiophores that are distinct from creeping hyphae, unbranched, straight or flexuose, brown, thick-walled. Conidiogenous cells are terminally integrated, polyblastic, cylindrical, straight or flexuose, pale brown, sometimes secondarily septate, fertile part subhyaline, having scattered pimple-shaped, apically pointed, conidium-bearing denticles, and conidia are solitary, subhyaline to pale brown, smooth or finely verrucose, rather thin-walled, with a wing-like gelatinous sheath, obovoid to fusoid, aseptate or septate, truncate base, unpigmented hilum, schizolytic conidial secession (Crous et al. 2015d). *Xenodactylariaceae* members have conidiophores reduced to conidiogenous cells of hyphae, erect to flexuous, hyaline, smooth, with one to several denticulate apical loci, conidia occurring in branched chains, hyaline smooth, subcylindrical and septate (Crous et al. 2018a).

Sexual morph: *Ascomata* solitary or gregarious, immersed under a black clypeus, subglobose to conical venter, short-papillate, ostiolate, glabrous, periphysate ostioles. *Peridium* leathery, two-layered, outer layer hyaline to pale brown, inner layer filled with cells of *textura angularis* to *textura prismatica*. *Paraphyses* septate, cylindrical, longer than the asci. *Asci* eight-spored, unitunicate, cylindrical, with a slender long pedicel, apex broadly rounded with a inamyloid apical ring. *Ascospores* ellipsoidal, hyaline, three-septate, thin-walled, loosely verruculose with granular content, uniseriate, without sheath or appendages (adapted from Réblová et al. 2016a). Asexual morph: *Cultures* have submerged mycelia that are hyaline, thin-walled. *Conidiophores* erect from creeping hyphae, unbranched, straight or flexuose, brown, thick-walled. *Conidiogenous cells* terminally integrated, polyblastic, cylindrical, straight or flexuose, pale brown, pimple-shaped with conidium-bearing denticles. *Conidia* solitary, subhyaline, smooth or slightly verrucose, thin-walled, with a wing-like gelatinous sheath, obovoidal or fusiform, narrowly truncated base with a slightly prominent unpigmented hilum, schizolytic conidial secession (adapted from Crous et al. 2015d, Réblová et al. 2016a) (Fig. 234).

Families included in *Myrmecridiales*

Myrmecridiaceae Crous

Evolution

Myrmecridium taxa have both aseptate conidia and septate conidia e. g. *M. schulzeri* var. *tritici* (Jie et al. 2013) and *M. phragmitis* (Crous et al. 2011b). The phylogenetic analysis carried out by Jie et al. (2013) has revealed that the genus *Myrmecridium* has a close relationship with *Rhodoveronaea* (sexual state = *Annulatascaceae*) and *Ophiostoma* (*Ophiostomataceae*) in the *Sordariomycetes*. Crous et al. (2020b) have shown through phylogenetic analysis that *Myrmecridiales* has a close relationship with *Paramichloridiales*. Sugita & Tanaka (2022) have shown that *Myrmecridiales* is closely related to *Annulatascales* and *Thyridiales* based on combined LSU, RPB2 and TEF1 sequence analysis. While the sexual states of *Annulatascaceae* family have massive refractive apical rings, the apical apices of *M. montsegurinum* have smaller apical rings that are commonly found in diaporthaceous members, whereas members of *Thyridiaceae* also have compact and inconspicuous apical rings in asci (Sugita & Tanaka 2022). In contrast to the hyphomycetous anamorphs of *Myrmecridiales* producing macronematous conidiophores, the *Thyridiales* produce coelomycetous anamorphs (pycnidial conidiomata) and, if hyphomycetous, then

micronematous conidiophores with monophialidic conidiogenous cells. The divergence time for *Myrmecridiales* has been estimated to be 113 MYA (Hyde et al. 2020d).

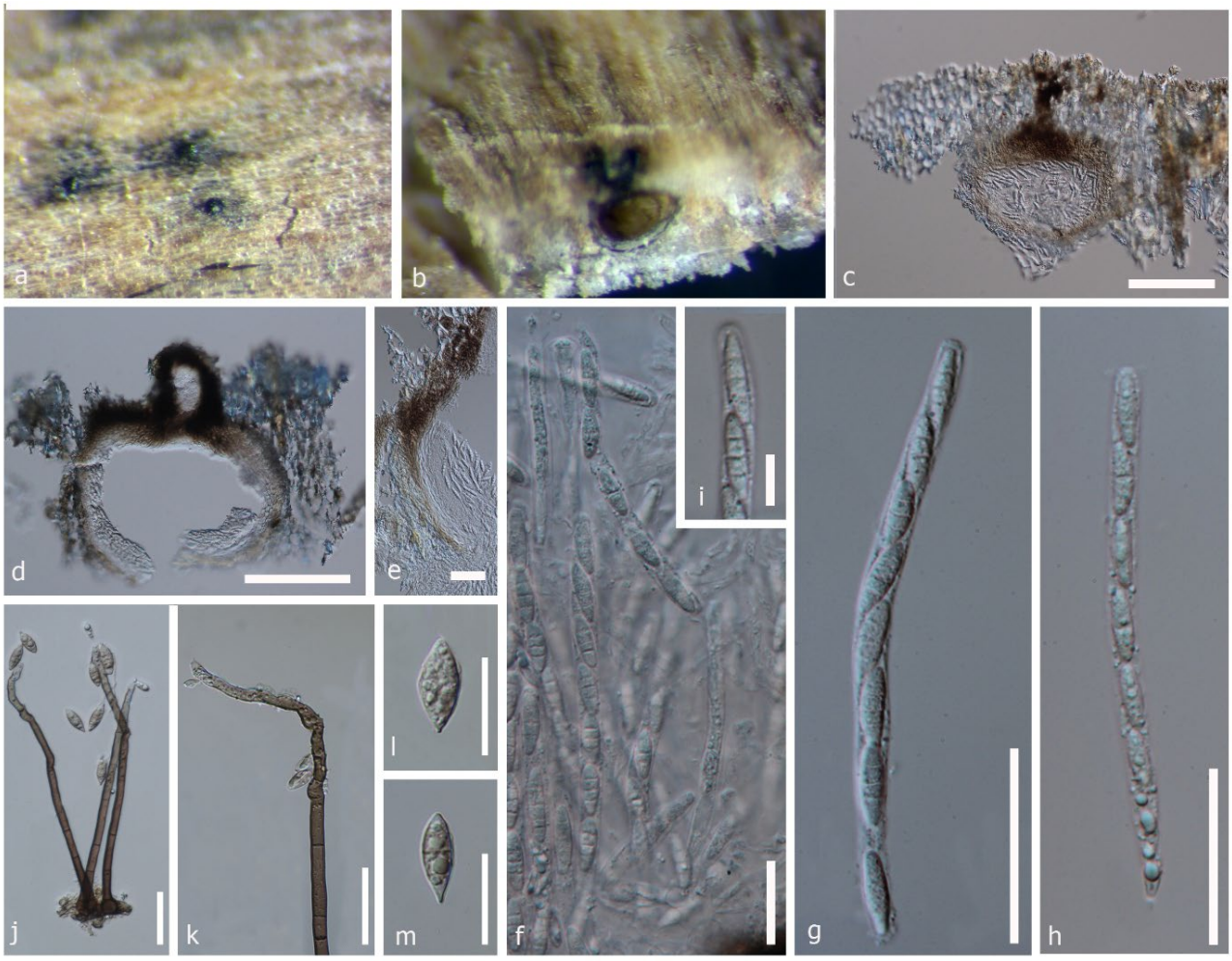


Figure 234 – Sexual and asexual morphs of *Myrmecridiales*. a, b Ascomata on substrate. c, d Vertical section through ascoma. e Peridium, f Paraphyses. g, h Asci. i Ascospores. j, k Conidiophores. l, m Conidia (a–h *Myrmecridium montsegurinum*, j–m *Neomyrmecridium naviculare*). Scale bars: c = 100 µm, d = 150 µm, e = 50 µm, f, g–k = 30 µm, l, m = 20 µm.

Justification of order and problems

Ramichloridium along with *Rhinocladiella* and *Veronaea* are polyphyletic and hence, based on a phylogenetic analysis, employing partial sequences of LSU and ITS, Arzanlou et al. (2007) segregated ramichloridium-like taxa into eight genera, including five new genera. Several of these genera were found to be distantly related in *Dothideomycetes,* while others were found in *Chaetothyriomycetes* and *Sordariomycetes*. While the type species of *Ramichloridium* along with a few other *Ramichloridium* species resides in the *Capnodiales* clade (*Mycosphaerellaceae* and *Teratosphaeriaceae* of *Dothideomycetes*), the other taxa belonged to other higher hierarchical groups: *Rhinocladiella* and *Veronaea* (*Herpotrichiellaceae*, *Chaetothyriales*), *Veronaeopsis* (*Venturiaceae*, *Pleosporales*, *Dothideomycetes*), *Pleurothecium* (*Chaetosphaeriales*, *Chaetothyriomycetes*), *Pseudovirgaria*, *Radulidium* and *Myrmecridium* (*Sordariomycetes* genera i*ncertae sedis*), and *Rhodoveronaea* (*Annulatascaceae*, *Sordariomycetes*) (Arzanlou et al. 2007). *Ramichloridium schulzeri*, based on which the genus *Myrmecridium* (*M. schulzeri*) has been raised, produces hyaline mycelium, conidia pale to unpigmented with pimple-like denticles, clustered near *Thyridium* and the *Magnaporthaceae* (Arzanlou et al. 2007). Subsequently, several other species were added to the genus and the genus remained as a distinct and undefined clade in *Sordariomycetes* and hence, a new family, *Myrmecridiaceae*, in a new order *Myrmecridiales*, has been introduced

(Crous et al. 2015d) and placed in *Diaporthomycetidae*. Based on multi-gene analyses including LSU, SSU, TEF1 and RPB2 sequence data, Hongsanan et al. (2017a) showed *Myrmecridiales* has close affinities with *Distoseptisporaceae* and *Magnaporthales*. Whereas Hyde et al. (2020b), through their phylogenetic analysis involving a combined set of LSU, SSU, TEF1 and RPB2 showed that *Myrmecridiales* taxa are closely related to *Annulatascales* and *Magnaporthales* within *Diaporthomycetidae*. *Myrmecridium montsegurinum* has been found with the sexual state, has some similarities to *Annulatascaceae* members including the uniseriate arrangement of ascospores in an ascus with a prominent amyloid-negative apical ring and long-pedicellate, cylindrical asci. *Annulatascaceae* members have massive discoid, wedge-shaped apical rings in asci and rarely bipartite asci. Further, the anamorphic stage of *Annulatascaceae* has been reported only in the genus *Chaetorostrum* which has taeniolella-like anamorph (with brown phragmocondia), unlike hyaline ellipsoidal, aseptate conidia with pimple-like denticles found in *Myrmecridium*. Due to the above reasons the erection of an order *Myrmecridiales* to accommodate *Myrmecridium*, *Neomyrmecridium* in the family *Myrmecridiaceae* and *Xenodactylaria* in the family *Xenodactylariaceae* is justified.

Significance

Ecological and economic roles

Members belonging to *Myrmecridiales* occur in a wide range of habitats and sources, including in soil, dung, plant tissues and soft corals (Thilagam et al. 2015, Serrano et al. 2020), both in terrestrial and aquatic water habitats. Three species are reported from freshwater habitats (Luo et al. 2019b) in rhizosphere of sugarcane and have potential as biocontrol agents against pathogens (Romao-Dumaresq et al. 2016). *Myrmecridium schulzeri* has been reported to be an endophyte of the epiphytic orchid *Laelia speciosa* (Avila-Diaz et al. 2013). This species has also been reported to be a very good decomposer of oakwood and pinewood, occurring in the third stage of fungal succession during decomposition. *Myrmecridium obovoideum* was described by Jie et al. (2013) from a farmland soil in Guizhou Province, China. Tibpromma et al. (2017) described *Myrmecridium fluviae* from a freshwater sample in Korea. *Myrmecridium schulzeri* was also found to be an endophyte in the medicinal plant *Bauhinia forficata* (Bezarra et al. 2015). This fungus has been shown by them to be a good producer of cellulases, xylanases and lipases. Peinter et al. (2016) reported, *Myrmecridium hiemale*, from snow-covered alpine soil as an eurypsychrophile (psychrotolerant) that can grow at 0-10 ºC but better between 10 ºC to 20 ºC. *Myrmecridium schulzeri* has been isolated from the pigeon feces collected from Mafikeng, the North West province of South Africa, but is not reported to have any human health significance (Syakalima et al. 2019). *Myrmecridium* species, as soil dwellers, have been implicated in the death of notoginseng that is used in herbal medicine (Dong et al. 2016). Glyphosate, which is used as a pesticide and weedicide, is toxic to some crop plants also including wheat. *Myrmecridium* species abundantly colonize live and dying glyphosate-killed wheat roots, thus indicating a high glyphosate-tolerance and capability to degrade glyphosate (Schlatter et al. 2017).

Chemical diversity

Recently, a novel lactose oxidase has been identified from *Myrmecridium flexuosum* NJK-21 by Lin et al. (2019b). Lactobionic acid (LBA) is a high-value lactose derivative produced through the oxidation of lactose and it has applications in the cosmetics, pharmaceutical, food and chemical industries. Since no suitable strain or enzyme could be used to produce LBA, chemical or electrochemical transformation was used to produce LBA. However, these processes generate toxic by-products that cause environmental pollution. Though fermentation by certain microbes for the production of LBA is an option, the subsequent purification steps are difficult, which is a drawback. Hence, the direct enzymatic oxidation of lactose to LBA is a viable option. Among the different strains screened, *M. flexuosum* NUK-21 exhibited the highest activity towards lactose by producing a novel Lactose oxidase (LOD) enzyme which has Zn as the prosthetic group unlike flavin adenine dinucleotide (FAD) in most other oxidase enzymes produced by different fungi. The authors suggest that the novel LOD produced by *M. flexuosum* NUK-21 could prove useful in the production of LBA in the future and be applied in the pharmaceutical and food industries. Zhang et al. (2012a) reported

a moderate antibacterial activity from secondary metabolites isolated from *Myrmecridium schulzeri* colonizing soft corals (Gorgonians) in the South China Sea.

Other relevant data and future recommendations

Myrmecridium schulzeri has been widely reported from different environments and geographic regions. This cosmopolitan nature could be due to its adaptability. When more sexual state taxa of this genus are reported, more information on its morphology could be deciphered. The ascospores of *M. montsegurinum* have a tendency to develop distosepta as seen in the photomicrographs (Réblová et al. 2016a), but such distosepta are incipient in nature. In the recent phylogenetic analyses based on multi-gene regions, *Myrmecridiales* are somewhat closely placed to *Distoseptisporaceae*. The aseptate nature of conidia and the wing-like sheaths around the conidia seem not to be universal in this genus or the family *Myrmecridiaceae*.

***Ophiostomatales* Benny & Kimbr., Mycotaxon 12(1): 48 (1980)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Ophiostomatoid fungi, including members of the orders *Ophiostomatales* (*Diaporthomycetidae*) and *Microascales* (*Hypocreomycetidae*) (De Beer & Wingfield 2013), are classified in *Sordariomycetes*, *Ascomycota* (Wijayawardene et al. 2022a). Two families and 15 genera are accepted in *Ophiostomatales* according to Wijayawardene et al. (2022a), with four newly erected genera (De Beer et al. 2022). Globalization and climate change have increased the possibility of new linkages between forest pests and pathogens as well as the occurrence of forest diseases and pest outbreaks (Wingfield et al. 2017, Wang et al. 2021b). Due to their close relationship and catastrophic effects on forests, insect-borne forest pathogens and their vectors are receiving more attention (Wingfield et al. 2017, Biedermann & Vega 2020, Wang et al. 2021b).

History

Ophiostomatales was established by Benny & Kimbrough (1980) to accommodate a single family, *Ophiostomataceae* (De Beer et al. 2013b), first described by Nannfeldt (1932). Later, Malloch & Blackwell (1993) erected the monotypic family *Kathistaceae* in *Ophiostomatales* to accommodate *Kathistes* based on sexual character similarities. However, the species produce yeast-like asexual morph that are different from other genera within *Ophiostomataceae*. *Ophiostomataceae* was treated in different orders before 1980 (De Beer et al. 2013b, 2022). The family was redescribed by Upadhyay (1981) with *Ceratocystis* serving as the type genus, *Ophiostoma*, *Sphaeronaemella*, *Grosmannia*, and *Europhium* as synonyms, based on morphological similarities such as their long-necked ascomata that produce sheathed ascospores in sticky droplets (Malloch & Blackwell 1993). However, DNA sequence data showed that *Ophiostoma* and *Ceratocystis* belong to two different orders (Spatafora & Blackwell 1994). The first molecular study of *Ophiostomatales* was carried out by Berbee & Taylor (1992a). They discussed the placement of the human pathogen, *Sporothrix schenckii*, in *Ophiostoma* based on 18s ribosomal RNA gene sequence. These two species have a similar asexual morph, but the sexual morph of *S. schenckii* was not observed. The study showed that *S. schenckii* is phylogenetically related to *Ophiostoma stenoceras* and *O. ulmi*. They concluded that it is possible to link sexual and asexual fungi in molecular phylogeny based on DNA sequences (Berbee & Taylor 1992a). The first study on generic boundaries was carried out by Zipfel et al. (2006). Using a multi-gene phylogenetic analysis, Zipfel and colleagues showed that *Ophiostoma*, *Ceratocystiopsis*, and *Grosmannia* are phylogenetically distinct genera (Zipfel et al. 2006, De Beer et al. 2022). De Beer & Wingfield (2013) updated the *Ophiostomatales* based on all reported LSU and ITS sequences. They recognized 18 species complexes among the several genera of *Ophiostomatales*, redefined *Ophiostoma sensu stricto*, *Raffaelea sensu stricto*, *Ceratocystiopsis*,

Fragosphaeria and *Graphilbum*, and included 266 species in their work. However, they came to the conclusion that the rDNA-based phylogenies were insufficiently reliable to determine the generic status of the *Sporothrix schenckii-Ophiostoma stenoceras* species complex or other lineages within what they classified as *Leptographium sensu lato*. Their study also indicated that the ambrosial species of *Raffaelea* did not comprise a monophyletic group. Since then, many studies have been conducted on taxonomic resolving (Ando et al. 2016, Jankowiak et al. 2017, Yin et al. 2019, 2020) and describing new taxa within *Ophiostomatales* (Romon et al. 2014, Musvuugwa et al. 2015, 2016, Simmons et al. 2016, Chang et al. 2017b, Marincowitz et al. 2020). The generic boundaries within the *Ophiostomatales* have recently been reconsidered and revised by De Beer et al. (2022) using multi-gene analyses of combined ITS, LSU, TEF1-α and RPB2 sequence data. The results of this study have provided support for the delineation of most of the genera that have been recognized during the course of the last decade in *Ophiostomatales*. This study also revealed robust novel lineages describing four new genera. The study has also resolved the remaining one fungus-one name issues that were not dealt with in the revision of De Beer & Wingfield (2013). Finally, they updated the generic taxonomy of *Ophiostomatales,* representing 16 distinct lineages within the order. In the study, they accepted *Esteya*, *Ceratocystiopsis*, *Graphilbum*, *Aureovirgo*, *Raffaelea*, *Sporothrix*, *Fragosphaeria* and *Hawksworthiomyces* as currently accepted genera, *Leptographium* and *Ophiostoma* as re-defined genera and re-instated genera *Grosmannia* and *Dryadomyces*, whereas *Harringtonia*, *Heinzbutinia*, *Jamesreidia* and *Masuyamyces* were introduced as new genera (De Beer et al. 2022).

General description

Ophiostomatales genera produce either sexual or asexual morph stages. However, the sexual stage has not been reported in some genera, including *Afroraffaelea*, *Dryadomyces*, *Esteya*, *Harringtonia*, and *Hawksworthiomyces* (De Beer & Wingfield 2013, De Beer et al. 2022). *Ophiostomatales* genera are mostly distinguished by producing globose to subglobose or pyriform perithecial ascomata, with moderately long to long (snake-like) necks, which are pale brown to brown, becoming black when they mature. However, a few genera have short-necked perithecia (such as *Ceratocystiopsis* and *Raffaelea*), or even lack a neck (such as *Leptographium*). Additionally, some genera form a brush-like or collar-like structure at the apex of the neck (such as *Ceratocystiopsis*, *Crysosphaeria*, *Graphilbum*, *Leptographium*, *Ophiostoma*, *Raffaelea* and *Sporothrix*). *Fragosphaeria* produces cleistothecial ascomata with an easily fragmented wall. Asci are subglobose, clavate or fusiform, evanescent. Ascospores are hyaline to subhyaline, 1-celled and considerably varied in shape. However, *Sporothrix longicollis*, previously described as *Spumatoria longicollis* (Giraldo et al. 2017), produces 2-celled ascospores. In the asexual stage, the genera are extremely diverse, with forming five distinct asexual morphs, including hyalorhinocladiella-like (such as *Ceratocystiopsis*, *Esteya*, *Graphilbum*, *Grosmannia*, *Intubia*, *Masuyamyces* and *Ophiostoma*), leptographium-like (such as *Aureovirgo*, *Grosmannia*, *Leptographium* and *Ophiostoma*), pesotum-like (such as *Graphilbum*, *Grosmannia*, *Leptographium*, *Masuyamyces* and *Ophiostoma*), raffaelea-like (such as *Harringtonia*, *Raffaelea* and *Masuyamyces*), and sporothrix-like (such as *Chrysosphaeria*, *Fragosphaeria*, *Grosmannia*, *Heinzbutinia*, *Intubia*, *Jamesreidia*, *Ophiostoma* and *Sporothrix*) (De Beer et al. 2022).

Sexual morph: *Ascomata* perithecial or cleistothecial. *Perithecial* bases globose, subglobose or pyriform, pale brown, brown to black with age, with short or moderate long to long neck, nearly cylindrical to cylindrical, straight or slightly curved; upper part simple or with structures including brush-like or collar-like structures. *Ostiolar hyphae* absent or present, convergent, parallel or divergent. *Asci* evanescent, clavate, subglobose or fusiform. *Ascospores* mostly hyaline, 1-celled or 2-celled (only *Sporothrix longicollis*), naked or enclosed in sheath falcate, including a variety of shapes such as ellipsoidal, short cylindrical to oblong, reniform, cucullate, allantoid and ossiform (De Beer et al. 2022). Asexual morph: *Conidiophores* micronematous, semimacronematous or macronematous, mononematous or synnematous, simple or branched, single or aggregated in sporodochia; hyaline to subhyaline or pigmented, smooth to verrucous. *Conidiogenous cells* integrate

or discrete, flask-shaped, cylindrical, subulate, monillioid or oblong, polyblastic or sympodial, smooth or denticulate, with inconspicuous scars or with inconspicuous annellations. *Conidia* mostly 1-celled, varied in shape including oblong to ellipsoidal, obovoid, clavate to broadly clavate, pyriform, subalantoid, bacilliform tapering toward one end, smooth, straight or curved, hyaline or subhyaline (adapted from De Beer et al. 2022) (Fig. 235).

Families included in *Ophiostomatales*

Kathistaceae Malloch & M. Blackw.
Ophiostomataceae Nannf.

Ophiostomatales genera *incertae seids*
Harringtonia Z.W. de Beer & Procter
Jamesreidia Z.W. de Beer & M. Procter
Masuyamyces Z.W. de Beer & M. Procter

Evolution

The evolution of *Ophiostomatales* is poorly understood (Wingfield & De Beer 2018). The earliest fossils of *Ophiostomatales* date back to the Jurassic period (about 150 MYA), and they are believed to have originated in the Southern Hemisphere, most likely in Gondwana, the supercontinent that included present-day Africa, Antarctica, Australia, Madagascar and South America (McLoughlin 2001, Taylor et al. 2009a). *Ophiostomatales* are known to have evolved in a symbiotic relationship with bark beetles, which feed on the inner bark of trees. The fungi grow in the galleries that the beetles excavate, and in return, the fungi provide the beetles with a food source and protection from other microbes (Six 2012, Seybold et al. 2018, Ayres et al. 2000). The evolution of *Ophiostomatales* has been shaped by their interactions with their environment, including their host trees, bark beetles, and other microbes. For example, some species of *Ophiostomatales* produce toxins that inhibit the growth of competing fungi, while others produce volatile compounds that attract bark beetles (Harrington 2005, Hofstetter & Moser 2014, Fischer & Lu 2015). Recent research has shown that the evolution of *Ophiostomatales* is driven in part by horizontal gene transfer, which is the transfer of genetic material between organisms that are not directly related. This process allows *Ophiostomatales* to acquire new traits that may be beneficial for their survival and reproduction (Dhillon et al. 2015, Li et al. 2018). Overall, the evolution of *Ophiostomatales* is a complex and ongoing process that involves interactions with a variety of organisms and environmental factors. Further research is needed to fully understand the mechanisms driving the evolution of these fascinating fungi (Six & Wingfield 2011, Wingfield & De Beer 2018).

Justification of order and problems

The order has been justified based on a combination of morphological, ecological, and molecular characteristics (Zipfel et al. 2006). However, there are some problems and challenges associated with the *Ophiostomatales*. The taxonomy of the *Ophiostomatales* was previously confused due to the convergent evolution of morphological characters used to delimit unrelated fungal taxa (De Beer et al. 2022). However, DNA-based methods have resolved much of this confusion. Wijayawardene et al. (2022a) have listed *Kathistes*, *Mattirolella*, and *Termitariopsis* as *Ophiostomatales* genera, belonging to *Kathistaceae*. Based on a MycoBank search (accessed on May 14, 2023), species of these three genera have been described during 1920–1990, and there are no molecular data (only LSU for *Kathistes calyculata* and *Kathistes analemmoides*) to support their taxonomic placement within *Ophiostomatales*. De Beer et al. (2022) also did not include these genera

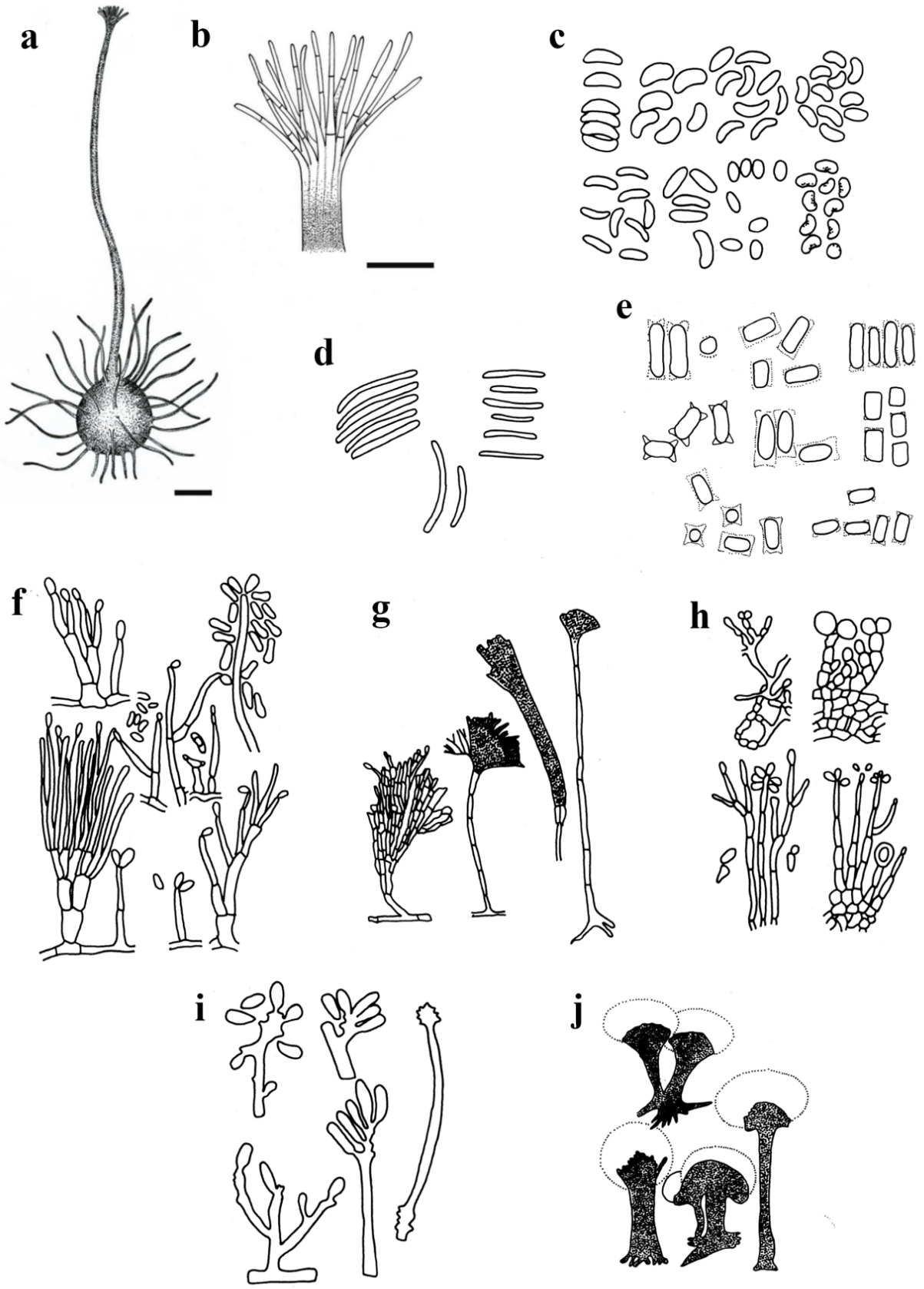


Figure 235 – Morphology of *Ophiostomatales*. *Ophiostoma pilifera* (a, b) a Ascomata. b Ostiolar region with ostiolar hyphae (redrawn from Osorio 1985). Ascospore types of *Ophiostomatales* (c–e) c Type A. d Type B. e Type E (redrawn from De Beer et al. 2013). Conidiophore types of *Ophiostomatales* (f–j) f Hyalorhinocladiella-like. g Leptographium-like. h Raffaelea-like. i Sporothrix-like. j Pesotum-like (redrawn from De Beer et al. 2013).

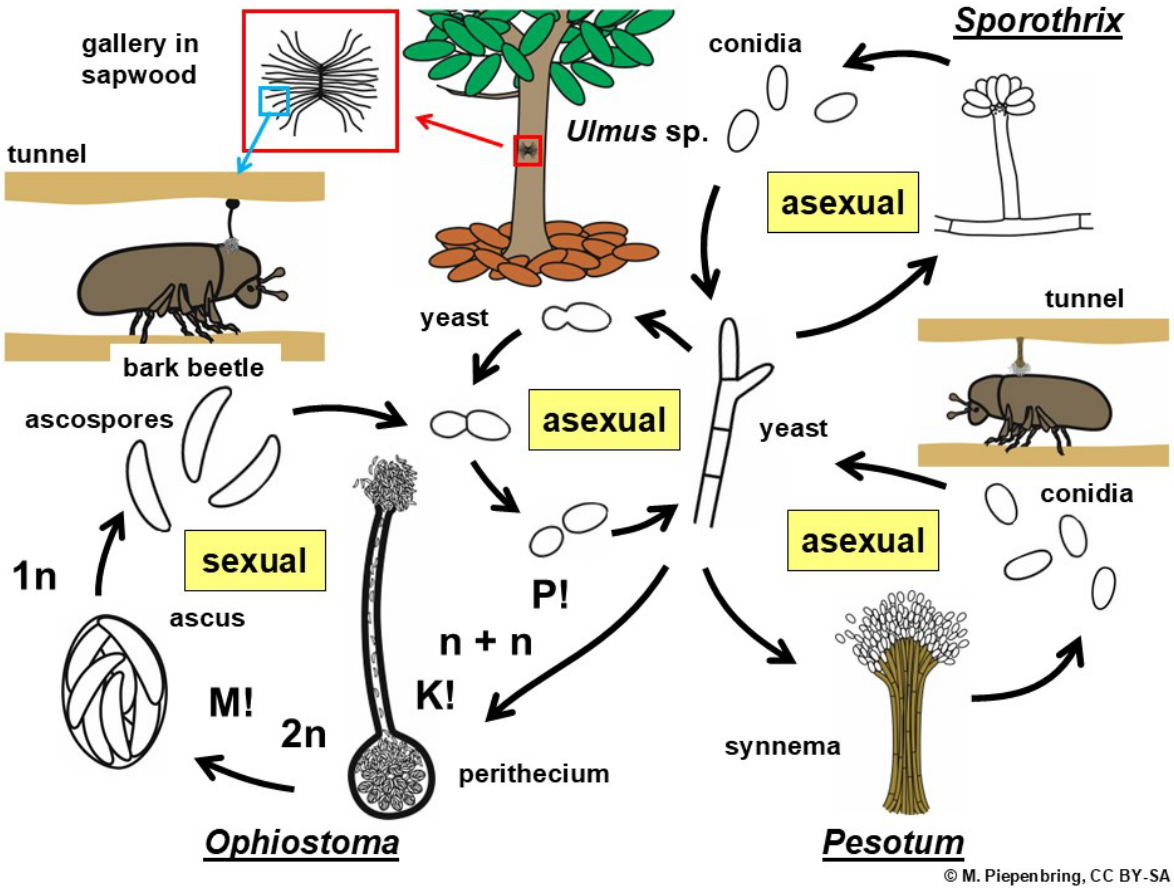


Figure 236 – Sexual and asexual life cycles of *Ophiostomatales* (From Mycological teaching diagrams by Meike Piepenbring (2023)). Abbreviations: 1n = haploid, 2n = diploid, P! = plasmogamy, K! = karyogamy, M! = meiosis. Black and white circles represent haploid nuclei of different mating types, circles of both colors represent diploid nuclei.

in their study. However, they showed that *Spumatoria longicollis*, previously described by Giraldo et al. (2017), shares characteristics with *Kathistes* and is distinct from *Ophiostomatales* based on its coprophilous nature and ascospore morphology, but phylogenetically (LSU and TEF-1α) it is placed within the *Sporothrix inflata* species complex. Additionally, Bateman et al. (2017) described *Afroraffaelea*, a new monotypic genus within *Ophiostomatales* based on SSU, LSU, and TUB2. Nonetheless, De Beer et al. (2022) discussed that four known isolates of *Afroraffaelea ambrosiae* clustered together as one species; however, the clade was inconsistently grouped in the single gene trees. For example, in the LSU and TEF-1α trees, the isolates grouped with *Graphilbum*; in the ITS tree, they clustered with *Dryadomyces*; and in the RPB2 tree, they were placed between *Hawksworthiomyces* and *Heinzbutinia*. Moreover, its sexual morph was not observed, and no representative asexual structure was found to adduce *Ophiostomatales*. Therefore, one of the main issues in *Ophiostomatales* is the lack of a robust phylogenetic framework that accurately reflects the evolutionary relationships among the member taxa. This is partly due to the rapid radiation of the order and the presence of many cryptic species with similar morphological features (Harrington 2005, Six 2012). In addition, the taxonomic status of some genera and species within the order remains controversial and subject to ongoing revisions based on new molecular and morphological data (De Beer et al. 2022).

Significance

Ecological and economic roles

Ophiostomatales includes species that are causative agents of plant and human diseases and are common associates with insects such as bark and ambrosia beetles (*Coleoptera*: *Curculionidae*,

Platypodinae and *Platypodinae*) (Harrington 2005, Musvuugwa et al. 2016, Wang et al. 2021b, De Beer et al. 2022). *Sporothrix schenckii* causes human sporotrichosis (De Beer et al. 2016). Moreover, most species are either non-pathogenic or weak pathogens and some can kill trees with or without contribution by their vector insects (Zubaer et al. 2021). *Ophiostomatales* taxa are ecologically important as many of them can thrive as saprobes in wood (Seifert 1993). The blue-stain-producing species of *Ophiostomatales* such as *Ophiostoma minus* and *Ophiostoma piliferum*, are responsible for significant economic losses in the forestry industry as it is difficult to export stained timbers and lumber products (Zubaer et al. 2021). Species of *Leptographium* are also commonly associated with bark beetles, and cause sapstain on a variety of trees, leading to degrade valuable tree logs and causing considerable financial losses (Romon et al. 2007, Yin et al. 2019). *Ophiostoma novo-ulmi*, one of the most devastating tree pathogens in the world, causes Dutch elm disease (Hessenauer et al. 2020). Members of *Ophiostomatales* are commonly referred to as "blue-stain fungi" because they are responsible for the blue staining of wood caused by their growth in the sapwood of trees (Jankowiak et al. 2021). The presence of *Ophiostomatales*-associated diseases can have significant economic implications for the forestry industry (Pautasso et al. 2012, Wingfield et al. 2015). Some species are plant pathogens and can cause diseases in trees and are associated with various tree diseases, such as Dutch elm disease, pine wilt disease, and oak wilt disease. These pathogens can impact forest health and have ecological consequences by affecting tree populations and community dynamics (Billings et al. 2001, Brasier & Kirk 2010, Vicente et al. 2022, Copeland et al. 2023). Outbreaks of diseases caused by *Ophiostomatales* can result in the decline and death of valuable timber species, leading to economic losses for the timber industry (Gonthier et al. 2007, Santini et al. 2013). Some species within *Ophiostomatales* have been introduced to regions outside their natural range and have become invasive species. For example, the spread of Dutch elm disease caused by *Ophiostoma ulmi* and *Ophiostoma novo-ulmi* has resulted in the widespread mortality of elm trees, impacting urban and rural landscapes (Brasier 2000, 2001). *Ophiostomatales* taxa form symbiotic relationships with bark beetles and ambrosia beetles. They colonize the galleries formed by these beetles within trees, providing them with a habitat and a nutrient-rich environment. In return, the beetles aid in the dispersal of *Ophiostomatales* spores to new host trees (Hofstetter et al. 2006, Six & Wingfield 2011, Six 2012). While some *Ophiostomatales* species are detrimental to forests, others can be used beneficially as agents of biological control. For instance, certain *Ophiostomatales* strains have been employed for controlling invasive bark beetle populations that damage forests by disrupting their reproductive biology (Klepzig & Six 2004, Six 2012, Biedermann et al. 2019). Many species are involved in wood decay processes, breaking down lignocellulosic material in dead or dying trees. This decomposition contributes to nutrient cycling in forest ecosystems and helps recycle organic matter (Blanchette 1995, Dighton & White 2017). *Kathistaceae* is another family of *Ophiostomatales* containing four genera, including *Kathistes*, *Mattirolella*, *Termitaria*, and *Termitariopsis*. The species of this family are mostly ectoparasitic to insects, including termites and ants. Species of *Kathistes* are coprophilous and were reported commonly from herbivore dung, usually dispersing by insects (Malloch & Blackwell 1993). Globalization and climate change have increased the possibility of new linkages between forest pests and pathogens as well as the occurrence of forest diseases and pest outbreaks (Wingfield et al. 2017, Wang et al. 2021b). Due to their close relationship and catastrophic effects on forests, insect-borne forest pathogens and their vectors are receiving more attention (Wingfield et al. 2017, Biedermann & Vega 2020, Wang et al. 2021b). Understanding the ecological and economic roles of *Ophiostomatales* is crucial for managing and conserving forest ecosystems, mitigating disease outbreaks, and sustaining the economic value of timber resources.

Chemical diversity

Ophiostomatales have been studied for their chemical diversity, as they produce bioactive compounds with potential applications in medicine, agriculture, and industry (Kandasamy et al. 2016, 2023, Wang et al. 2020a). One of the key chemical groups produced by *Ophiostomatales* taxa is polyketides. These are complex organic compounds synthesized by a group of enzymes called polyketide synthases (Cox 2007, Chooi & Tang 2012). Polyketides from *Ophiostomatales* exhibit

diverse structures and biological activities. For example, some polyketides have shown antimicrobial properties, making them potential candidates for the development of novel antibiotics. Others have demonstrated anti-inflammatory or anticancer activities, indicating their therapeutic potential (Lee et al. 2001, Oh et al. 2008, Ibrahim et al. 2022, Nawrot-Chorabik et al. 2022). Furthermore, *Ophiostomatales* are also known for producing volatile organic compounds (VOCs). These VOCs are small organic molecules that are released into the environment and can influence various biological interactions. *Ophiostomatales* VOCs have been found to play important roles in fungal ecology, including communication and defense mechanisms. They can attract or repel insects, modulate fungal growth and development, and even impact the behaviour of other organisms in the ecosystem (Bruce et al. 2004, Davis et al. 2013, Hung et al. 2015, Kandasamy et al. 2016). In addition, *Ophiostomatales* produce a variety of other secondary metabolites, including terpenoids, alkaloids, and peptides. These compounds possess a wide range of biological activities and have been investigated for their potential as pharmaceuticals, agrochemicals, and industrial products (Morath et al. 2012, Sbaraini et al. 2017).

Other relevant data and future recommendations

The study of *Ophiostomatales* chemical diversity provides valuable insights into the remarkable capabilities of these fungi to produce a vast array of bioactive compounds. Continued research in this field has the potential to unlock novel natural products with significant societal and economic implications (Six 2012, Netherer et al. 2021).

***Pararamichloridiales* Crous, Persoonia 39: 357 (2017)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Pararamichloridiales consists of a solitary family *Pararamichloridiaceae*. This family comprises one genus *Pararamichloridium*, with its type species *P. livistonae*. The overall classification of *Pararamichloridiales* places it within *Sordariomycetes*. *Pararamichloridiales* is characterized by its branched conidiophores, which exhibit a range of colors from almost transparent (subhyaline) to brown, and they are septate. Crous et al. (2017a) stated that the conidiophores possess polyblastic, terminal, and intercalary conidiogenous cells that generate individual, hyaline, aseptate, clavate to ellipsoid conidia. This genus encompasses four species, *viz*. *P. aquisubtropicum*, *P. caricicola*, *P. livistonae* and *P. verrucosum*. According to the systematic study of Crous et al. (2017a), no sexual morph has been discovered within the genus *Pararamichloridium*. Through the use of phylogenetic data from LSU and ITS sequences, it has been demonstrated that *Pararamichloridiales* constitutes a well-defined and distinct group with robust statistical support.

History

Pararamichloridiales was described by Crous et al. (2017a). This order was composed of the monotypic family *Pararamichloridiaceae*, which encompassed two genera, *Pararamichloridium* and *Woswasia*. *Pararamichloridium* was named based on its morphological similarity to *Ramichloridium*, a fungus belonging to *Dissoconiaceae* (*Capnodiales*, *Dothideomycetidae*) (Wijayawardene et al. 2022a). The type, *Pararamichloridium livistonae*, is distantly grouped from *Ramichloridium apiculatum* (Videira et al. 2017). Its close phylogenetic association to *Spadicoides verrucosa* was described by Rao & De Hoog (1986). This indicates that *Pararamichloridium livistonae* and *Spadicoides verrucosa* are likely to share a recent common ancestor as compared to *Ramichloridium apiculatum* (Videira et al. 2017). However, *Spadicoides verrucosa* can be distinguished from *Pararamichloridium* in having pale brown, verruculose conidia. Despite this difference, it is evident that *Spadicoides verrucosa* does not belong to the genus *Spadicoides*, as indicated by its close phylogenetic relationship to *Pararamichloridium*.

In the study of Crous et al. (2017a), *Woswasia atropurpurea*, *Xylochrysis lucida*, and *Cyanoannulus petersenii* formed a separate branch, quite distant from the *Pararamichloridium* clade. Subsequently, Zhang et al. (2017a) removed *Woswasia* from the *Pararamichloridiaceae* due to its close phylogenetic relationship with *Xylochrysis* and *Cyanoannulus*, placing it within *Woswasiaceae* (a family in *Diaporthomycetidae* of uncertain position). This reclassification has been confirmed by subsequent studies (Hyde et al. 2020b, d, Wijayawardene et al. 2020). With the recently introduced family, *Neoeriomycopsidaceae*, the order presently accommodates two families, which are listed below.

General description

The unique characteristics that differentiate this genus include conidiophores that may be branched or unbranched, exhibiting a medium brown coloration and being septate. The conidiogenous cells are also medium brown and possess denticulate structures. Conidia produced by this genus are solitary, hyaline, smooth, and granular, with a clavate shape and they are aseptate (Crous et al. 2017a).

Sexual morph: Undetermined. Asexual morph: *Mycelium* consisting of hyaline, smooth, septate, branched, hyphae. *Conidiophores* erect, solitary, straight to flexuous, septate, branched at apex or not, subcylindrical, subhyaline to medium brown, smooth. *Conidiogenous cells* terminal and intercalary, subcylindrical, subhyaline to medium brown, smooth, polyblastic, denticulate. *Conidia* solitary, hyaline, smooth, aseptate or septate, thin-walled, clavate to ellipsoid or fusoid, slightly curved, tapering toward the apex with unbranched appendage (adapted from Crous et al. 2017a, 2023) (Fig. 237).

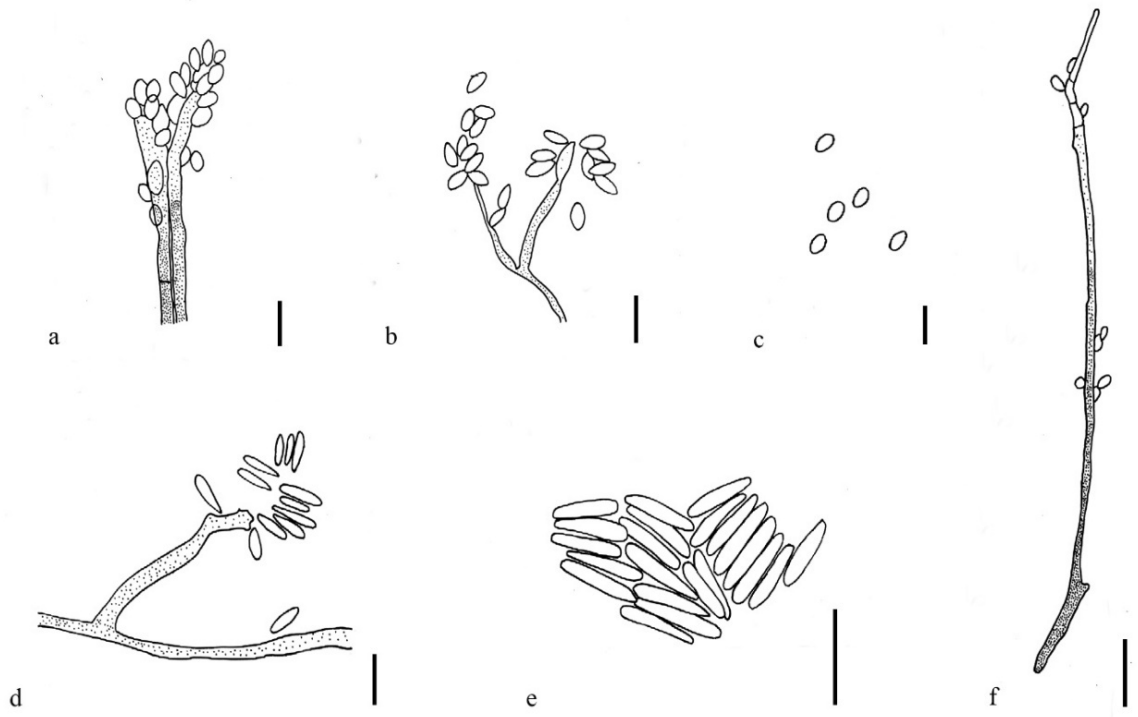


Figure 237 – Morphology of *Pararamichloridiales.* a, b, d, f Conidiogenous cells and conidia (a, f *Pararamichloridium aquisubtropicum,* b *P. caricicola,* d *P. livistonae*). c, e Conidia (c *P. aquisubtropicum,* e *P. livistonae*). Scale bars: a–e = 10 µm, e = 20 µm.

Families included in *Pararamichloridiales*

Pararamichloridiaceae Crous

Neoeriomycopsidaceae Crous

Evolution

The phylogenetic tree constructed using multi-locus sequence data from the ITS, LSU, SSU, and RPB2 markers showed that *Pararamichloridium livistonae* and *P. verrucosum* grouped together, forming a distinct clade as indicated by Crous et al. (2017a). The estimated divergence time for *Pararamichloridiales* is around 101.5 MYA (Crous et al. 2017a).

Justification of order and problems

Pararamichloridiaceae, which included *Pararamichloridium* and *Woswasia* and was proposed by Crous et al. (2017a). However, based on morphological traits, phylogenetic analysis, and molecular dating, Zhang et al. (2017a) reclassified *Woswasia*, along with *Xylochrysis* and *Cyanoannulus*, as families of uncertain position (*incertae sedis*) within *Diaporthomycetidae*. In a recent multi-loci phylogenetic analysis using ITS, LSU, SSU, and RPB2, *Pararamichloridium livistonae* (CBS 143166) and *P. verrucosum* (CBS 128.86) were closely related, forming a distinct clade with strong support. In contrast, *Woswasia atropurpurea* (CBS 133167), *X. lucida* (CBS 135996), and *Cyanoannulus petersenii* (R044a and R044b) constituted a separate branch that was genetically distant from the *Pararamichloridium* clade. These findings, coupled with the close phylogenetic relationship observed between *Woswasia*, *Xylochrysis*, and *Cyanoannulus* within the family *Woswasiaceae*, lead to the recommendation that *Woswasia* should be excluded from the family *Pararamichloridiaceae* (Crous et al. 2017a).

Significance

Ecological and economic roles

The taxa are reported as saprobes and are involved in the decomposition of dead or waste organic matter, particularly in terrestrial and freshwater habitats (Padaruth 2023). These species have been identified in various parts of the world, including Australia, China, India, Indonesia and Thailand. An intriguing report from Indonesia documents an isolate of *Pararamichloridium* found in association with a healthy banana plant (Napitupulu et al. 2021). Additionally, a study by Ogórek et al. (2020) found that *P. caricicola* was isolated from the wing membranes of female greater mouse-eared bats (*M. myotis*) during their spring emergence from the "Nietoperek" underground hibernation site.

Chemical diversity

No relevant studies are available for the chemical diversity of *Pararamichloridiales*.

Other relevant data and future recommendations

The ecological significance of *Pararamichloridium* species as saprobes, which aid in nutrient cycling by breaking down organic matter (Crous et al. 2017a, Chaudhary et al. 2022). The adaptability of *Pararamichloridium* species is underscored by their widespread distribution, found in a multitude of continents. This fact opens up discussions on biogeography and factors that influence species dispersal (Crous et al. 2017a, Ogórek et al. 2020, Padaruth 2023). Further molecular studies are needed to clarify the familial relationships within *Pararamichloridiaceae*, to deepen our understanding of the evolution and divergence of these species (Hyde et al. 2020b, d, Wijayawardene et al. 2020).

Phomatosporales **Senan., Maharachch. & K.D. Hyde, Mycosphere 7(5): 631 (2016)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Phomatosporales belongs to the class *Sordariomycetes* in *Ascomycota,* and it contains a single family *Phomatosporaceae,* comprising five genera (Hyde et al. 2024b). *Phomatospora* is the largest genus in *Phomatosporales,* which accommodates over 100 species (MycoBank 2025). The species

in *Phomatospora* are mainly distinguished by their sexual morph characters. *Phomatospora* was classified as a member of *Sphaeriales*, *Diaporthales*, or *Xylariales* (Barr 1970, 1994, Rappaz 1992, Fallah & Shearer 1998). *Lanspora* was introduced as a monotypic genus in *Sphaeriales* (Hyde & Jones 1986). Subsequently, *Phomatospora* and *Lanspora* were placed in *Sordariomycetes* genera *incertae sedis* (Lumbsch & Huhndorf 2007, Fournier & Lechat 2010, Crous et al. 2015c). On the basis of the multi-gene phylogenetic analyses and morphological characterization, *Phomatosporales* was introduced by Senanayake et al. (2016), which contained a new monotypic genus *Tenuimurus,* besides *Phomatospora* and *Lanspora*. *Phomatosporales* is characterized morphologically by its sexual morph. Ascomata ostiolate, papillate, and immersed; asci 8-spored, unitunicate, with J- apical ring; ascospores mostly uniseriate, aseptate, hyaline, with striations or appendages. The taxa are widely distributed in terrestrial, freshwater and marine environments, and is mainly saprobic on herbaceous stems, submerged wood or decaying twigs (Senanayake et al. 2016, Luo et al. 2019b, Hyde et al. 2020d, Dong et al. 2023).

History

Phomatosporales contains a single family *Phomatosporaceae* which was formally established by Senanayake et al. (2016), and was invalidly established by von Arx (1951). *Phomatosporaceae* accommodates *Phomatospora*, *Lanspora, Tenuimurus, Conicotenuis*, and *Minimispora* that were established in 1875, 1986, 2016, and 2023 respectively (Hyde & Jones 1986, Senanayake et al. 2016, Dong et al. 2023). *Phomatospora berkeleyi* as the first species in *Phomatospora* that was introduced in 1875 which replacing the synonym *Sphaeria phomatospora*. Before molecular biology was used in mycology, *Phomatospora* was placed as a member of *Diaporthaceae* in *Diaporthales* (Barr 1970). Subsequently, it was placed in *Xylariales* because *P. berkeleyi*, and *P. arenaria* were shown to produce a sporothrix-like anamorph in culture (Rappaz 1992, Barr 1994). Lumbsch & Huhndorf (2007), supported the placement of *Phomatospora* in *Sordariomycetes* genera *incertae sedis*. *Lanspora* was established as a member of *Halosphaeriaceae* in *Sphaeriales* in 1986 which contained a single species, *L. coronata* (Hyde & Jones 1986). Subsequently, the phylogenetic analyses based on LSU, SSU, and ITS showed *Lanspora* was close to *Phomatospora* (Crous et al. 2015c). *Lanspora cylindrospora* (Hyde et al. 2020b) and *L. dorisauae* (Pang et al. 2023) were introduced as the second and the third species in *Lanspora*, respectively. Three monotypic genera *Tenuimurus*, *Conicotenuis*, and *Minimispora* were introduced to *Phomatosporales* in 2016 and 2023, respectively (Senanayake et al. 2016, Dong et al. 2023). Until now (February 2025), over 110 species are assigned to *Phomatosporales*.

General description

The characters for separation of the three genera *Lanspora*, *Phomatospora*, *Tenuimurus*, *Conicotenuis*, and *Minimispora* in *Phomatosporales* are based on ascospores and paraphyses, except molecular phylogeny evidence (Senanayake et al. 2016, Hyde et al. 2020d, Dong et al. 2023). *Tenuimurus* accommodates species primarily having smaller ascospores (≤10 μm) as compared to other species in *Phomatosporales* and having hyaline paraphyses (Senanayake et al. 2016). *Minimispora* accommodates species having smaller ascomata (≤10 μm diam.) as compared to other species in *Phomatosporales* (Dong et al. 2023). *Conicotenuis* accommodates species having distinct fusiform ascospores (Dong et al. 2023). *Lanspora* accommodates species having ascospores with crown-like appendages or lacking appendages and not having paraphyses (Senanayake et al. 2016, Hyde et al. 2020b). Although *Lanspora cylindrospora* has small ascospores (≤10 μm), *L. cylindrospora* clusters with type species *L. coronata* in LSU, SSU, ITS, TEF1-α, and RPB2 phylogenetic analyses and neither of them has paraphyses (Hyde et al. 2020b). *Phomatospora* accommodates species having large ascospores (≥10 μm) with filamentous or sheet-like appendages (Senanayake et al. 2016). In addition, the asexual morph of *Phomatospora* is described as being sporothrix-like, but in *Lanspora* and *Tenuimurus* it is undetermined (Webster 1955, Reid & Booth 1966, Rappaz 1992).

Sexual morph: *Ascomata* solitary, seldom gregarious, immersed or gradually erumpent with age, subglobose or globose, light brown to black, coriaceous, sometimes developing under a small blackened clypeus, ostiolate, with a papilla or neck. *Peridium* comprising small, brown pseudoparenchymatous cells, sometimes thickened in upper part. *Paraphyses* absent or numerous, hypha-like, aseptate or septate, distally tapering, hyaline. *Asci* 8-spored, unitunicate, cylindrical or oblong-fusiform, thin-walled, short-pedicellate or sessile, with a small refractive nonamyloid J- apical ring. *Ascospores* mostly uniseriate, sometimes overlapping uniseriate, rarely biseriate, hyaline, ellipsoidal to fusiform, usually aseptate or 1–3-septate, not constricted at the septum, sometimes bi-guttulate at the ends of the cell, with longitudinal striations or filamentous appendages at both ends or a sticky mucilaginous sheath. Asexual morph: *Sporothrix*-like (adapted from Rappaz 1992) (Fig. 238).

Families included in *Phomatosporales*

Phomatosporaceae Senan. & K.D. Hyde

Evolution

In the study of Senanayake et al. (2016) based on LSU, SSU and ITS phylogeny, *Phomatosporales* formed a clade distantly related to other existing orders in the *Diaporthomycetidae*, for which this order was established. In recent studies based on combined LSU, SSU and ITS with one or two sequences of TUB2, TEF1-α, and RPB2, the separation of *Phomatosporales* from other orders in *Sordariomycetes* is also well-supported (Luo et al. 2019b, Hyde et al. 2020b, d, Pang et al. 2023). The divergence time for *Phomatosporales* is proposed as 91 MYA by using the maximum clade credibility tree of families in *Sordariomycetes* (Hyde et al. 2020d).

Justification of order and problems

Phomatosporales was established partially because the species of *Phomatosporales* formed a well-supported clade in multi-gene phylogenetic analyses (Senanayake et al. 2016). However, since most species of *Phomatospora* were established before molecular phylogeny was used in mycology, only eleven species in *Phomatosporales* were shown in the different phylogenetic analyses including *Conicotenuis fusiformis*, *Lanspora coronata*, *L. cylindrospora*, *L. dorisauae*, *Minimispora superficialis*, *Phomatospora bellaminuta*, *P. biseriata*, *P. striatigera*, *P. uniseriata*, *P. viticola*, and *Tenuimurus clematidis* (Senanayake et al. 2016, Luo et al. 2019b, Phookamsak et al. 2019, Hyde et al. 2020b, d, Dong et al. 2023, Pang et al. 2023). Nearly 90% of species in *Phomatosporales* are not analyzed for molecular phylogeny because their molecular data are not available. Even the type species for *Phomatospora*, *P. berkeleyi* remains unavailable for molecular phylogeny. It is a question whether those *Phomatospora* spp. that were early established only on morphology belong to this newly established *Phomatosporales*.

Significance

Ecological and economic roles

Phomatosporales is a widely distributed order in terrestrial, freshwater and marine environments (Hyde 1988, Barr 1994, Fallah & Shearer 1998, Senanayake et al. 2016). Most species of *Phomatosporales* are endophytic or saprobic on herbaceous stems, grass culms, coriaceous leaves, or wood from terrestrial environment (Barr 1994, Senanayake et al. 2016). Other species of *Phomatosporales* are mainly saprobic on drifted or submerged wood, or decaying twigs originating from freshwater or marine environments (Hyde 1992b, Hyde et al. 1999, Luo et al. 2019b, Dong et al. 2023, Pang et al. 2023). Some species in *Phomatosporales* show some morphological adaptation to freshwater or marine environments. Their ascospores have appendages or slimy sheaths, which could facilitate subsequent attachment to substrates (Hyde 1993, Raja & Shearer 2008, Senanayake et al. 2016). Eight species of *Phomatosporales* are known from marine environments including *Lanspora coronata*, *L. dorisauae*, *Phomatospora acrostichi*, *P. bellaminuta*, *P. kandeliae*, *P. nypicola*, *P. nypae* and *P. phragmiticola* (Hyde & Jones 1986, Hyde 1988, 1992b, 1993, Kohlmeyer et al. 1995, Poon & Hyde 1998, Hyde et al. 1999, Pang et al. 2023).

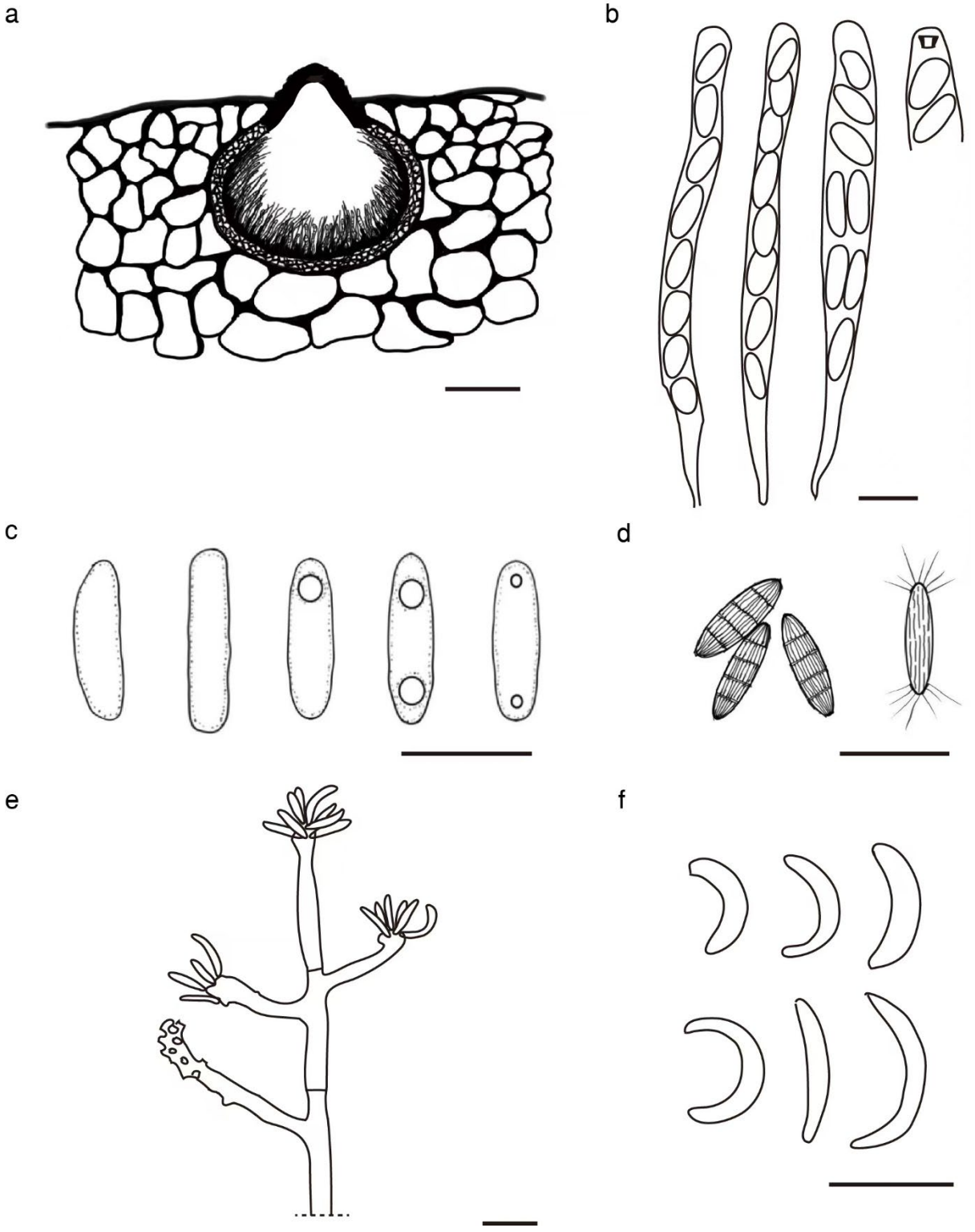


Figure 238 – Morphology of *Phomatosporales.* a Ascomata (*Phomatospora berkeleyi*). b Asci (*Phomatospora berkeleyi* and *Phomatospora biseriata*) and ascus tips (*Phomatospora acrostichi*). c Ascospores (*Phomatospora berkeleyi* and *Phomatospora biseriata*). d Striations (*Phomatospora triseptata*) and appendages (*Phomatospora muskellungensis*) of ascospores. e Sporothrix-like asexual morph (*Phomatospora angelicae*). f Conidia (*Phomatospora berkeleyi*). (Redrawn from Hyde 1988, Rappaz 1992, Fallah & Shearer 1998, Raja & Shearer 2008, Senanayake et al. 2016). Scale bars: a = 100 μm, b–f = 10 μm.

Eight species of *Phomatosporales* are reported from freshwater including *Conicotenuis fusiformis*, *Minimispora superficialis*, *Phomatospora aquatica*, *P. berkeleyi*, *P. luteotingens*, *P.*

muskellungensis, *P. striatigera* and *P. triseptata* (Scheuer 1988, Fallah & Shearer 1998, Vijaykrishna & Hyde 2006, Raja & Shearer 2008, Fournier & Lechat 2010, Luo et al. 2019b, Dong et al. 2023). Since most species of *Phomatosporales* are saprobic on various decaying plant materials in terrestrial, freshwater or marine ecosystems, they are presumed to secrete enzymes for plant decomposition, which lead to soft rotting (Abdel-Raheem & Shearer 2002, Senanayake et al. 2016).

Chemical diversity

Natural product chemistry in *Phomatosporales* is rarely reported. A new 8-acetoxy pestalopyrone and a known pestalopyrone with antimalarial activity (IC_{50} was 37 μM) against *Plasmodium falciparum* were isolated from *Phomatospora bellaminuta* (Cao & Clardy 2011). Except that, the mycelia water-soluble extract from *P. berkeleyi* was found to be toxic to the pine-wood nematode against *Bursaphelenchus xylophilus* (Dong et al. 2004).

Other relevant data and future recommendations

Information about the species in *Phomatosporale*s is mainly about their distribution and characters for the sexual morph. Most species in *Phomatosporales* lack molecular data for phylogenetic studies. Comprehensive studies on the asexual morph, secondary metabolites, ecological roles and activity screening results are worthy of further study. In addition, further study is required to determine whether morphological features (such as striations and appendages of ascospores) can be linked to molecular phylogeny.

Pinibarreniales **J. Luo & Ning Zhang, Mycologia 116(5): 841 (2024)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Sordariomycetidae*

Introduction & History

Pinibarreniales was recently established by Luo et al. (2024) to accommodate a monotypic family *Pinibarreniaceae* and genus *Pinibarrenia* that was typified by *Pinibarrenia chlamydospora* based on the evidence from morphological and phylogenetic analyses along with ecological characters. The order formed a distinct clade within *Sordariomycetidae* in the phylogenetic analysis conducted based on ITS, 28S, and RPB2 sequence data. *Pinibarreniales* showed 67.17% to 83.76% similarity for ITS and 76.28%–94.45% similarity for 28S with 10 orders that are assigned within *Sordariomycetidae* . The BLAST search result revealed that seventy-three environmental ITS sequences had 97% to 99% identities to *Pinibarrenia* strains, and several strains also showed similar ecology, such as *Ericaceae* as a host (Luo et al. 2024).

General description

The order has been established only on asexual morphology and the close morphological association with members of *Sordariomycetidae* is discussed in Luo et al. (2024).

Sexual morph: Not observed. Asexual morph: Hyphomycetous. *Hyphae* branched, septate, smooth. *Conidiophores* micronematous, simple, erect, unbranched to branched, septate. *Conidiogenous cells* erect, terminal, phialidic, cylindrical to ampulliform. *Conidia* ellipsoidal, aseptate, straight to curved. *Chlamydospores* terminal or intercalary, usually in long chains or clusters, ovoid to subglobose, smooth, thick-walled (adapted from Luo et al. 2024) (Fig. 239).

Families included in *Pinibarreniales*

Pinibarreniaceae J. Luo & N. Zhang

Evolution

The ecology of *Pinibarreniales* is also supported by the environmental sequence identity by sharing similar habitat and edaphic conditions. Further, the order could presumably have a lineage of

fungi that initially formed an association with *Ericaceae* plants and adapted to acidic and oligotrophic environments (Luo et al. 2024).

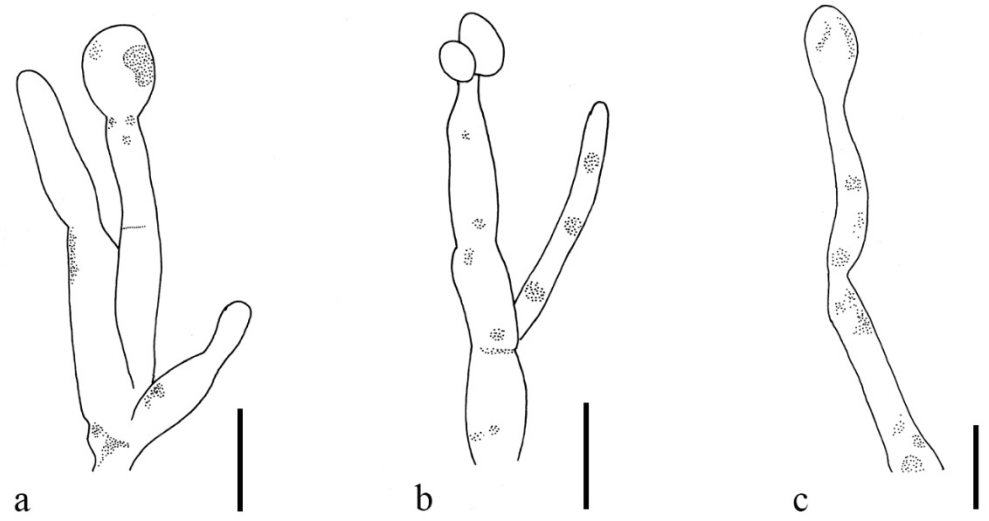


Figure 239 – Morphology of *Pinibarreniales*. a, c Chlamydospores. b Conidiophores and conidia (*Pinibarrenia chlamydospora*) (drawn from Luo et al. 2024). Scale bars: a, b = 5 μm, c = 10 μm.

Justification of order and problems

The order has been recently established based on morphological, phylogenetic, ecological and sequence similarity analyses (Luo et al. 2024).

Significance

Ecological and economic roles

Pinibarrenia chlamydospore was isolated from the healthy roots of highbush blueberry in the New Jersey Pine Barren as an endophyte. However, a plant-fungal interaction experiment conducted between strains of *Pinibarrenia chlamydospore* (PB23.R23, RB23.R23, and RB23.R45) with *Arabidopsis thaliana* seeds resulted in negative impacts on the growth of seeds and assumed to have potential for a pathogenic lifestyle (Luo et al. 2024).

Chemical diversity

No relevant studies are available for the chemical diversity of *Pinibarreniales*.

***Pisorisporiales* Réblová & J. Fourn., Persoonia 34: 43 (2014)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Pisorisporiomycetidae*

Introduction

Pisorisporiales is an order of aquatic and terrestrial fungi in the class *Sordariomycetes* introduced by Réblová et al. (2015a). They incorporated genera *Achroceratosphaeria* and *Pisorisporium* and raised a new family *Pisorisporiaceae* based on phylogenetic analysis of DNA sequences from protein-coding and ribosomal nuclear loci (RPB2, LSU and SSU). Currently, the genus *Brocchiosphaera*, which was introduced by Yamaguchi et al. (2020) and the family *Pisorisporiaceae* are placed under *Pisorisporiales*. *Pisorisporiaceae* is typified by *Pisorisporium*, and this genus is characterized by astromatic, black, immersed to superficial perithecial ascomata, persistent paraphyses, unitunicate, persistent asci with an amyloid apical ring and hyaline, fusiform, cymbiform to cylindrical, transversely multi-septate ascospores with conspicuous guttules (Réblová et al. 2015a). The taxa of *Pisorisporiales* include *Achroceratosphaeria potamia*, *A. incolorata*,

Brocchiosphaera brocchiata, *B. bulbiformis* and *B. microspora*, *Pisorisporium cymbiforme* and *P. glaucum*. They are morphologically comparable and can be distinguished mainly by the shape and septation of ascospores, the shape of asci and the amyloidity of the apical ring (Samuels et al. 1987, Barrasa et al. 1993).

History

Réblová et al. (2010) introduced the ascomycete genus *Achroceratosphaeria*, with *A. incolorata* (= *Ceratosphaeria incolorata*) and *A. potamia* through the morphological studies and phylogenetic analysis of combined LSU and SSU sequence data. *Achroceratosphaeria incolorata* is characterized by the fasciculate peculiar appearance, eccentric necks, and paler in their upper part (Réblová 1998). Réblová et al. (2015a) introduced a new family *Pisorisporiaceae* and order *Pisorisporiales*, representing a new lineage of aquatic fungi, which includes the genera *Achroceratosphaeria* and *Pisorisporium*. The new genus *Pisorisporium* contains two species, with *P. cymbiforme* as the type species (Réblová et al. 2015a). Yamaguchi et al. (2020) split the genus *Candelabrum* into two clades based on phylogeny and taxonomic data; the *C. spinulosum* group (*C. clathrosphaeroides*, *C. desmidiaceum*, *C. japonense*, *C. spinulosus*) nested in *Leotiomycetes*, and *C. brocchiatum* group (*C. brocchiatum* and *C. microsporum*) clusters in *Sordariomycetes*. Hence, Yamaguchi et al. (2020) transferred all species of the *C. spinulosum* group to the new genus *Brocchiosphaera* and proposed two new combinations, *B. brocchiata* and *B. microspora*, and additionally introduced a new species, *B. bulbiformis*.

General description

In *Pisorisporiales*, sexual morphs are only found in *Achroceratosphaeria* and *Pisorisporium* while asexual morph are only found in *Brocchiosphaera* (Réblová et al. 2015a, Yamaguchi et al. 2020). Ascomata of the *Pisorisporium* are gradually erumpent to superficial, papillate or with a short beak, glabrous, enter subglobose to broadly conical, laterally or basally flattened, black, but the *Achroceratosphaeria* are venter globose to subglobose sometimes depressed, subhyaline to pale brown; neck cylindrical, hyaline to subhyaline to grey, occasionally hairy, periphysate (Réblová et al. 2010, 2015a). The ascomata walls of *Pisorisporium* are black, leathery to fragile, 2-layered, and the outer layer is partly carbonaceous; the *Achroceratosphaeria* are pigmented dark brown, opaque to light brown to subhyaline (Réblová et al. 2010, 2015a).

Sexual morph: *Ascomata* perithecial, astromatic, solitary or in small groups, subhyaline to pale brown to black, immersed to superficial, papillate or with a long, hyaline or black, upright or obliquely lying neck, ostiolate, periphysate. *Peridium* leathery to fragile, comprising two layers, partly carbonaceous in the outer layers. *Hamathecium* comprising abundant, persistent, cylindrical, septate, hyaline paraphyses. *Asci* 8-spored, unitunicate, cylindrical-clavate, pedicellate, stipitate with a pronounced amyloid or inamyloid apical ring. *Ascospores* overlapping uniseriate to biseriate, hyaline, fusiform, cylindrical to cymbiform, transversely multi-septate, lacking a mucilaginous sheath or appendages, with or without guttules. Asexual morph: *Mycelium* immersed, branched, septate, hyaline. *Conidiophores* macro- to semimacronematous, mononematous, unbranched, hyaline and arising from repent hypha. *Conidiogenous cells* monoblastic, terminal. *Conidia* solitary, acrogenous, composed of dichotomous or trichotomous branches, terminating cells are ornamented with minute tubercles, developing into a globose or subglobose propagule, hyaline to orange conidia, floating on the surface of the water (adapted from Yamaguchi et al. 2020) (Fig. 240).

Families included in *Pisorisporiales*

Pisorisporiaceae Réblová & J. Fourn.

Pisorisporiales genus *incertae sedis*

Brocchiosphaera K. Yamag., Chuaseehar. & Nakagiri

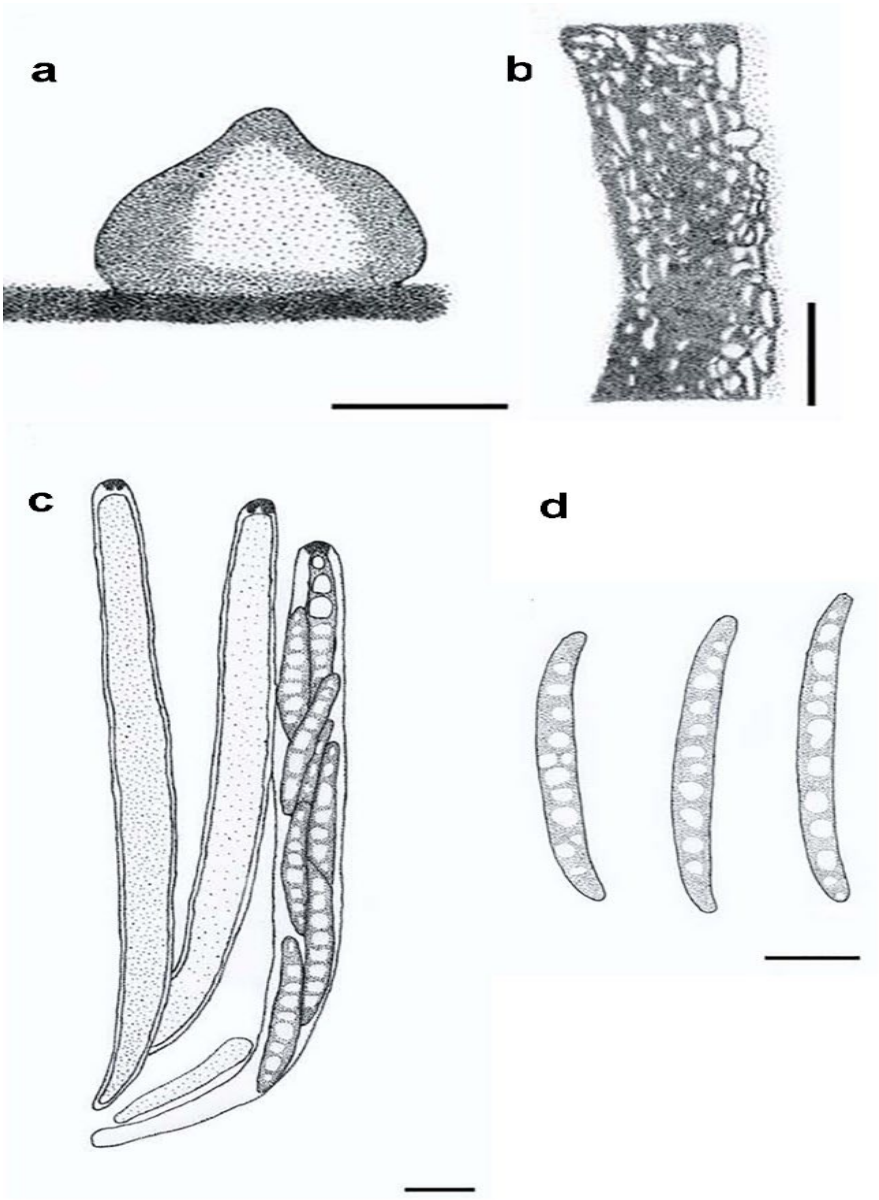


Figure 240 – *Pisorisporium cymbiforme.* a Ascomata. b Vertical sections of the ascomatal wall. c Asci. d Ascospores. (a, d from PRM 924377 holotype, b from PRM 924379, c from PRM 924378) (redrawn from Maharachchikumbura et al. 2016). Scale bars: a = 200 μm, b = 20 μm, c, d = 10 μm.

Justification of order and problems

Morphologically, the ascospores and asci of *Pisorisporium* are similar to members of *Ceratosphaeria*, *Ceratosphaerella* and *Pseudohalonectria* of *Magnaporthaceae* (Réblová et al. 2015a). They all have fusiform, cylindrical to cymbiform, multi-septate, hyaline ascospores. Still, the *Pisorisporium* has an inamyloid reaction of the apical ring and long, sometimes flexuous protruding necks of ascomata different from them (Réblová et al. 2015a). In addition, the ascospores are predominantly 2-seriate within the ascus in *Pisorisporium*, but *Pseudohalonectria* and *Ceratosphaeria phialidica* have cylindrical to cymbiform asci with ascospores arranged in a fascicle or rarely 4-seriately (Réblová et al. 2015a).

Based on combined LSU, SSU and RPB2 sequence analysis, *Pisorisporiales* shows a sister relationship with the orders *Koralionastetales* and *Lulworthiales* in an unsupported clade (Réblová et al. 2015a). However, there are no morphological similarities among members of the *Koralionastetales*, *Lulworthiales* and *Pisorisporiales* (Réblová et al. 2015a). They are situated basal to the *Hypocreomycetidae* based on weakly supported Bayesian and maximum likelihood analyses (Spatafora et al. 2006, Zhang et al. 2006, Schoch et al. 2007). Molecular data do not sufficiently

support the relationship between *Pisorisporiales* and other orders, and there are only a few sequence data for this order.

Significance

Ecological and economic roles

Most species of *Pisorisporiales* are grown on submerged wood and driftwood in freshwater habitats (Réblová et al. 2010, 2015a). They decompose wood with their saprobic activity (Hyde et al. 2020d).

Chemical diversity

No relevant studies are available for the chemical diversity of *Pisorisporiales*.

Other relevant data and future recommendations

The members of *Pisorisporiales* are predominantly found in regions encompassing Europe and Asia, and there is currently only one family, three genera, and seven species in this order (Samuels et al. 1987, Barrasa et al. 1993, Maharachchikumbura et al. 2016). In future research, it is recommended to conduct extensive studies in different regions (Hyde et al. 2024c), leading to discovery new species and supplementing more molecular data.

Planisphaeriales **J.F. Zhang, Jian K. Liu & K.D. Hyde, Fungal Diversity 222: 113 (2023)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Sordariomycetidae*

Introduction & History

Planisphaeriales was recently established to accommodate a monotypic family *Planisphaeriaceae* and the genus *Planisphaeria* with two new species (*P. karsti* and the type species *P. reniformispora*). The order formed a distinct lineage within *Sordariomycetidae* based on LSU, SSU, TEF1-α and RPB2 sequence data (Zhang et al. 2023c). The order further formed a sister clade relationship to *Phyllachorales* without strong statistical support and they together formed a close clade to *Boliniales*. The order shares similar morphological features to both *Phyllachorales* and *Boliniales* but differs in non-stromatic ascomata with a broad crack at the apex with ascospores that are reniform or narrowly ovoid, hyaline, one- celled (Maharachchikumbura et al. 2016, Hyde et al. 2020d, Zhang et al. 2023c).

General description

Members of *Planisphaeriales* are characterized by uni-loculate ascomata with a fattened base and a broad crack at the apex, similar texture of peridium, unitunicate, 8-spored asci and hyaline, non-septate ascospores. However, the generic type *Planisphaeria reniformispora* differs from *P. karsti* in having reniform ascospores that are surrounded by a thick mucilaginous sheath, whereas *P. karsti* has ellipsoid ascospores that are guttulate, verrucose, narrowed towards one end and rounded at the other end (Zhang et al. 2023c). Sexual morph: *Ascomata* perithecial, immersed to erumpent through the host tissue, with broadly crack at the apex, gregarious or scattered, depressed subglobose to obpyriform, with a fattened base, coriaceous, brown to black, clypeate, periphysate. *Peridium* composed of several layers of subhyaline to hyaline, thin-walled, elongated cells of *textura angularis* merging with red-brown pseudoparenchymatous cells. *Paraphyses* dissolved or persistent at age. *Asci* unitunicate, clavate, pedicellate, with or without apical rings. *Ascospores* hyaline, non-septate, reniform or narrowly ovoid, rarely in irregular shapes, straight or curved, with or without mucilaginous sheath. Asexual morph: not observed (adapted from Zhang et al. 2023c) (Fig. 241).

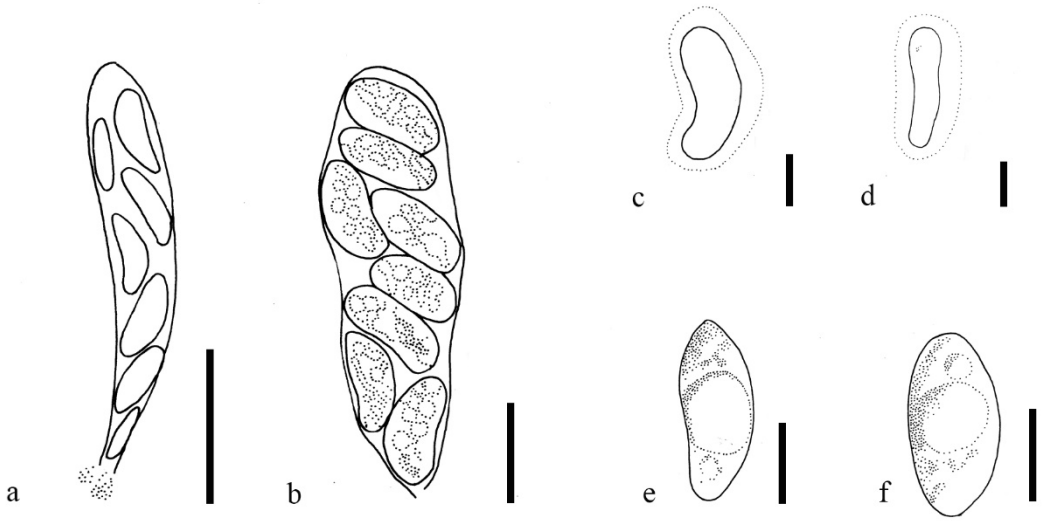


Figure 241 – Morphology of *Planisphaeriales*. a, b Asci (a *Planisphaeria reniformispora*, b *P. karsti*). c–f Ascospores (c, d *P. reniformispora*, e, f *P. karsti*). (drawn from Zhang et al. 2023c). Scale bars: a = 20 μm, b = 30 μm, e, d = 5 μm, e, f = 10 μm.

Families included in *Planisphaeriales*

Planisphaeriaceae J.F. Zhang, Jian K. Liu & K.D. Hyde

Justification of order and problems

The order has been established based on morphology and phylogenetic analyses, yet more fresh collections with sequence data are essential to support its placement (Zhang et al. 2023c).

Significance

Ecological and economic roles

Planisphaeriales species are reported as ***s***aprobic on dead branches of unidentified woody plants from karst landforms of Guizhou Province, China (Zhang et al. 2023c).

Chemical diversity

No relevant studies are available regarding the chemical diversity of *Planisphaeriales.*

***Pleurotheciales* Réblová & Seifert, Persoonia 37: 63 (2015) [2016]**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Savoryellomycetidae*

Introduction

Pleurotheciales is the largest order in *Savoryellomycetidae* (Hongsanan et al. 2017a). The order was introduced by Réblová et al. (2016c) based on a multi-locus phylogenetic analysis including ITS, SSU, LSU, TUB2, RPB2, and MCM-7 sequence data. *Pleurotheciales* species formed a distinct, well-supported clade separate from other taxa, with *Savoryellales* as its closest sister taxon (Réblová et al. 2016c). Most of the species in this order have been isolated as saprobes on decaying plants and wood debris and a large number is known to inhabit freshwater habitats (Hongsanan et al. 2017a, Luo et al. 2019b). In rare instances, some species were isolated as human pathogens, such as

Phaeoisaria clematidis which causes keratomycosis (Guarro et al. 2000). *Pleurotheciales* is made up of one family, *Pleurotheciaceae*, with 15 genera.

History

Pleurotheciales was established to accommodate several freshwater and terrestrial genera with uncertain taxonomic resolutions (Réblová et al. 2016c). These fungi exhibited astromatic, partially submerged to superficial ascomata with unitunicate asci featuring inamyloid apical rings and septate ascospores that are hyaline to subhyaline (Réblová et al. 2012). Initial analyses of specific genetic markers, including the SSU, LSU and RPB2, revealed a close relationship between *Phaeoisaria*, *Pleurotheciella*, *Pleurothecium*, and *Sterigmatobotrys*, with a central clade focused on *Pleurothecium* (Réblová et al. 2012). Expanding the analysis with more taxon sampling provided further clarity on the taxonomic placement of these genera. By examining LSU, SSU and RPB2, it became evident that these genera formed a distinct, well-supported clade that is clearly separate from *Savoryella* (Réblová et al. 2016c). Consequently, the order *Pleurotheciales* was established, consisting of only one family, *Pleurotheciaceae* (Réblová et al. 2016c). Upon its establishment, this order included ten genera: *Helicoon*, *Pleurothecium*, *Brachysporiella*, *Phragmocephala*, *Melanotrigonum*, *Sterigmatobotrys*, *Taeniolella*, *Pleurotheciella*, *Adelosphaeria*, and *Phaeoisaria*. Some of these genera are known to be polyphyletic such as *Helicoon*, *Brachyosporiella* and *Taeniolella*.

Initially, only *Helicoon farinosum* was included as a representative of this polyphyletic genus. This species was consistently placed within *Pleurotheciales* in subsequent studies (Maharachchikumbura et al. 2016, Goh & Kuo 2018, Luo et al. 2019b). In the analysis of ITS sequences, *Helicoon* species were found in different orders, demonstrating that not all *Helicoon* species belong in *Pleurotheciales* (Goh & Kuo 2018). *Helicoon subglobosum* and *H. gigantisporum* clustered with other *Tubeufiales* sp., *Helicoon sessile* in *Orbiliales* and *Helicoon maioricense* and *H. fuscosporum* in *Venturiales* (Goh & Kuo 2018). In 2019, Dayarathne established the genus *Helicoascotaiwania* to accommodate *Ascotaiwania hughesii*, the sexual morph of *Helicoon farinosum*. This was reclassified as *Helicoascotaiwania hughesii* under *Pleurotheciale*s (Dayarathne et al. 2019). The phylogenetic placement of *Helicoon hughesii* was supported by Réblová et al. (2020a), however, it was proposed that the correct epithet for the species is *Helicoascotaiwania farinosa* since *Helicoon farinosum* holds priority over *Ascotaiwania hughesii* (Réblová et al. 2020a). The classification of *Helicoascotaiwania* under *Pleurotheciales* was accepted by Hyde et al. (2020b), removing *Helicoon* from the order.

Brachysporiella setosa is currently named as *Monotosporella setosa* (MycoBank 2025). Although *Monotosporella* was initially considered as a synonym of *Brachyosporiella* (Ellis 1959), the analysis of LSU sequences revealed that *Brachysporiella navarrica* clustered differently, under *Kirschsteiniotheliaceae* while *Monotosporella setosa* remained in the *Pleurotheciaceae* clade (Hernández-Restrepo et al. 2017). This led to the proposal to consider the two genera as distinct. *Monotosporella* remains in *Pleurotheciales*, but it is noteworthy that this classification is based solely on *Monotosporella setosa* (Hernández-Restrepo et al. 2017, Dayarathne et al. 2019, Luo et al. 2019b, Réblová et al. 2020a). The addition of sequences of other species of *Monotosporella* may lead to changes in its classification.

Taeniolella rudis was initially included in *Pleurotheciales* and was recovered in a clade together with other *Sterigmatobotrys* species (Réblová et al. 2016c). Previously, Réblová & Seifert (2011) noted morphological similarities between *Taeniolella* and *Sterigmatobotrys*, such as the sterigmatobotrys-like conidiophores in *Taeniolella* conidia, showing a close relationship between the two genera. Based on both molecular data and distinctive morphological characteristics of the synanamorph, *T. rudis* was reassigned to the genus *Sterigmatobotrys* (Ertz et al. 2016). Further analysis of LSU sequences showed that *T. rudis* did not group with *T. exiis*, the type species of *Taeniolella* (Ertz et al. 2016). Thus, it was reassigned as *Sterigmatobotrys* and *Taeniolella* was removed from *Pleurotheciales*. *Taeniolella* is currently classified under *Mytilinidiales* (Ekanayaka et al. 2017a).

After 2016, several genera have been added to *Pleurotheciales* primarily based on molecular analysis. *Anapleurothecium* was introduced, based on analysis of LSU sequences (Hernández-Restrepo et al. 2017). This formed a clade with *Helicoascotaiwania* and *Monotosporella* as the closest taxa. Morphologically, *Anapleurothecium* resembles *Pleurophragmium,* but it differs due to its larger denticles and conidia, which are darkly pigmented (Hernández-Restrepo et al. 2017). They are, however, phylogenetically distinct. *Dematipyriforma* was introduced as a genus in *Savoryellales* with *Dematipyriforma aquilaria* as the type species (Sun et al. 2017b). Since the isolate did not produce a sexual morph, it could not be compared morphologically with *Ascotaiwania* and *Savoryella* species, the closest taxa in the tree (Sun et al. 2017b). Based on a multi-locus analysis of LSU, SSU, ITS and RPB2, *D. aquilaria* was recovered in a well-supported clade in *Pleurotheciales* (Dong et al. 2021a). With the introduction of new species in the genus, *D. nigrospora* and *D. muriformis*, the taxonomic placement of this genus was confirmed as they clustered with species in *Pleurotheciales* (Bao et al. 2022).

Additional genera have been incorporated into *Pleurotheciales* through molecular analysis, including *Neomonodictys*, *Rhexoacrodictys*, *Saprodesmium*, and *Coleodictyospora*. *Neomonodictys* was established to accommodate *Neomonodictys muriformis*, a species found in freshwater (Dong et al. 2021b). This is morphologically similar to *Monodictys* by having monoblastic, hyaline to brown conidiogenous cells and pyriform or clavate conidia, however, they are phylogenetically distant (Dong et al. 2021b). *Monodictys* is *incertae sedis* in *Dothideomycetes* while *Neomonodictys* groups with species under *Pleurotheciales* in *Sordariomycetes* (Wijayawardene et al. 2018, Dong et al. 2021b). *Rhexoacrodictys* was included in *Pleurotheciales* based on analysis of LSU, SSU, RPB2 and TEF sequences (Luo et al. 2019b). This phylogenetic placement was further confirmed by Dong et al. (2021b). *Saprodesmium* was established as a genus to accommodate *Saprodesmium dematiosporum*, which was recovered as an independent branch between *Dematipyriforma* and *Rhexoacrodictys* in *Pleurotheciales* based on LSU, SSU, ITS and RPB2 sequences (Dong et al. 2021b). A new species of *Coleodictyospora*, *C. muriformis*, was introduced and this was found to form a well-supported clade in *Pleurotheciales* with *Pleurothecium* as a sister taxon (Dong et al. 2021b). This justified the classification of *Coleodictyospora* in *Pleurotheciales*. However, out of the three species in this genus, only *C. muriformis* has molecular data. The type genus, *C. cubensis*, and another species *C. micronesiaca* were introduced based solely on morphological characteristics.

The monotypic genus *Carpoligna* clusters with species in *Pleurotheciales*. Initially, it was found in a well-supported clade with *Pleurotheciella centenaria* (Ertz et al. 2016), and in a later combined analysis, *Carpoligna pleurothecii* forms a clade with *Pleurothecium semifecundum* (Dayarathne et al. 2019). *Carpoligna pleurothecii* is the sexual morph of *Pleurothecium recurvatum*, and is the reason why previous lists did not include *Carpoligna* in the genera of *Pleurotheciales* (Fernández et al. 1999, Hyde et al. 2020b, Wijayawardene et al. 2022a).

The classification of fungi within the *Pleurotheciales* has relied heavily on molecular data since its establishment. Molecular analyses have been instrumental in resolving taxonomic uncertainties and clarifying the relationships between different genera and species within this order. As more sequences from various species classified under *Pleurotheciales* become available, it is likely that the taxonomic placement and classification of these fungi will become even more refined and accurate.

General description

Members of this taxa have perithecial ascomata with hyphomycetous asexual stages, and diverse morphologies specially in the asexual morphs (Réblová et al. 2016c, Dong et al. 2021b).

Sexual morph: *Ascomata* perithecial without stromata. *Ostiole* periphysate. *Hamathecium* consists of paraphyses. *Asci* unitunicate, featuring an inamyloid apical ring. *Ascospores* hyaline or versicolorous, with hyaline polar cells and brown middle cells, transversely multi-septate. Asexual morph: *Conidiophores* macronematous or semi-macronematous, typically found loosely fasciculate or aggregated in indeterminate synnemata. *Conidigenous cells* holoblastic, either monoblastic or with

sympodial extension, conidial succession rhexolytic or schizolytic. *Conidia* hyaline, brown or versicolorous, septate or aseptate (adapted from Réblová et al. 2016c) (Figs. 242, 243).

Families included in *Pleurotheciales*

Pleurotheciaceae Réblová & Seifert.

Evolution

Pleurotheciales is classified under the subclass *Savoryellomycetidae* in *Sordariomycetes* (Hongsanan et al. 2017a). *Pleurotheciales*, has a stem age of 139–143 MYA (Hongsanan et al. 2017a, Dayarathne et al. 2019), falling within the recommended range for the age of fungal orders which is typically between 130-250 MYA (Hongsanan et al. 2017a, Hyde et al. 2017a, Dayarathne et al. 2019). An ancestral character analysis of Samarakoon et al. (2022), suggested that *Savoryellomycetidae* has a freshwater ancestor. This finding may explain why many species within the *Pleurotheciales* order are commonly isolated from freshwater habitats (Réblová et al. 2016c).

Justification of order and problems

When *Pleurotheciales* was initially introduced, it was noted that the morphology of these fungi was inconspicuous, making it difficult to classify them in *Sordariomycetes* (Réblová et al. 2016c). In fact, it is also challenging to differentiate these fungi from each other in the absence of culture and/or molecular data (Réblová et al. 2016c). As a result, the establishment of this order relied heavily on molecular data. Several taxa within *Pleurotheciales* were initially considered polyphyletic, including *Helicoon*, *Brachysporiella*, and *Taeniolella* (Réblová et al. 2016c). However, these genera are no longer classified under *Pleurotheciales* since the specific species used in the initial analysis were transferred into genera that are well within *Pleurotheciales* (Ertz et al. 2016, Hernández-Restrepo et al. 2017, Réblová et al. 2020a). It is important to note that some genera in the order, such as *Monotosporella* and *Coleodictyospora* are represented by only one species in the phylogenetic analyses since these are the only species with available molecular data (Réblová et al. 2020a, Dong et al. 2021b). The phylogenetic placement of these genera will be further be confirmed as more molecular data from other species becomes available. The addition of other genera to this order after its establishment was primarily based on robust phylogenetic placement, making these classifications reliable (Hernández-Restrepo et al. 2017, Luo et al. 2019b, Dong et al. 2021b, Bao et al. 2022).

Significance

Ecological and economic roles

Species within *Pleurotheciales* are predominantly found as saprobes in freshwater habitats (Réblová et al. 2016c, Luo et al. 2019b, Dong et al. 2021b). However, there are instances of some genera, like *Phaeoisaria,* being reported from marine sediments and others, such as *Dematipyriforma*, were isolated as endophytes (Cheng et al. 2014, Sun et al. 2017). As saprobes, they facilitate decomposition and nutrient cycling in the environment that they inhabit. As endophytes, these fungi may potentially have a beneficial effect on their hosts, however, there haven't been any reported studies on the specific role of *Pleurotheciales* species as endophytes to date. It is noteworthy that some species within this order, such as *Phaeoisaria clematidis* and *Pleurothecium recurvatum* have been documented as a cause of fungal infections in humans (Guarro et al. 2000, Chew et al. 2010). These findings suggest that while the majority of the *Pleurotheciales* species are saprobic, they also exhibit other lifestyles, including endophytic and potentially pathogenic roles. Nevertheless, there is a limited number of reports regarding their activities as endophytes and pathogens, indicating the need for further research to better understand these aspects of their biology and ecology.

Chemical diversity

To date, there are no reports of chemical diversity from species in *Pleurotheciales*.

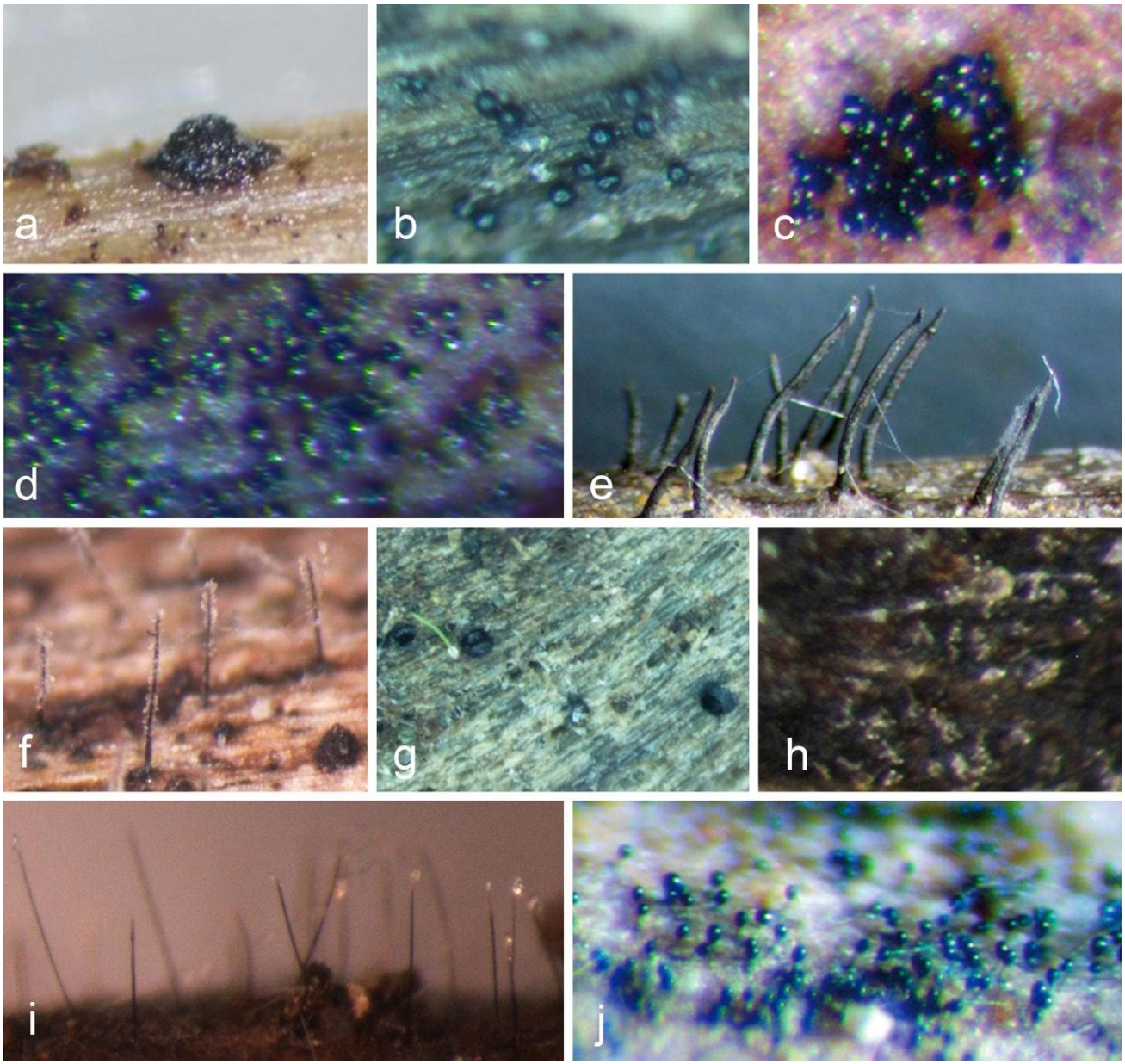


Figure 242 – Colonies on natural substrate of *Pleurotheciales* species. a *Coleodictyospora muriformis*. b *Dematiosporium aquaticum*. c *Dematipyriforma muriformis*. d *Neomonodictys muriformis*. e *Phaeoisaria filiformis*. f *Phaeoisaria clematidis*. g *Pleurotheciella fusiformis*. h *Pleurotheciella aquatica*. i *Pleurothecium recurvatum*. j *Rhexoacrodictys fimicola*.

Other relevant data and future recommendations

The establishment of the order *Pleurotheciales* was driven by molecular data, as it encompassed a diverse array of fungi. Many of these species share morphological similarities with unrelated fungi, making morphology alone insufficient for their accurate classification (Réblová et al. 2016c). Some of the genera initially included in the *Pleurotheciales* were found to be polyphyletic which necessitated the use of molecular data to accurately classify and differentiate species (Ertz et al. 2016, Hernández-Restrepo et al. 2017, Dayarathne et al. 2019). For genera like *Monotosporella* and *Coleodictyospora*, which are represented by only one species with available molecular data, the addition of more molecular sequences will be crucial to confirm their phylogenetic placement within *Pleurotheciales*. As additional molecular sequences become available for species within this order, it is expected that the taxonomic position and relationships of these fungi will be further clarified, providing a more accurate understanding of their evolutionary history and diversity.

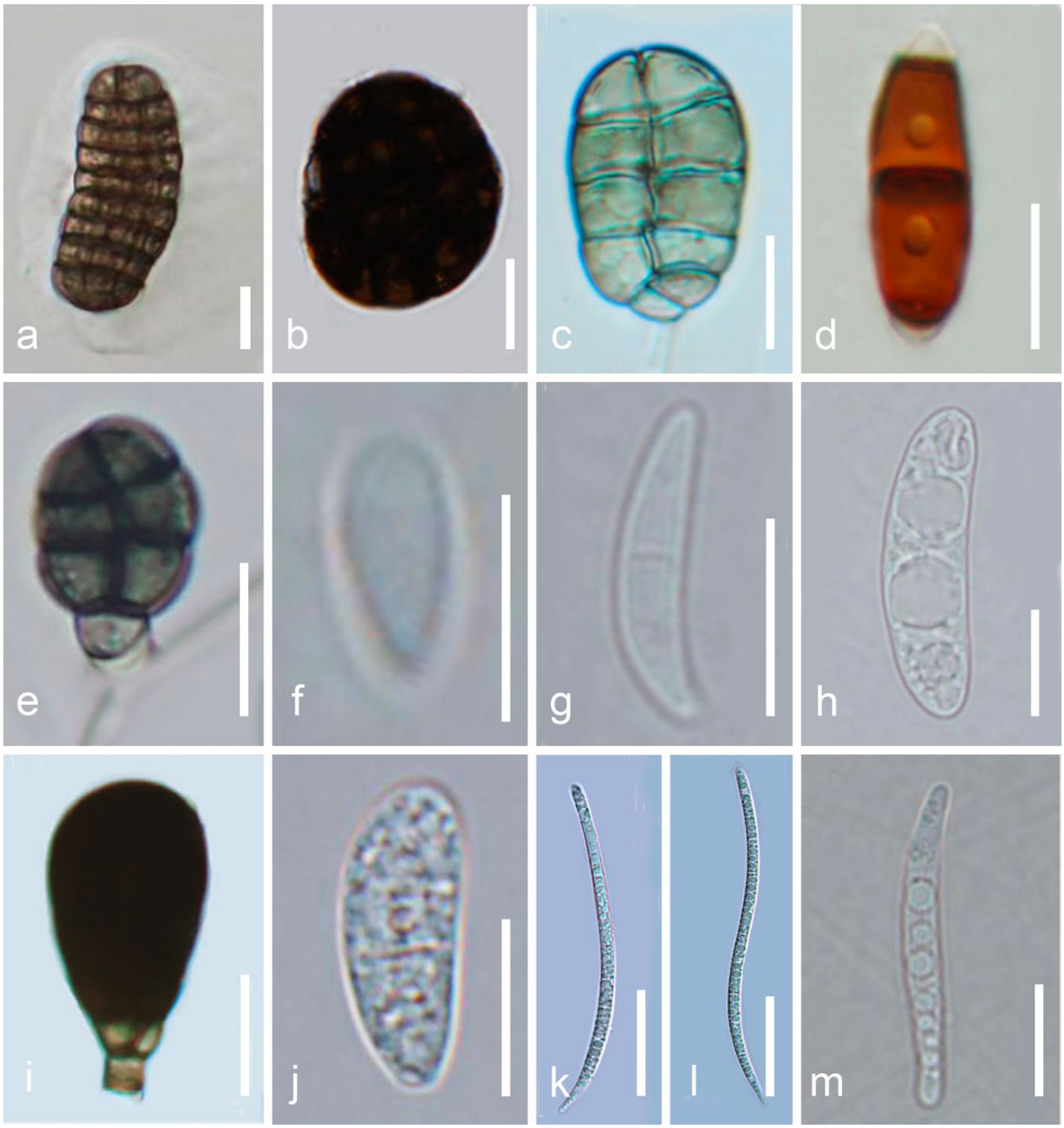


Figure 243 – Spores of *Pleurotheciales* species. Conidia of: a *Coleodictyospora muriformis*. b *Dematiosporium aquaticum*. c *Dematipyriforma muriformis*. d *Helicoascotaiwania hughesii*. e *Neomonodictys muriformis*. f *Phaeoisaria clematidis*. g *Pleurotheciella fusiformis*. h *Pleurothecium recurvatum*. i *Rhexoacrodictys fimicola*. j *Sterigmatobotrys uniseptata* Ascospores of: k-l *Phaeoisaria filiformis*. m *Pleurotheciella fusiformis*. Scale bars: a–e, g–j, m = 10 µm, f = 5 µm, k–l = 30 µm.

Pseudodactylariales **Crous, Persoonia 39: 421 (2017)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Sordariomycetidae*

Introduction

Pseudodactylariales was introduced by Crous et al. (2017a) to accommodate two dactylaria-like species, *Pseudodactylaria hyalotunicata* and *P. xanthorrhoeae*. Currently, *Pseudodactylariales*

includes a solitary family, *Pseudodactylariaceae*, with a single genus, *Pseudodactylaria*. The taxonomic assignment of *Pseudodactylariales* to the class *Sordariomycetes* was established by Crous et al. (2017a). Members of *Pseudodactylariales* exhibit a dactylaria-like morphology, but differ from *Dactylaria* by having 1-septate conidia encased in a mucoid sheath (Crous et al. 2017a).

History

Tsui et al. (1997) introduced a distinct *Dactylaria* species, *D. hyalotunicata*, originating from submerged wood, which differs from other similar species by having hyaline conidiophores and relatively small conidia with a hyaline gelatinous sheath. However, *D. hyalotunicata* was treated as a synonym under *Pseudodactylaria* when the genus *Pseudodactylaria* was established by Crous et al. (2017a) based on the combination of morphology and multi-gene phylogenetic analysis. Simultaneously, *Pseudodactylariales* was introduced, and the newly proposed family *Pseudodactylariaceae* (Crous et al. 2017a). Subsequently, a growing number of *Pseudodactylaria* species have been introduced (Lin et al. 2018, Yang et al. 2023b).

General description

Sexual morph: Undetermined. Asexual morph: hyphomycetous. *Conidiophores* hyaline, subcylindrical, straight to flexuous, unbranched or branched, thick-walled, septate. *Conidiogenous cells* terminal, integrated, subcylindrical, denticulate. *Conidia* solitary, aggregating in slimy mass, fusoid-ellipsoid, hyaline, smooth-walled, guttulate, septate, surrounded by a thin mucilaginous sheath (adapted from Hyde et al. 2020d) (Fig. 244).

Families included in *Pseudodactylariales*

Pseudodactylariaceae Crous

Evolution

The divergence time for *Pseudodactylariales* was estimated as 128 MYA (Hyde et al. 2020d).

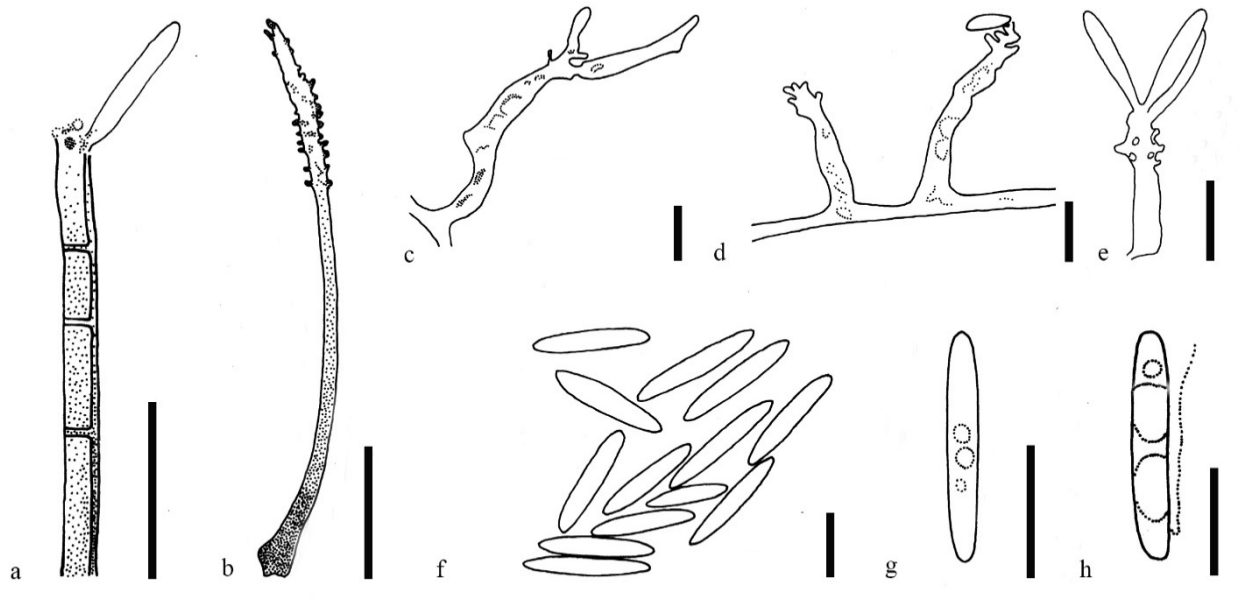


Figure 244 – Asexual morphology of *Pseudodactylariales*. a Conidiogenous cells with conidia (*Pseudodactylaria denticulata*). b Conidiophores with conidiogenous cells (*Pseudodactylaria uniseptata*). c–e Conidiophores (c *Pseudodactylaria xanthorrhoeae*, d *Pseudodactylaria xanthorrhoeae*, e *Pseudodactylaria brevis*). f–h Conidia (f *Pseudodactylaria xanthorrhoeae*, g *Pseudodactylaria denticulata*, h *Pseudodactylaria uniseptate*) (drawn from Crous et al. 2017a, Lin et al. 2018, Yang et al. 2023b). Scale bars: a = 20 µm, b = 30 µm, c–f, h = 10 µm, g = 15 µm.

Justification of order and problems

Morphologically, species within the order *Pseudodactylariales* exhibit considerable resemblance to those found in *Dactylaria* and closely related genera, posing a challenge in their differentiation based solely on morphological characteristics.

Significance

Ecological and economic roles

Pseudodactylariales species mainly occur as saprobes in both terrestrial and aquatic habitats in Australia, China, and Thailand (Crous et al. 2017a, Lin et al. 2018, Yang et al. 2023b) and are important in nutrient cycling.

Chemical diversity

Comprehensive investigations into the chemical production within *Pseudodactylariales* remain unexplored. This underscores the need for further research, especially in light of the growing number of reported species within this order.

Other relevant data and future recommendations

Pseudodactylariales species have now been collected in Australia, China, and Thailand, and thus, numerous regions have never been studied for this order. Consequently, we anticipate that thorough investigations will unveil a multitude of new species.

***Phyllachorales* M.E. Barr, Mycologia 75(1): 11 (1983)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Sordariomycetidae*

Introduction

Phyllachorales is an order of obligate plant biotrophic fungi currently containing about 2000 species names (including potential synonyms) distributed in 72 genera. Species of *Phyllachorales* are leaf-inhabiting microfungi with shiny black stromata, which gave them the common name "tropical tar spot fungi." Most known species are tropical and subtropical in distribution (Piepenbring et al. 2011), with only a few (ca. 10%) in temperate regions. Due to their biotrophic nutrition mode, high host-specificity is assumed, and species concepts are based partly on the host plants. *Phyllachorales* belongs to the class *Sordariomycetes*. The taxa of *Phyllachorales* are characterized by their biotrophic nature and the formation of perithecial stromata that are primarily immersed in the plant tissues, often clypeate, and strongly melanized. Traditionally, two families were recognized within the order: *Phyllachoraceae* and *Phaeochoraceae* (Theissen & Sydow 1915, Hawksworth et al. 1995, Hyde et al. 1997). Two other families were recently added: *Telimenaceae* (Mardones et al. 2017) and *Neopolystigmataceae* (Guterres et al. 2022). Thus, *Phyllachorales* currently comprises four families, which can be separated by a combination of the host and the morphology of the fruiting body. *Phyllachoraceae* is the largest family within the order, with almost 1,200 described species. The largest genus is *Phyllachora*, which has more than 900 spp. and only a few further genera include more than 20 species described: *Coccodiella*, *Ophiodothella*, and *Trabutia*. Further genera include less than ten described species, and 14 are monotypic. *Phyllachoraceae* include species with immersed stromata, reduced pseudostroma growing on *Poaceae*, and species with erumpent to superficial stromata occurring in several monocot and eudicot host plants. *Phaeochoraceae* contains 28 accepted species in the genera *Cocoicola*, *Phaeochora*, *Phaeochoropsis*, and *Serenomyces*. *Phaeochoraceae* include species characterized by immersed to erumpent stromata without a clypeus, occurring exclusively on *Arecaceae*. *Telimenaceae* contains only the genus *Telimena*. This family was erected to place many *Phyllachora*-like species, i.e. with immersed perithecia in the mesophyll of the leaves on eudicot and non-*Poaceae* monocots. *Neopolystigmataceae* includes only the genus *Neopolystigma* and two species characterized by a bright-colored, epiphyllous, or subepidermal pseudostroma growing of *Fabaceae*.

History

The history of the classification of *Phyllachorales* is strongly linked to its type genus *Phyllachora* (Cannon 1991, Pearce 2006). Over the past 150 years, there have been multiple shifts in the systematic placement of tropical tar spot fungi, with changes occurring between loculoascomycetes and pyrenomycetes, as well as the taxonomic status for the order *Phyllachorales* or the family *Phyllachoraceae*.

The genus *Phyllachora* was introduced on an herbarium label in Fuckel's exsiccate series "Fungi Rhenani" with the single species, *P. agrostis* (Fuckel 1867 in Cannon 1991). This species is currently accepted as *Scirrhia agrostis* within *Dothideales*. Fuckel (1870) expanded the genus to include 18 species and placed it into *Dothideaceae*, which subsequent authors considered as the first publication of *Phyllachora* (Cannon 1991). Subsequently, the genus *Phyllachora* was lectotypified with *Phyllachora graminis* (Pers.) Fuckel as a generic type (Clements & Shear 1931), and the genus name in the sense of Fuckel (1870) was conserved to allow continued use in its currently accepted circumscription (Holm 1975). *Phyllachora* included leaf or steam-inhabiting fungi with stromatic development, hyaline, and aseptate ascospores. For many years, its placement within the *Dothideaceae*, specifically in the section *Hyalosporae*, was widely accepted by several authors, including Saccardo (1876, 1883b, 1928) and Cooke (1885). However, these studies focused on adding new species and did not delve into higher-level relationship discussions.

Theissen & Sydow (1915) recognized the family *Phyllachoraceae* for the first time in their classic work "Die *Dothideales*." The family was described for fungi immersed in host plant tissue beneath the cuticle or epidermis, with a black covering layer called clypeus and significant stromatic development. Much of our contemporary understanding of tropical tar spot fungi classification and morphological diversity derives from this work. This study subdivided *Phyllachoraceae* into three subfamilies (*Trabutiineae*, *Scirrhiineae*, and *Phyllachorineae*) primarily based on the depth of fungal tissue embedded in the leaves. The genus *Catacauma* was established for species with stroma positioned between the epidermis and the palisade layer, the genus *Trabutia* for species with stroma between cuticle and epidermis, and *Phyllachora* for species with stroma deeply immersed in the mesophyll of the leaf. Further criteria for distinguishing genera within each subfamily included characteristics of the ascospores, such as color and septation, as well as the presence or absence of paraphyses.

Orton (1924) and Petrak (1924) were the first authors who independently suggested that phyllachoraceous fungi should not be considered closely related to *Dothideales*, primarily based on distinctive stromatal characteristics, particularly the well-developed perithecial walls. Petrak (1924) additionally pointed out the affinities between *Phyllachora* and other genera, including *Physalosporina*, *Polystigma*, and *Sphaerodothis*. He also suggested that the depth of immersed ascomata in the host tissue was unreliable for taxonomic purposes. Nevertheless, several authors continue to follow Theissen & Sydow (1915), overlooking Petrak's treatment (Seaver & Chardón 1926, Stevens 1927, Chardón 1928, 1929, 1932, 1946, Seaver 1928a, Sydow 1930, Chardón & Toro 1934).

Nannfeldt (1932) replaced the name *Phyllachoraceae* with *Polystigmataceae* and positioned this family within the order *Sphaeriales*. This classification was primarily based on the presence of unitunicate asci and the perithecial ascomata. Luttrell (1951a) classified ascomycetes with perithecia based on characteristics of the centrum; *Phyllachoraceae* was also included in *Xylariales*. Arx & Müller (1954) maintained the *Polystigmataceae* within the *Sphaeriales* and delimited 18 genera, including species with aseptate spores. Subsequently, several other genera with septate and filiform ascospores were incorporated into the family (Müller & von Arx 1962, Eriksson & Hawksworth 1990).

The order *Phyllachorales* was formally described by Barr (1983b) and placed in the subclass *Edaphomycetidae* based on habit and the position of the ascomata. Subsequently, Cannon (1988) proposed a close relationship between the *Phyllachorales* and *Diaporthales*, citing similarities in their centrum structure. Barr (1990b) reassigned the family *Phyllachoraceae* into *Xylariales*, primarily due to the presence of a xylaria-like centrum. Hawksworth et al. (1995) re-established the

order *Phyllachorales* with the only family *Phyllachoraceae*. A second family, *Phaeochoraceae*, was established by Hyde et al. (1997) to accommodate species associated with palms that lacked a clypeus. This family was provisionally assigned to *Phyllachorales* since the family was erected (Hyde et al. 1997). The uncertain affinities of *Phyllachorales* within *Sordariomycetes* were suggested by Eriksson (2006), a notion later corroborated with molecular data by Maharachchikumbura et al. (2015), with *Boliniales* identified as a sister group. The monophyly of *Phyllachorales*, including members of the two traditional families, *Phyllachoraceae* and *Phaeochoraceae*, and the new family *Telimenaceae*, was confirmed by Mardones et al. (2017).

General description

The life cycle of species of *Phyllachorales* begins when hyphae from germinating ascospores develop pigmented appressoria of clavate to obclavate shape, that penetrate the plant tissue (Fig. 245). Afterwards, the hyphal invasion of the host tissue starts, spread intra and intercellularly within the epidermis and parallel to the vascular bundles, finally resulting in the formation of cavities and perithecia covered by black clypei.

Sexual morph: Species of *Phyllachorales* may cause inconspicuous, moderate, or strong infections on living leaves or stems, which can be seen as blackened stromatic material of various shapes (Fig. 245 – a-k). They often cause the bleaching of the leaf tissue, producing a yellow to reddish discoloration zone around the stromata (Fig. 245 – a-c). In a few cases, necrotic tissue can be observed surrounding the stromata (Fig. 245 – d), which, according to Parbery (1978), is caused by mycoparasites and not by the phyllachoraceous fungus. The stromata may be visible as solitary or gregarious spots that can be discrete (Fig. 245 – g) or coalesce into large crusts (Fig. 245 – i). They can be located at the margins of the leaves, along the leaf veins (Fig. 245 – h) or scattered all over the leaves (Fig. 245 – g). The visible part of the stroma corresponds to the clypeus, a shield of black fungal cells restricted to the epidermal cells of the host and covering the perithecia (Fig. 245 – c). Stromata are primarily black, due to fungal melanin (Fig 245 a-d), except in species of *Neopolystigma* which have brightly colored stromata (Fig. 245 – d-e, Fig. 246 – a) and some *Phyllachora* spp. and *Stigmatula* spp. with poorly developed blackened tissue. In the case of members of the family *Phaeochoraceae*, the clypeus is absent (Fig. 245 – k, Fig. 246 – b). The term amphigenous is used to describe a clypeus visible on both sides of the leaf (Fig. 245 – c, d), the clypeus is epiphyllous when it is only visible on the adaxial side of the leaf (Fig. 246 – e), and hypophyllous when it is only visible on the abaxial side of the leaf (Fig. 245 – f) (Parbery & Langdon 1964).

In graminicolous species of *Phyllachora*, Parbery (1963b) noted that the clypeus originates within the epidermal cells of the host independently from the perithecia rather than as an extension from the ostiolar region of the perithecium. The perithecium develops deep in the mesophyll and expands until its ostiolar region meets the clypeus (Fig. 245 – c-f) (Parbery 1963b). Branched and hyaline hyphae start to grow closely adjacent to the perithecium to form a pseudostroma, defined as a fungal stroma composed of fungal tissue and remnants of host tissue. The hyphae expand the host tissue, become brown and more densely packed, and fill the intercellular spaces. Delimitating all these structures is complex and differs significantly in each species. The pseudostroma may range between strongly developed (Fig. 246 – d, f) to almost reduced, e.g., in species of *Phyllachora* on grasses (Fig. 246 – c) (Parbery and Langdon 1964). The expansion of the clypeus varies, and it is not always congruent with the diameter of the perithecia. Occasionally, there is no invasion of the lower epidermis, or it is so limited that a clypeus fails to form. (Fig. 246 – f) (Parbery 1963b). The size and shape of the blackened regions may be affected by the vascular tissues of the host plants or the level of ultraviolet radiation experienced by the fungus (Parbery 1964, Cannon 1991).

The stromata are uni-, few-, or multi-loculate, depending on the number of perithecia (Fig. 246 – c-f). The shape of the perithecia is globose, lenticular, pyriform, or deformed by adjacent vascular bundles. The perithecia may be superficial, erumpent, or completely immersed within the leaf. In *Phyllachora* spp. and *Telimena* spp., the perithecium is immersed within the leaf and can be seen occupying the mesophyll tissue (Fig. 246 – c-f). In *Catacauma* spp., the perithecium is inserted above the mesophyll between the epidermal and palisade cells, and in *Trabutia* spp. is between the cuticle

and the epidermis (Fig. 246 – h). Also, several other transitional positions can be observed. The position, size, and shape of the perithecia may be significantly influenced by large vascular bundles or other mechanical tissues in the host leaf (Parbery 1963b, Cannon 1991). If the stromata are erumpent or salient, as in species of *Camarotella*, the perithecia are partly submerged in the plant tissue, and the stromata do not develop an epidermal clypeus but a dark and compact outer layer surrounding the perithecia (Fig. 246 – g). For genera with superficial stromata, e.g., *Coccodiella* or *Erikssonia*, the superficial part of the stromata is known as epistroma and the small part of the stromata, which penetrates and is attached to the host tissue receives the name of hypostroma (Fig. 246 – i).

Hymenial structures are highly variable in phyllachoraceous fungi. Most species have paraphyses, which are filiform, septate, very thin-walled, and occasionally branched at the base (Cannon 1991). The paraphyses seem to be ephemeral and degenerate by the time of ascospore release (Cannon 1988). They usually have the same length as the asci but can also be longer or form fascicles. The asci are unitunicate, usually eight-spored, persistent, and with an apical ring that does not stain blue in iodine. The shape of the ascus varies from cylindrical to clavate and is determined mainly by the ascospores and their arrangement within the ascus. While in some species, an ascus crown can be easily observed, e.g., in *Phyllachora* spp. on grasses (Parbery 1963a), in some other species, any apical structure in the ascus tip can be distinguished even in fresh collections. Ascospores in members of *Phaeochoraceae* are olive to brown with striate ornamentation, while in the other families, they are usually hyaline, smooth, and thin-walled. The shape ranges from globose to filiform. Ascospores are mostly aseptate, but species with uni- to tri-septate ascospores are also known. A gelatinous sheath can be seen surrounding the ascospore.

Asexual morph: Within the *Phyllachorales*, most sexual-asexual connections are either unknown or not fully understood. The genus *Phyllachora* is frequently associated with a spore state developing aseptate hyaline scolecospores. This state was described as an anamorph with the name *Linochora* Höhn. (Höhnel 1910). Locules of *Linochora* species are mostly irregularly convoluted or pycnidial and occur either contemporaneously or a little before the teleomorph (Parbery 1978, Cannon 1991, Trampe 2010). Scolecospores of the *Linochora* state are considered to be spermatial in function (Parbery 1963a, b). Parbery (1996) proposed the term andromorph "to accept it as part of the sexual reproductive apparatus of the fungus and not as an asexual product." Spermatiogenous cells develop directly from a thin, fertile layer of short and thin-walled cells or may rise from one to multiple branched spermatiophores (Parbery 1963a). The shape of the spermatiogenous cells is mostly cylindrical, tapering slightly towards the tip and presenting an apical wall thickening, which resembles a small collarette that results from percurrent proliferation (Cannon 1991). Spermatia are mostly filiform with a small swelling toward the base. Other anamorph-teleomorph connections have been reported for other genera within *Phyllachorales*, i.e. *Acerviclypeatus* Hanlin (anamorph of *Ophiodothella*, *Cyclodomus* Höhn. (anamorph of *Maculatifrondes*), *Diachorella* Höhn. (anamorph of *Diachora*), *Mycohypallage* B. Sutton (anamorph of *Deshpandiella*), *Oswaldina* Rangel (anamorph of *Apiosphaeria*), *Polystigmina* Sacc. (anamorph of *Polystigma*), *Pseudothiopsella* Petr. (anamorph of *Pseudothiella*) and *Rhodosticta* Woron. (anamorph of *Polystigma*) (adapted from Petrak 1928, Sutton 1963, Hanlin 1990, Dianese et al. 1994, Cannon 1996, Hyde et al. 1996, Hyde & Cannon 1999).

Families included in *Phyllachorales*

Neopolystigamataceae Dianese & Guterres
Phaeochoraceae K.D. Hyde, P.F. Cannon & M.E. Barr.
Phyllachoraceae Theiss. & H. Syd.
Telimenaceae Mardones, T. Trampe & M. Piepenbr

Phyllachorales genera *incertae sedis*
Marinosphaera K.D. Hyde
Neoxylomyces M.S. Calabon, Boonmee, E.B.G. Jones & K.D. Hyde



Figure 245 – Infected leaves and stromata of *Phyllachorales.* a *Telimena engleri* on *Anthurium* sp. (*Araceae*). b *Diatractium ingae* on *Inga* sp. (*Fabaceae*). c *Phyllachora* sp. on *Chusquea* sp. (*Poaceae*). d *Telimena balansae* on *Cedrela odorata* (*Meliaceae*). e–f *Neopolystigma pusillum* on *Andira inermis* (*Fabaceae*). g *Telimena hydrangeae* on *Hydrangea* sp. (*Hydrangeaceae*). h *Phyllachora hoyosensis* on *Ficus* sp. (*Moraceae*). i *Trabutia xylosmae* on *Xylosma prockia* (*Salicaceae*). j *Camarotella costaricensis* on *Acrocomia aculeata* (*Arecaeae*). k *Serenomyces phoenicis* on *Phoenix canariensis* (*Arecaceae*). Scale bars: a, b, c, d, e, g, h, i, j = 1 cm, f, k = 1 mm.

Evolution

Species of *Phyllachorales* have acquired their obligate biotrophic nature only once at the beginning of their radiation and have retained it ever since. Ancestral State Reconstruction Analysis supports the hypothesis that the ancestor of *Phyllachorales* had a clypeus and black stromata (Mardones et al. 2017). Therefore, the clypeus was lost only once in *Phaeochoraceae*, and the brightly colored stromata apparently evolved in *Neopolystigmataceae*. Most species have immersed

perithecia in the leaves, and species with superficial or erumpent perithecia appear to be restricted to the family *Phyllachoraceae*, where the transitions have taken place multiple times, i.e. *Coccodiella*, *Camarotella*, *Neophyllachora*.

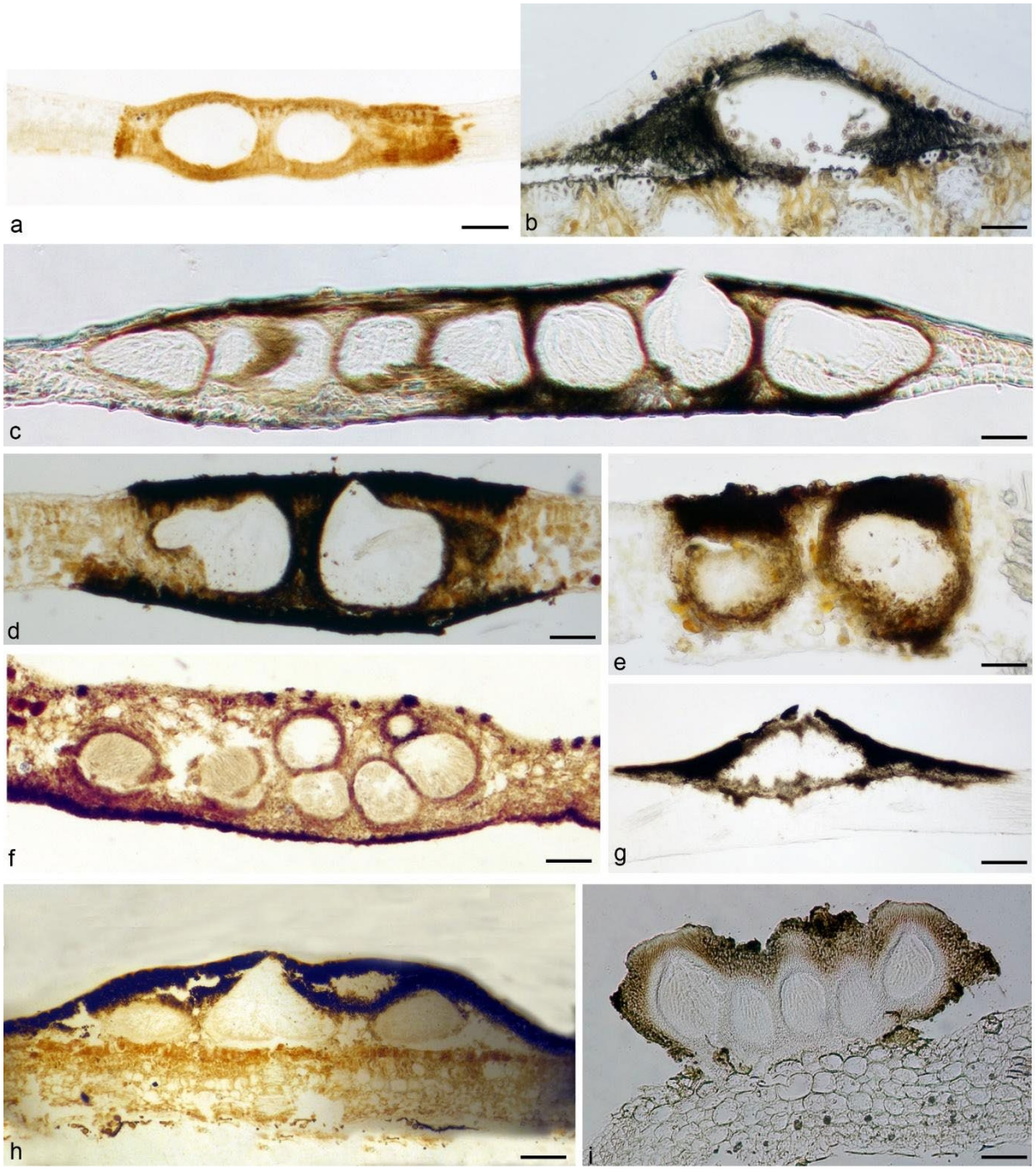


Figure 246 – Perithecia of *Phyllachorales* in different positions in the leaves. a Brightly colored stromata of *Neopolystigma pusillum* (*Neopolystigmataceae*) immersed in the mesophyll of the leaf. b Subcuticular perithecium without a clypeus of *Serenomyces phoenicis* (*Phaeochoraceae*). c Immersed perithecia of *Phyllachora graminis* (*Phyllachoraceae*) with amphigenous ascomata. d Immersed perithecia of *Telimena bicincta* (*Telimenaceae*) with amphigenous ascomata. e Immersed perithecia of *Telimena balansae* (*Telimenaceae*) with epiphyllous ascomata. f Immersed perithecia of *Telimena rinoreae* (*Telimenaceae*) with hypophyllous ascomata. g Erumpent perithecium of *Camarotella costaricensis* (*Phyllachoraceae*). h Perithecia of *Trabutia xylosmae* located between the cuticle and the epidermis of the leaf. i Superficial perithecia (epistroma) of *Coccodiella miconiae* (*Phyllachoraceae*). Scale bars: a–i = 100 µm.

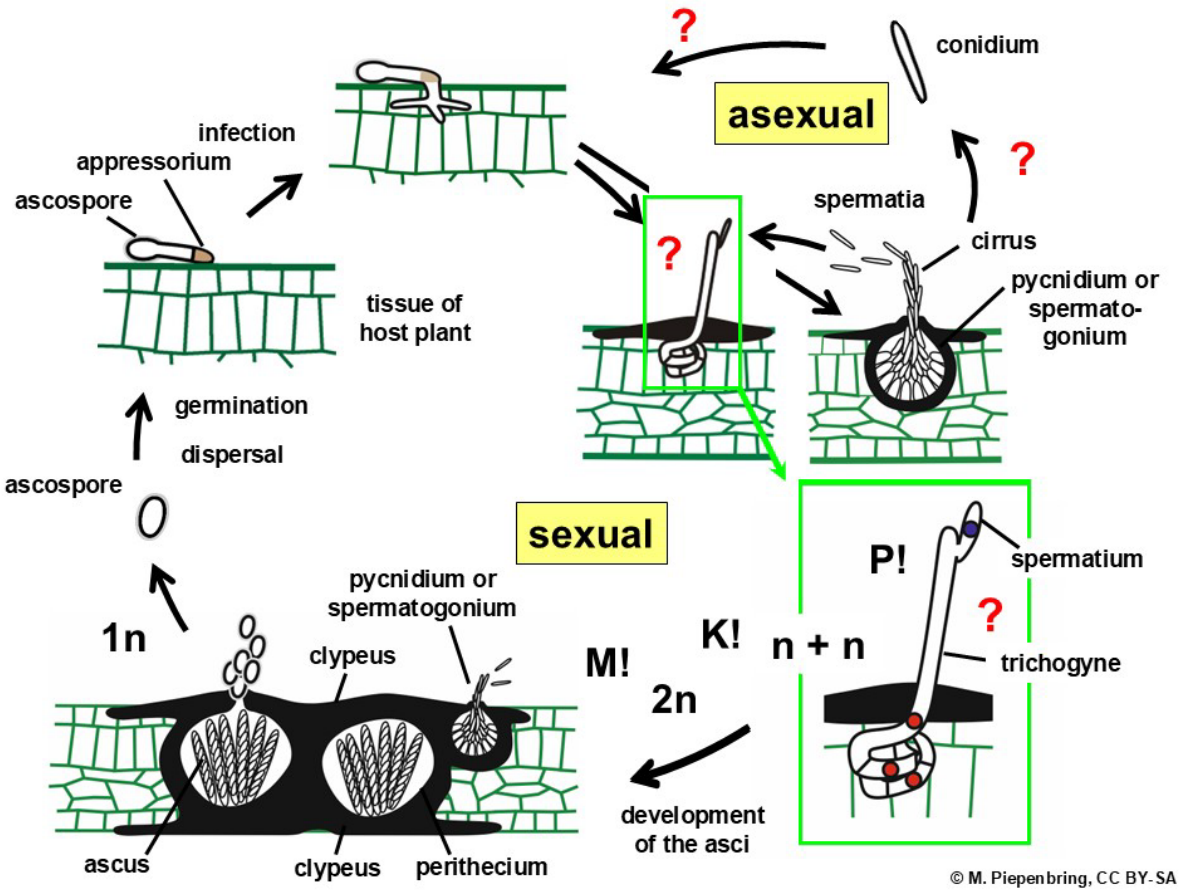


Figure 247 – Sexual and asexual life cycles of *Phyllachorales* (From Mycological teaching diagrams by Meike Piepenbring (2023)). Abbreviations: 1n = haploid, 2n = diploid, P! = plasmogamy, K! = karyogamy, M! = meiosis. Black and white circles represent haploid nuclei of different mating types, circles of both colors represent diploid nuclei.

Species of *Phyllachorales* are obligate biotrophs and are thought to be host-specific. Studies of species of *Phyllachorales* on the host families *Poaceae* and *Fabaceae* suggested that tropical tar spot species are not restricted to a single host species but may occur on species belonging to a group of closely related genera (Parbery 1978, Cannon 1991, 1997). *Phyllachorales* primarily infect monocots, eudicots, and other angiosperms (basal groups and magnoliids). They show host-switching patterns similar to rusts (*Pucciniales*, *Basidiomycota*) or epifoliar *Meliolaceae* (*Meliolales*, *Ascomycota*), suggesting host jumps as a key mode of evolution. Phylogenetic analyses indicate close relationships with monocots, with several host-switches inferred within and between monocots and eudicots (Mardones et al. 2017, 2018a, b, Guterres et al. 2022). Phyllachoraceous fungi likely originated on monocots, then expanded to include eudicot families. Host-jumps from monocots to eudicots occurred multiple times independently, with accompanying morphological changes, such as from immersed perithecia in graminicolous species to erumpent and superficial stromata in *Camarotella* spp., *Coccodiella* spp., and *Neophyllachora* spp.

Justification of order and problems

Several studies based on multi-locus phylogenetic analyses of 2–4 loci provide relatively adequate support for the monophyly of the order, including members of the four accepted families (Mardones et al. 2017, 2018a, Guterres et al. 2022), supporting the evolutionary significance of the unifying features of *Phyllachorales* - the biotrophic nature and the formation of perithecial stromata, primarily immersed in the plant tissues and often clypeate and strongly melanized. On the other hand, the published *Phyllachorales* phylogenies (Dos Santos et al. 2016, Mardones et al. 2017, 2018a, b, 2020, 2022, Dayarathne et al. 2017, Yang et al. 2019b, Guterres et al. 2022, Li et al. 2022a, 2023a)

clearly show that several nodes below the family level are not well-supported. These phylogenies have used primarily nuclear ribosomal DNA (ITS, SSU and LSU) and, to a lesser extent, TEF and RPB2. Due to the poor resolution, broad generic concepts have been adopted. For example, within *Phyllachora*, Mardones et al. (2017) showed that unidentified species of *Phyllachora* on *Chusquea* (*Bambusoideae* and *Poaceae*) form a clade completely separated from the clade that contains *P. graminis* (type species of *Phyllachora*) and *P. maydis*. Within *Telimena*, most phylogenies showed that there are at least three clades that somewhat correlate to the plant clades rosids, asterids, and non-*Poaceae* monocots (*Araceae* and *Arecaceae*), but with poor node support (Mardones et al. 2017, 2018a, 2020, 2022).

However, there are several genera with no available DNA to confirm their place within the order, i.e. those with erumpent or superficial stromata (e.g., *Erikssonia* and *Oxodeora)*, subcuticular stromata (e.g., *Trabutia*) or filiform ascospores (e.g., *Ophiodothella*). Additionally, in recent works, several taxa traditionally placed on *Phyllachorales* have been excluded from the order based on molecular data: *Polystigma* spp. on *Rubus* spp. (*Rosaceae*) were transferred to subclass *Xylariomycetidae* (Habibi et al. 2015), *Apiosphaeria guaranitica*, the causal agent of the brown crust disease in *Bignoniaceae*, was transferred to *Diaporthaceae* in *Diaporthales* (Guterres et al. 2018), *Phaeochorella parinarii* to *Phaeochorellaceae* in *Diaporthales* (Guterres et al. 2019) and *Phyllachora ambrosiae* to *Cryptophyllachora ambrosiae* in *Sordariomycetidae* (Kiss et al. 2018).

Significance

Ecological and economic roles

The species of *Phyllachorales*, as obligate biotrophs, grow on living plant tissues and produce appressoria for nutrient acquisition and penetration of the epidermal cells of the host, but causing minimum damage to the plant tissues. Tropical tar spot fungi have been found as endophytes (Higginbotham et al. 2013), but most species have been reported as weak pathogens. Some species, such as *Phyllachora lespedezae* on species of *Fabaceae*, *P. graminis* on several grasses, and *P. sacchari* on *Sorghum* sp., have been reported as pathogens (Parbery 1978, Cannon 1991). Several other species (e.g., *Coccostromopsis chamaedoreae*, *Ophiodothella orchidearum*, *P. alyxiae*, *P. gratissima*, and *P. sacchariare*, among others) have been associated with some crop and ornamental plants (USDA-APHIS Agricultural Risk Management database). Recently, in the United States and Brazil, some species have been reported as important emerging pathogens affecting maize and coconut palm, respectively (e.g., *P. maydis* and *Camarotella* spp.) (Vitória et al. 2008, Valle-Torres et al. 2020, Broders et al. 2022). Additionally, due to their high host affinity, some of these fungi (e.g., *Coccodiella* spp.) hold promise as biological control agents of invasive weeds (e.g., *Ambrosia artemisiifolia* and *Miconia calvescens*) (Seixas et al. 2007, Alves et al. 2010, Kiss et al. 2018).

Chemical diversity

Relevant studies are not available for the chemical diversity of *Phyllachorales*.

Other relevant data and future recommendations

There is ongoing uncertainty surrounding the delineation of families, genera, and species, along with their distinguishing characteristics within *Phyllachorales*. Defining family, genus, and species concepts in *Phyllachorales* is crucial not only to clarify the identity of economically significant species but also to facilitate the study of the evolutionary mechanisms behind host-specificity and pathogen diversification. *Phyllachorales* predominantly infect monocotyledonous or eudicotyledonous host plants, with occasional occurrences in other angiosperm groups like magnoliids and basal groups. However, our understanding of *Phyllachora*-like fungi on magnoliids and basal groups remains limited. Extensive collections on these host plants are needed to ascertain host-specificity.

Additionally, revisions to genus boundaries within *Phyllachoraceae* and *Telimenaceae*, including potential new genera, may be segregated. Other genera and species not on *Poaceae* remain classified in *Phyllachoraceae*. These have fruiting bodies that are not immersed, thus obscuring the taxonomic utility of the position of the fruiting body. It is likely that further molecular sequence data

of the remaining *Phyllachora* spp. not occurring in *Poaceae*, will show that these species do not belong to *Phyllachora sensu stricto* but to *Telimenaceae* due to their non-grass host. Well-supported phylogenies and additional taxon sampling are needed to define family, genus, and species concepts in *Phyllachorales* confidently. The *Neopolystigmataceae* and *Phaeochoraceae* families, with one and four genera and two and 28 species, respectively, are currently found only to infect host families *Fabaceae* and *Arecaceae*. Presently, about 45 phyllachora-like species are on *Fabaceae* in South America and approximately 30 on *Arecaceae* globally. There is a possibility that species on these plants previously classified as *Polystigma* or *Phyllachora* may need reclassification.

Rhamphoriales **K.D. Hyde & Hongsanan, Fungal Diversity 107: 94 (2021)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Rhamphoriales was established to accommodate a single family *Rhamphoriaceae* based on phylogenetic and divergence time estimates analyses along with morphological data within *Diaporthomycetidae* (*Sordariomycetes*) (Hyde et al. 2021a).

History

Rhamphoriaceae was recently introduced by Réblová & Štěpánek (2018) to accommodate *Rhamphoriopsis*, *Rhodoveronaea*, *Xylolentia*, a dematiaceous hyphomycete *Linkosia multiseptum* with a generic type *Rhamphoria* within *Sordariomycetes*. *Rhamphoria* is typified by *R. delicatula* (Niessl 1876) and presently comprises 13 species (Species Fungorum 2025) and the taxa are reported in both sexual and asexual morphs. The genus was placed in the subfamily *Rhamphorioidae* of the *Diaporthaceae* based on morphology (Munk 1957). *Rhodoveronaea* was introduced to accommodate *R. varioseptata,* which was reported in its asexual morph from Germany. Subsequently, Réblová (2009) reported the sexual morph of *R. varioseptata* from Sweden. Réblová & Štěpánek (2018) added two new genera *Rhamphoriopsis*, and *Xylolentia,* when they established the family *Rhamphoriaceae*. The family formed a monophyletic clade and was close to *Sporidesmiaceae* in the combined phylogenetic analysis conducted based on SSU, LSU and RPB2 sequence data, which was also revealed in the study of Hyde et al. (2020d). However, *Rhamphoriaceae* differs from *Sporidesmiaceae* in several morphological features. *Rhamphoriaceae* has a two-layered peridium, and hyaline or brown, ellipsoidal, obovoid, clavate, fusiform to fusiform-clavate ascospores, lacking mucilaginous sheaths or appendages, whereas *Sporidesmiaceae* has a three-layered peridium, and hyaline, fusiform ascospores with a thin sheath. In the asexual morph, *Rhamphoriaceae* differs from *Sporidesmiaceae* in having different conidiogenous cells (polyblastic, monoblastic, denticulate vs. monoblastic, terminal, and percurrent) and conidia (ellipsoidal to obovoid, aseptate or septate, hyaline or brown vs. obclavate, subobtuse at apex, truncate at base, transversely euseptate or distoseptate, brown) (Réblová & Štěpánek 2018, Hyde et al. 2020d, 2021a). Thus, a new order *Rhamphoriales,* was established to accommodate *Rhamphoriaceae* (Hyde et al. 2021a).

General description

Rhamphoriales members are reported in both sexual and asexual morphs. The sexual morphs are characterized by perithecial ascomata, absence of stromatic tissues or clypeus, two-layered peridium, unitunicate, pedicellate asci with a J-, apical ring, cylindrical paraphyses and dictyoseptate or transversely septate ascospores (Réblová & Štěpánek 2018). *Rhamphoria* and *Rhodoveronaea* share similarities in their asexual morph in having dematiaceous hyphomycetes with the same mode of conidiogenesis, but differ in sexual morph (Hyde et al. 2020d).

Sexual morph: *Ascomata* perithecial, immersed or particularly erumpent becoming superficial, papillate or with a central cylindrical or rostrate neck. *Ostiole* periphysate. *Peridium* leathery to fragile, comprising two layers. *Paraphyses* consisting of septate, cylindrical paraphyses. *Asci* 8-spored, unitunicate, cylindrical or cylindrical-clavate, persistent, with a J-, apical ring. *Ascospores*

overlapping uniseriate, hyaline or brown, ellipsoidal, obovoid, clavate, fusiform to fusiform-clavate, dictyoseptate or transversely septate, lacking mucilaginous sheaths or appendages, sometimes produce ascoconidia.

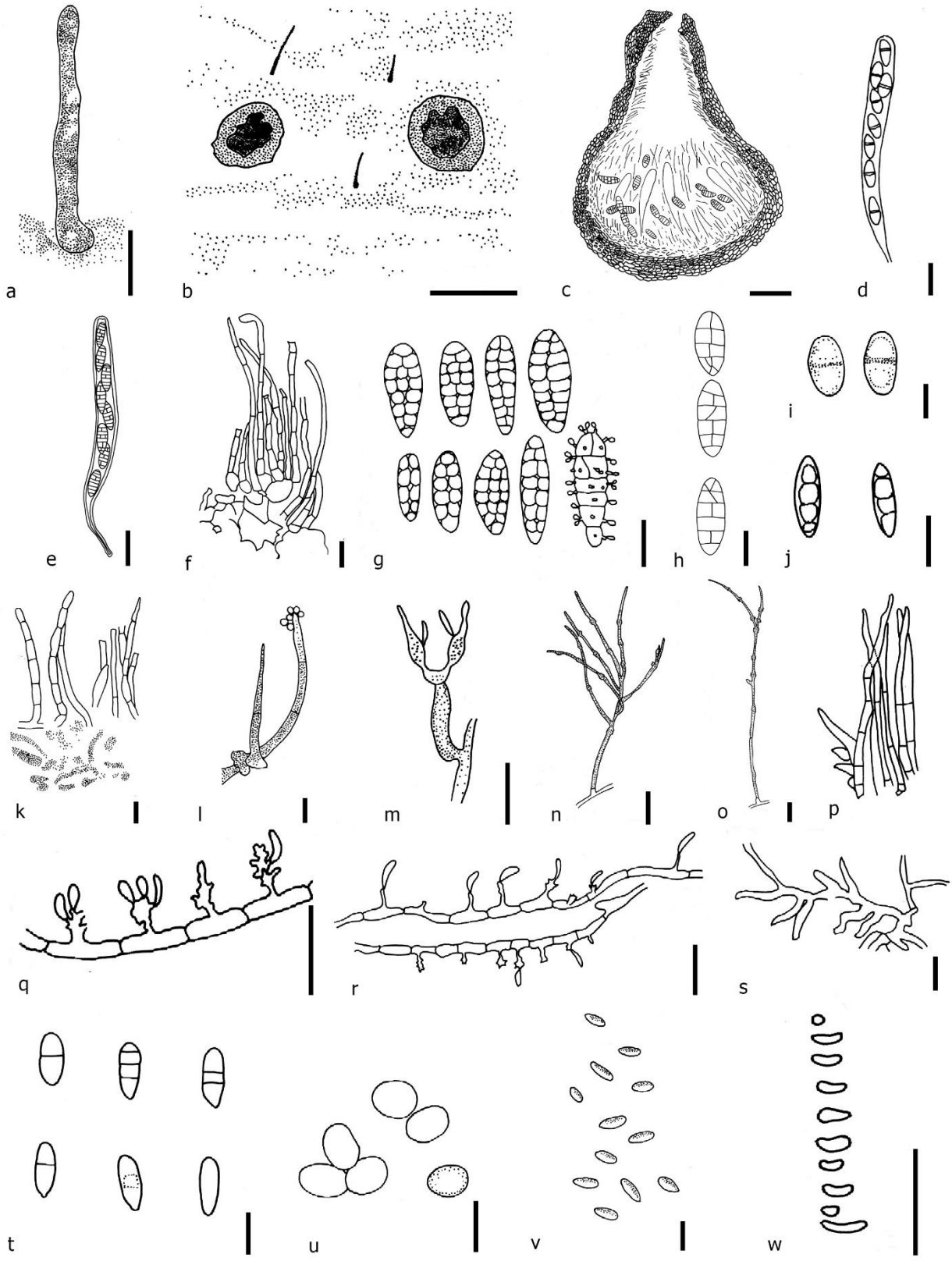


Figure 248 – Morphology of *Rhamphoriales*. a, b Appearance ascomata on substrate (a *Rhamphoriopsis muriformis*, b *Rhamphoria delicatula*). c Vertical section through ascoma (*Rhamphoria bevanii*). d, e ascus (d *Xylolentia brunneola*, e *Rhamphoria bevanii*). f Paraphyses

(*Xylolentia brunneola*). g–j Ascospores (g *Rhamphoria pyriformis*, h *Rhamphoria obliqua*, i *Xylolentia brunneola*, j *Rhodoveronaea varioseptata*). k–o Conidiophore (k *Xylolentia brunneola*, l *Xylolentia brunneola*, m, n, o *Rhamphoria pyriformis*). p Phaeoisaria-like conidiophores on natural substrate (*Rhamphoriopsis muriformis*). q Conidiogenous cells on vegetative hyphae in old cultures (*Rhamphoria pyriformis*). r Anamorph in young cultures (*Rhamphoria pyriformis*). s Conidiophores and conidia (*Rhamphoriopsis muriformis*). t–w Conidia (t *Rhodoveronaea varioseptata*, u *Xylolentia brunneola*, v *Rhamphoriopsis muriformi,* s, w *Rhamphoria pyriformis*) (redrawn from Sivanesan 1976, Muller & Samuels 1982, Réblová 2009, Réblová & Štěpánek 2018). Scale bars: a, b = 250 μm, c = 45 μm, d, f–j, k–t, w = 10 μm, e, h = 25 μm, I, u, v = 5 μm, n, o = 20 μm.

Asexual morph: *Hyphomycetous*. *Conidiophores* macronematous or semi-macronematous, mononematous or loosely fasciculate. *Conidiogenous cells* producing conidia holoblastically, conidial secession rhexolytic on sympodially extending polyblastic conidiogenous cells, or schizolytic on monoblastic conidiogenous cells. *Conidia* hyaline, aseptate or septate (adapted from Réblová & Štěpánek 2018, Hyde et al. 2020d) (Fig. 248).

Families included in *Rhamphoriales*

Rhamphoriaceae Réblová

Evolution

The stem age of *Rhamphoriales* was reported as 133 MYA for divergence time estimate analyses (Hyde et al. 2021a).

Justification of order and problems

The inclusion of *Linkosia multiseptum* within *Rhamphoriaceae* was doubtful and the uncertainty was also questioned by Hyde et al. (2020d). The strain *L. multiseptum* HKUCC 10825 clustered within the order in the phylogenetic analyses conducted by Réblová et al. (2018). However, the species differs from the extant members of the order in the lack of conidiophores, presence of distoseptate, thick-walled conidia and ampulliform, monoblastic conidiogenous cells. Shenoy et al. (2006) stated the polyphyletic nature of the genus based on LSU sequence data. However, due to the deficiency of information available for holotype material, the placement within the order is doubtful. Wu & Diao (2022) transferred this species to *Chaetosphaeriaceae* based on morphology and phylogeny with several new collections from China, including *L. multiseptum*. However, the placement within the order is doubtful due to the absence of molecular data available for the type *L. coccothrinacis* (Wu & Diao 2022).

The production of ascoconidia from ascospores has been considered as the distinguishing feature of *Rhamphoria pyriformis* from other members of *Rhamphoria*. *Rhamphoria separata* was mainly distinguished from *R. pyriformis* in the lack of the ability to produce ascoconidia (Munk 1948) which was also reported in the same locality as *R. pyriformis* and the same host branch (Munk 1957). However, reinvestigation of *R. separata* showed that budding ascospores were not always observed and which raised the doubt about production of ascoconidia as a distinguishing feature (Müller and Samuels 1982, Réblová & Štěpánek 2018). Thus, Réblová & Štěpánek (2018) synonymized *R. separata* under *R. pyriformis* and proposed the reinvestigation of species in *Rhamphoria* and the number of accepted species could be lower than reported.

Significance

Ecological and economic roles

The taxa are mostly reported as saprobe on decaying wood mostly from terrestrial habitats and rarely from freshwater habitats in Asia and Europe (Arzanlou et al. 2007, Réblová and Štěpánek 2018, Hyde et al. 2020d, Chen et al. 2024).

Savoryellales **Boonyuen, Suetrong, Sivichai, K.L. Pang & E.B.G. Jones, Mycologia 103(6): 1368 (2011)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Savoryellomycetidae*

Introduction

The order *Savoryellales* (*Ascomycota*) is one of the most typical groups of predominantly widespread aquatic fungi on submerged wood from marine and freshwater habitats, mangroves, coastal sand dunes, as well as brackish water-cooling towers (Jones et al. 2016, Dayarathne et al. 2019). It accommodates a single family *Savoryellaceae*, which comprises seven genera, *viz*. *Aquabispora*, *Ascotaiwania*, *Bactrodesmium*, *Canalisporium*, *Dematiosporium*, *Neoascotaiwania*, and *Savoryella* (the type genus) (Cooke 1883, Jones & Eaton 1969, Nawawi & Kuthubutheen 1989, Sivanesan & Chang 1992, Boonyuen et al. 2011, Jaklitsch & Réblová 2015, Hernández-Restrepo et al. 2017, Luo et al. 2019b, Réblová et al. 2020a, Yang et al. 2023b). *Ascotaiwania*, *Canalisporium*, *Neoascotaiwania* and *Savoryella* are holomorphic, *Bactrodesmium* and *Dematiosporium* are represented by their asexual morphs, while *Aquabispora* is only known its sexual morph with 2-spored asci. The asexual-sexual morph connections of the above genera were confirmed by cultural characteristics and molecular data (Boonyuen et al. 2011, Réblová et al. 2016c, 2020a, Yang et al. 2016a, Hernández-Restrepo et al. 2017, Zhang et al. 2019b).

History

The taxonomic history of *Savoryellales* goes back to the discovery of a single fungus *Savoryella lignicola*, colonized on Scots pine test-blocks placed in a water-cooling tower for 168 days in the UK (Jones & Eaton 1969). The genus *Savoryella* (typified by *S. lignicola*), is named in the honour of John Savory, who has devoted much of his research work on the investigation of the soft rot decay in timber caused by the cellulolytic activity of fungi in water-cooling towers (Savory 1954a, b, Jones & Eaton 1969, Jones et al. 2016). Up to now, 17 *Savoryella* species have been reported from marine, brackish water, freshwater and terrestrial habitats, of which *Savoryella lignicola* is the most frequently collected species from marine/mangrove habitats (Maria & Sridhar 2003, Ananda & Sridhar 2004, Nambiar & Raveendran 2009, Alias et al. 2010, Manimohan et al. 2011, Jones et al. 2022), and freshwater habitat (e.g., González & Chavarría 2005, Kurniawati et al. 2010). The aquatic taxa *S. aquatica* and *S. lignicola* have both been shown to cause soft rot of wood decay (Mouzouras 1989a, Cai et al. 2003, Bucher et al. 2004a, b, Jones et al. 2016). *Savoryella appendiculata* has a high salinity optimum in the fungal growth (Jones et al. 2022). *Savoryella melanospora*, *S. nypae*, *S. paucispora* and *S. sarushimana* have been found in mangroves and driftwood in the coastal sand (Maria & Sridhar 2002, 2004, Manimohan et al. 2011, Suetrong et al. 2017, Zhang et al. 2019b, Manawasinghe et al. 2022). Recent studies regarding the survey of fungi response to different vegetations, temperature, soil, altitude and microhabitat, have shown that *Savoryella* species are one of the dominant groups in the cropland topsoil sample in the Qinghai-Tibetan Plateau (QTP) and the Qinghai Lake (Wei et al. 2021b, Gou et al. 2022). Members of *Savoryella* are characterized by immersed to superficial ascomata, papillate, periphysate, clavate to cylindrical, unitunicate, 8-spored or occasionally 2-spored asci with a nonamyloid apical thickening containing a pore, and ellipsoidal, 3-septate ascospores with brown central cells and hyaline polar end cells; the asexual morphs are two types: (type I) trichocladium-like, which characterized by inconspicuous or micronematous conidiophores and pyriform to obovoid conidia (Zhang et al. 2019b, Tian et al. 2024), and (type II) cylindrical conidiophores, terminal, determinate conidiogenous cells, and acrogenous, claviform, rostrate conidia (Xu et al. 2024a). The taxonomic history of *Savoryella* has been debated and tentatively placed in *Sphaeriales incertae sedis* (Kohlmeyer & Kohlmeyer 1979), *Ascomycetes incertae sedis* (Eriksson & Hawksworth 1986a), *Sordariales* (Jones & Hyde 1992) and *Halosphaeriales* (Read et al. 1993) based on morphological data, after which Vijaykrishna et al. (2006) made an initial attempt to date the origin of freshwater fungi based on phylogenetic analysis

of SSU sequence data and showed that *Savoryella* belongs to *Hypocreales*. Thereafter, Boonyuen et al. (2011) conducted phylogenetic analyses of *Savoryella* species based on a concatenated dataset (SSU, LSU, RPB1, RPB2, TEF1α and 5.8S rDNA), and their results showed that *Savoryella* has no affinities to any previously assigned orders, but formed a monophyletic group and closely related to species of *Ascotaiwania*, *Ascothailandia* and its asexual morph *Canalisporium*. The order *Savoryellales* was therefore established to accommodate these taxa and been placed in *Hypocreomycetidae*, *Sordariomycetes* (Boonyuen et al. 2011). While the name *Savoryellaceae* was originally proposed by Ranghoo (1998) without a description, it was formally published by Jaklitsch & Réblová (2015). With the extended phylogenetic evidence and molecular clock dating of *Savoryellales* and related taxa, the order is shown to be a sister clade to *Conioscyphales*, *Fuscosporales*, *Pleurotheciales*, and all of which are referred to *Savoryellomycetidae*, *Sordariomycetes* (Hongsanan et al. 2017a, Dayarathne et al. 2019).

Ascothailandia was linked to *Canalisporium* with the latter having priority due to the one fungus-one name ruling and the recommendations for competing sexual-asexually typified generic names (Nawawi & Kuthubutheen 1989, Sri-indrasutdhi et al. 2010, Hawksworth 2011, Taylor 2011, Réblová et al. 2016b, c). The holomorphic genus *Canalisporium* is characterized by perithecial, semi-immersed or superficial, globose or subglobose, dark brown to black ascomata with a long neck and periphysate ostiole, central or sometimes oblique, 8-spored asci, long cylindrical and unitunicate, apically truncate with a J- refractive apical ring, and fusiform, 3-euseptate and versicolored ascospores, surrounded by a thin layer of mucilage, and having effuse or punctiform colonies, with globose to subglobose or oval, holoblastic, thick-walled conidia, with 3–6 longitudinal septa and 4–6 transverse septa, supported by a pale brown small basal cell (Goh et al. 1998a, Sri-indrasutdhi et al. 2010, Goh & Kuo 2021, Yu et al. 2023).

Ascotaiwania (typified by *A. lignicola*) was shown to be polyphyletic, and few species have sequence data (Boonyuen et al. 2011, Jones et al. 2016, Réblová et al. 2016c). Those *Ascotaiwania sensu lato*, e.g., *A. persoonia* and *A. hughesii*, have been replaced in *Fuscosporales* and *Pleurotheciales*, respectively (Yang et al. 2016a). The sexual morph of *Ascotaiwania* is most similar to that of *Savoryella* but different in ascospores (fusiform, 3–7-septate, generally more than 3 septa, end cell pointed vs. ellipsoidal, 3-septate, end cell rounded). The asexual morph of *Ascotaiwania* have been observed as monodictys-like (in *A. lignicola*), trichocladium-like (in *A. hsilio*), and monotosporella-like (in *A. sawada*) (Sivichai et al. 1998, Chang 2001). Hernández-Restrepo et al. (2017) introduced *Neoascotaiwania* to *Savoryellales*, and distinguished *Neoascotaiwania* from *Ascotaiwania* in having 3-septate ascospores, an inamyloid apical ring in the asci, and the bactrodesmium-like asexual morph. Du et al. (2022) and Yang et al. (2022a) recently contributed to *Neoascotaiwania*.

Dematiosporium was introduced to *Savoryellales* by Luo et al. (2019b) based on a collection from a freshwater habitat (type *D. aquaticum*), which is a hyphomycete with dry, dark brown to black, mostly globose to subglobose, smooth conidia. Yu et al. (2023) recollected *D. aquaticum* and introduced *D. bambusicola*, together with the collection of *D. aquaticum* in Réblová et al. (2020a), the conidial morphology of *Dematiosporium* has been re-described, i.e. conidia dry, terminal, blastic, globose to subglobose, ellipsoidal or pyriform, pigmented, dictyosporous.

Bactrodesmium was proposed by Cooke (1883) for dematiaceous hyphomycetes forming sporodochia in the substrate and clavate, transversely septate conidia. One of its representative species *B. pallidum* was linked with *Savoryellales* by DNA sequence data in Hernández-Restrepo et al. (2017). Réblová et al. (2020a) re-evaluated this genus and resolved its taxonomic placement in *Savoryellales* based on phylogenetic evidence. *Bactrodesmium* is characterized by sporodochial colonies, mononematous, often fasciculate conidiophores, holoblastic conidiogenesis and acrogenous, solitary, dry, pigmented, transversely or rarely longitudinally septate conidia, and the conidia are seceding rhexolytically, exhibiting multiple secession patterns (Réblová et al. 2020a).

Aquabispora, typified by *Aq. setosa*, was added to *Savoryellales* by Yang et al. (2023b), which is represented by its sexual morph, *viz*. perithecial, superficial, subglobose to obpyriform, dark brown to black, setose, papillate ascomata, periphysate ostiole, broadly cylindrical to clavate, 2-spored asci,

with a inamyloid apical apparatus which has a central pore and retraction of plasmalemma, the ascospores are cylindrical-ellipsoidal, hyaline to brown, muriform, often surrounded by a mucilaginous sheath.

General description

Aquabispora is easily distinguished from other genera in *Savoryellaceae* in having the superficial, subglobose to obpyriform, setose ascomata, and 2-spored asci with cylindrical-ellipsoidal, muriform ascospores. *Ascotaiwania* is a holomorphic genus. Its ascomata partial to fully immersed, oblique to horizontal, the asci are cylindrical and long, present with nonamyloid massive ring, 8-spored ascospores, fusiform, 3–7-septate, generally more than 3-septa, end cell pointed, brown to black, mid brown central cells and smaller hyaline to subhyaline end cells. The asexual morphs are represented by two types, type I: triadelphia-like and monotosporella-like, effuse colonies and phragmoconidium; type II: monodictys-like, effuse colonies and dictyoconidium. *Bactrodesmium* represented by asexual morph, with sporodochium colonies and phragmoconidium. *Canalisporium* is also a holomorphic genus and its ascomata partially immersed, coriaceous, ostiolate, papillate, 8-spored asci, with a J- refractive apical ring, producing ovoid to fusoid, straight to curved, hyaline, 3-euseptate, surrounded by a thin layer of mucilage. The asexual morph is characterized by sporodochium colonies and dictyoconidium. *Dematiosporium* represented by asexual morph, with effuse colonies and dictyoconidium. *Neoascotaiwania* holomorphic genus with ascomata partial to fully immersed, oblique to horizontal, 8-spored asci, present with nonamyloid massive ring, and fusiform, 3-septate ascospores, brown to black, mid brown central cells and smaller hyaline to subhyaline end cells. The asexual morph characterized by effuse colonies and phragmoconidium. *Savoryella* holomorphic genus, represent ascomata that are superficial or partly immersed, coriaceous, pyriform, papillate, solitary or gregarious, 8-spored or occasionally 2-spored asci, cylindrical to clavate, with small discoid apical pore, and ellipsoidal, 3-septate ascospores, brown to black, mid brown central cells and smaller hyaline to subhyaline end cells. The asexual morphs are represented by two types, type I: trichocladium-like, effuse colonies and phragmoconidium; type II: cylindrical conidiophores, with claviform, rostrate conidia. The sexual morphs of the four holomorphic genera are similar to each other but can be distinguished from their ascospores shape. Whereas the two asexual morph genera are different in colonies and conidial shape.

Sexual morph: *Ascomata* perithecial, brown to black, immersed or superficial, globose to pyriform, coriaceous, often oblique or lying horizontally on the host with the neck facing upwards, periphysate, ostiolate, papillate. *Papilla* central or eccentric when lying horizontally to the host. *Peridium* membranous, comprising several layers of brown, thick-walled cells of *textura angularis*, inner layers hyaline. *Paraphyses* hypha-like, numerous or sparse, septate, partly deliquescing. *Asci* 2–8-spored, unitunicate, clavate to cylindrical, pedicellate, persistent, usually nonamyloid apical ring. *Ascospores* ellipsoidal to fusiform, transversely septate, versicolor ascospores with hyaline end cells and brown median cells, with or without polar mucilaginous pads or appendages. Asexual morph: *Colonies* sporodochial or effuse. *Conidiophores* mononematous, reduced, or short. *Conidiogenous cells* absent or if present erect, monoblastic, cylindrical. *Conidia* dry, subglobose, ellipsoidal, obovoid or pyriform, dictyoconidium or phragmoconidium, pigmented with transverse and longitudinal septa (Fig. 249).

Families included in *Savoryellales*

Savoryellaceae Jaklitsch & Réblová

Evolution

Savoryellales is one of the basal groups of *Sordariomycetes*. Molecular clock dating analysis showed that the divergence time of this order has a stem age of 268 MYA, indicating a subclass status. Most of *Savoryellales* members are aquatic fungi and are frequently discovered and reported in marine and mangrove ecology. The discovery of fossil fungi, e.g., *Monotosporella* sp. (Sadowski et al. 2012), which has been considered related to members of *Savoryellales*, also indicates their early

divergence. The fossil age of this species could help to determine the exact phylogenetic placement of other *Monotosporella* species in the future.

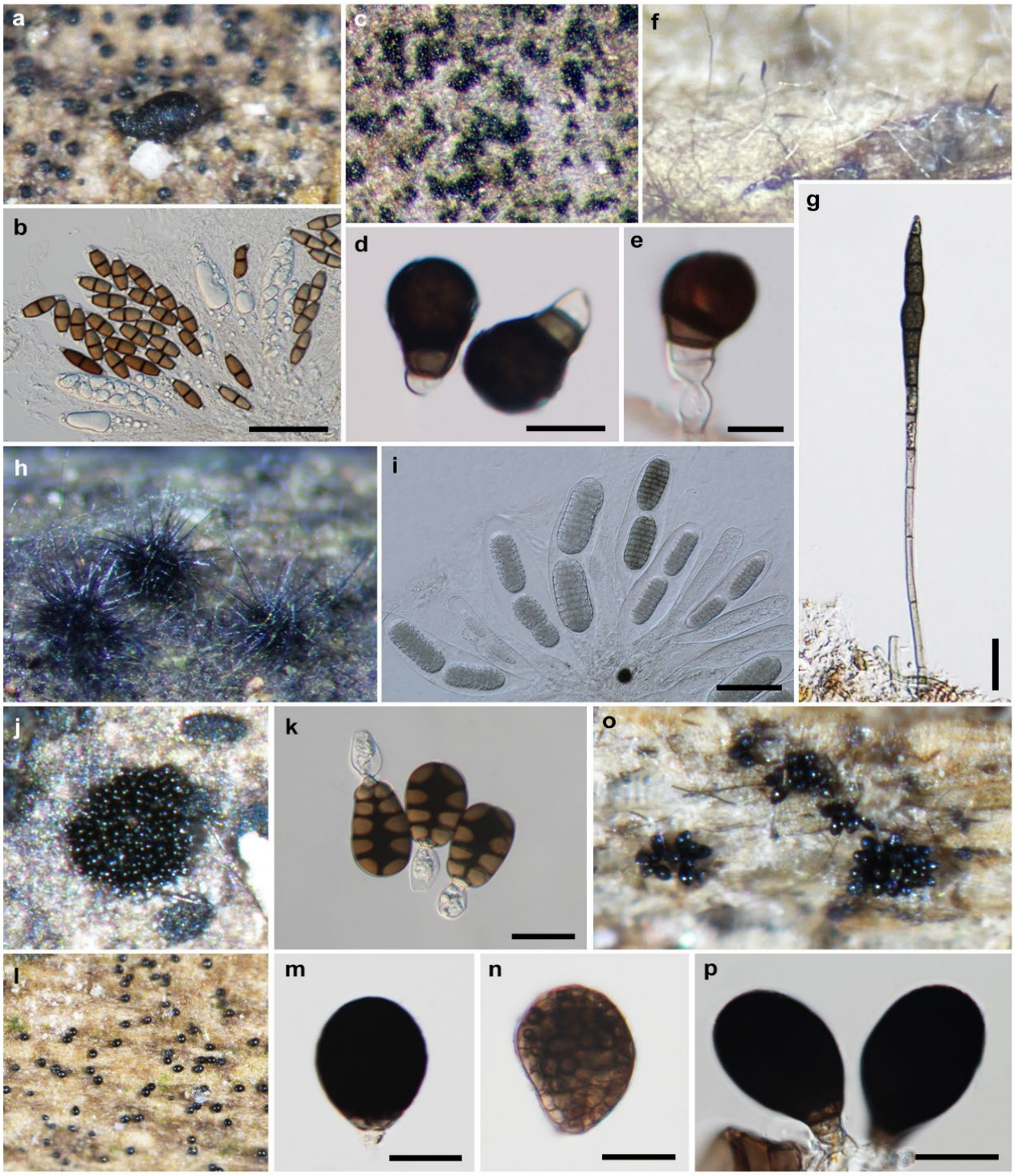


Figure 249 – Morphology of representative species in *Savoryellales*. a, h Ascomata (a *Savoryella bambusicola*, h *Aquabispora setosa*). b, i Asci and ascospores (b *Savoryella bambusicola*, i *Aquabispora setosa*). c, f, j, l, o Colonies on substrates (c *Savoryella nypae*, f *S. claviformis*, j *Canalisporium dehongense*, l *Dematiosporium bambusicola*, o *Neoascotaiwania guizhouensis*). e, g, k, p Conidiophores bearing conidia (e *Savoryella nypae*, g *Savoryella claviformis*, k *Canalisporium dehongense*, p *Neoascotaiwania guizhouensis*). d, m, n Conidia (d *Savoryella nypae*, m, n *Dematiosporium bambusicola*). (Pictures a, b adapted from Yu et al. (2023); c–e adapted from Zhang et al. (2019b); f, g adapted from Xu et al. (2024a); h, i adapted from Yang et al. (2023b); j, k adapted

from Yu et al. (2023); l–n adapted from Yu et al. (2023); o, p adapted from Du et al. (2022)). Scare bars: b = 50 μm; d, e = 10 μm; g, k, m, n, p = 20 μm; i = 100 μm.

Justification of order and problems

Many *Ascotaiwania* and *Triadelphia* species have not been sequenced, which may have affinities with *Savoryellales*. Further alignments are expected with the discovery of new genera and the sequencing of other taxa.

Significance

Ecological and economic roles

Many *Savoryellaceae* species were discovered from freshwater and marine habitats. They can cause soft rot decay of wood, especially when the wood is exposed to wet conditions, such as submerged wood in freshwater, marine environments, as well as water cooling towers.

Chemical diversity

Savoryella lignicola produces the extracellular cellulolytic enzymes endoglucanase, cellobiohydrolase, and β- glucosidase (Pointing et al. 1999). Cellulase and xylanase for wood decomposition were detected in an *in vitro* assay (Bucher et al. 2004b). After further extraction and industrialization, these enzymes that can decompose wood may be able to enzymatically decompose lignin in straw, pasture, and feed seed coats, improve the feeding quality of feed raw materials, and thereby increase their nutritional value.

Other relevant data and future recommendations

Many fungal metabolites have great potential in finding compounds with pharmacological effects, especially fungi in special environments. Most species in this family exist in aquatic and marine environments and future research can pay attention to the secondary metabolites of species in this family.

Sordariales **Chadef. ex D. Hawksw. & O.E. Erikss., Systema Ascomycetum 5(1): 182 (1986)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Sordariomycetidae*

Introduction

The order *Sordariales* (*Sordariomycetes*, *Ascomycota*) includes over 1500 taxa that possess a diverse array of taxonomic characters. Their ascomata have membranaceous or coriaceous walls and one- or two-celled ascospores often bearing appendages or sheaths (Huhndorf et al. 2004a). In the past, this order included up to 14 families, but after several revisions based on phylogenetic studies, it is currently divided into six different families, i.e. *Bombardiaceae*, *Chaetomiaceae*, *Diplogelasinosporaceae*, *Lasiosphaeriaceae*, *Lasiosphaeridaceae,* *Naviculisporaceae*, *Podosporaceae*, *Schizotheciaceae* and *Sordariaceae* (Hensen et al. 2023). However, a large number of taxa remain as *incertae sedis* awaiting to be placed in existing or potentially new families after molecular data is obtained (Marin-Felix & Miller 2022). The interest in this group of fungi is rising due to the production of bioactive compounds with interesting drug-like properties by several members in this order (Ibrahim et al. 2021, Charria-Girón et al. 2022). Moreover, these fungi are of great economic importance due to the production of enzymes able to degrade a wide range of substrates, including plastics (Vivi et al. 2019). *Sordariales* includes three of the most well-known model organisms of the fungal world, i.e. *Neurospora crassa*, *Podospora anserina*, and *Sordaria fimicola*.

History

In the past, the *Sordariales* contained 7 to 14 families (Hawksworth & Eriksson 1986, Eriksson 2001), which were placed in the order based on the putative ascomatal ontogenic characters involved in centrum development (Luttrell 1951a). Subsequently, this order was reduced to three families, i.e. *Chaetomiaceae*, *Lasiosphaeriaceae* and *Sordariaceae*, based on a phylogenetic analysis using LSU sequence data (Huhndorf et al. 2004a). However, *Chaetomiaceae* and *Lasiosphaeriaceae* were shown to be polyphyletic families so they were referred to as complexes. The polyphyly of *Lasiosphaeriaceae* was further discussed by Kruys et al. (2015) in a more robust phylogenetic study based on LSU, RPB2 and TUB2 sequence data. This family was divided into four different groups (I, II, III and IV) corresponding to four supported clades. Subsequently, Wang et al. (2019b) introduced the new family *Podosporaceae* to accommodate a well-supported lineage in the *Sordariales* (corresponding to group IV in Kruys et al. 2015) that occurred far from the clade containing *Lasiosphaeria*, the type genus of the *Lasiosphaeriaceae*. Subsequently, Marin-Felix et al. (2020) investigated additional members belonging to *Lasiosphaeriaceae* based on morphological and molecular data derived from ITS, LSU, RPB2 and TUB2 sequences. This family was restricted to the lineage including only clades representing *Lasiosphaeria* and *Mammaria*, and a clade nesting the type species of *Zopfiella* and other species characterized by ascospores with a septate upper cell (except for *Anopodium ampullaceum* with aseptate ascospores) together with the asexual morph species, *Ramophialophora humicola* (Marin-Felix & Miller 2022). Moreover, three families were introduced to accommodate lasiosphaeriaceous taxa forming well-supported lineages not related to *Lasiosphaeriaceae sensu stricto*, i.e. *Diplogelasinosporaceae*, *Naviculisporaceae* and *Schizotheciaceae* (Marin-Felix et al. 2020). Five new families were introduced by Huang et al. (2021b), but more data is needed to corroborate the proposals. Hitherto, genomic data supported the division of the order in nine families, validating *Lasiosphaeridaceae* and *Bombardiaceae* (Hensen et al. 2023). However, several unresolved lineages remain scattered throughout the order that are awaiting further study once more molecular data for sordarialean taxa are available.

General description

The *Sordariales* is one of the most morphologically diverse orders in the *Sordariomycetes*. Taxa belonging to this order are characterized by the production of ascomata with membranaceous or coriaceous ascomatal walls, and one- or two-celled ascospores often ornamented with mucilaginous appendages or sheaths (Miller & Huhndorf 2004). Ascospore morphology was traditionally used for delimiting genera in this order, but it has been demonstrated that ascomatal morphology is a better predictor of phylogenetic relationships (Miller & Huhndorf 2004, 2005) (see section Justification of order and problems for more details).

Sexual morph: *Ascomata* non-ostiolate or ostiolate, immersed to superficial, scattered or aggregated, glabrous or with hairs or setae covering the ascomata or on the neck, ascomatal wall mostly membranaceous, sometimes coriaceous, mostly brown to dark brown or black. *Paraphyses* and periphyses usually present. *Asci* unitunicate, from 4 to 8-spored, mostly cylindrical to clavate, short- or long-stipitate, without apical ring or sometimes with an apical ring or differentiation; apical ring distinct or inconspicuous; apical differentiation refractive and inamyloid mostly with a subapical globule or chamber. *Ascospores* uniseriate, biseriate or irregularly arranged in the asci, one- or two-celled, walls smooth or ornamented, e.g., pitted or warted, with 1 or 2, rarely more, germ pores, hyaline at first, then usually becoming colored when mature, sometimes with gelatinous appendages, cauda or sheath. Asexual morph: *Conidiophores* lacking, not distinctly differentiated from vegetative hyphae, or reduced to conidiogenous cells, rarely arising from an intercalary, thick-walled, pigmented foot cell. *Conidiogenous cells* phialidic, monophialidic, or sometimes polyphialidic, produced laterally or terminally. *Conidia* arthric or blastic; blastic conidia enteroblastic or holoblastic, arising singly, in chains or in masses, mostly 1-celled, rarely didymo-, phragmo- or muriform, usually smooth-walled, sometimes verrucose, usually hyaline, sometimes brown or dark brown. *Arthric conidia* terminal or intercalary, hyaline, oblong to cylindrical, with both ends truncated, smooth-walled, sometimes occurring in a slimy mass (Figs. 250, 251, 252).

Families included in *Sordariales*

Bombardiaceae S.K. Huang, Maharachch. & K.D. Hyde
Chaetomiaceae G. Winter
Diplogelasinosporaceae Y. Marin & Stchigel
Lasiosphaeriaceae Nannf.
Lasiosphaeridaceae S.K. Huang, Maharachch. & K.D. Hyde
Naviculisporaceae Y. Marin & Stchigel
Podosporaceae X. Wei Wang & Houbraken
Schizotheciaceae Y. Marin & Stchigel
Sordariaceae G. Winter

Sordariales genera *Incertae sedis*
Arnium Nitschke ex G. Winter
Camptosphaeria Fuckel
Cercophora Fuckel
Diffractella Guarro, P.F. Cannon & Aa
Emblemospora Jeng & J.C. Krug
Isia D. Hawksw. & Manohar.
Lockerbia K.D. Hyde
Periamphispora J.C. Krug
Strattonia Cif.
Tripterosporella Subram. & Lodha
Zygospermella Cain

Evolution

Sordariales contains taxa with a variety of coprophilous, herbicolous, lignicolous and terricolous ecological modes that have arisen multiple times throughout the group. Genera within the *Sordariales* have primarily been segregated based on their ascospore morphology (Lundqvist 1972). Ascospores can range from cylindrical, hyaline ascospores in *Lasiosphaeria* to ellipsoidal, brown apical cells and short to long, cylindrical to triangular, hyaline basal cells. Ascospore evolution has been hypothesized to have occurred along a continuum through either the gain or loss of the hyaline, typically basal cell (Chenantais 1919, Munk 1953, Boedijn 1962, Lundqvist 1972). However, numerous recent molecular studies have rejected this hypothesis by showing ascospore morphology to be extremely homoplastic. Multi-gene phylogenies show highly-supported monophyletic clades containing more than one, and usually multiple, ascospore morphologies (Miller & Huhndorf 2005, Kruys et al. 2015, Wang et al. 2019b, Marin-Felix et al. 2020, Huang et al. 2021b, Marin-Felix & Miller 2022). Current evidence suggests that evolutionary relationships in the *Sordariales* may be better predicted through ascomatal wall morphology and/or asexual states (Miller & Huhndorf 2005, Cai et al. 2006b, Marin-Felix et al. 2020).

Justification of order and problems

As mentioned above, ascospore morphology was traditionally used for inferring the taxonomic classification in the *Sordariales*, but it has been demonstrated that ascomatal morphology is a better predictor of phylogenetic relationships (Miller & Huhndorf 2004, 2005). This had already been observed for *Gelasinospora* and *Neurospora*, which differed only in the pattern of ascospore ornamentation, but the synonymy of both genera was based on molecular data since ascospore morphology was uninformative for separating these genera (Dettman et al. 2001, García et al. 2004). Another example that ascomatal wall morphology is a useful character for predicting relationships is found in the genus *Schizothecium*, which is recognized by species producing ostiolate ascomata with characteristic swollen agglutinated hairs or prominent protruding ascomatal wall cells (Cai et al. 2006b). With the increase in molecular data available for fungi belonging to the *Sordariales*, several genera and even families have been re-evaluated in the past years (Wang et al. 2016e, 2019b, c, Kruys et al. 2015, Marin-Felix et al. 2020). The taxonomic changes at the family level are explained above

(see History section). Regarding genera, an example involves *Chaetomium*, *Humicola* and *Thielavia*, which have been intensively studied due to their polyphyly in the past, resulting in the introduction of 22 new genera to accommodate well-supported lineages independent from the redefined former genera (Wang et al. 2016e, 2019b, c, 2022b). Even though numerous species have been transferred among genera based on recent phylogenetic studies in order to achieve a more natural classification, a large number of sordarialean taxa remain without a proper classification (Marin-Felix et al. 2020).

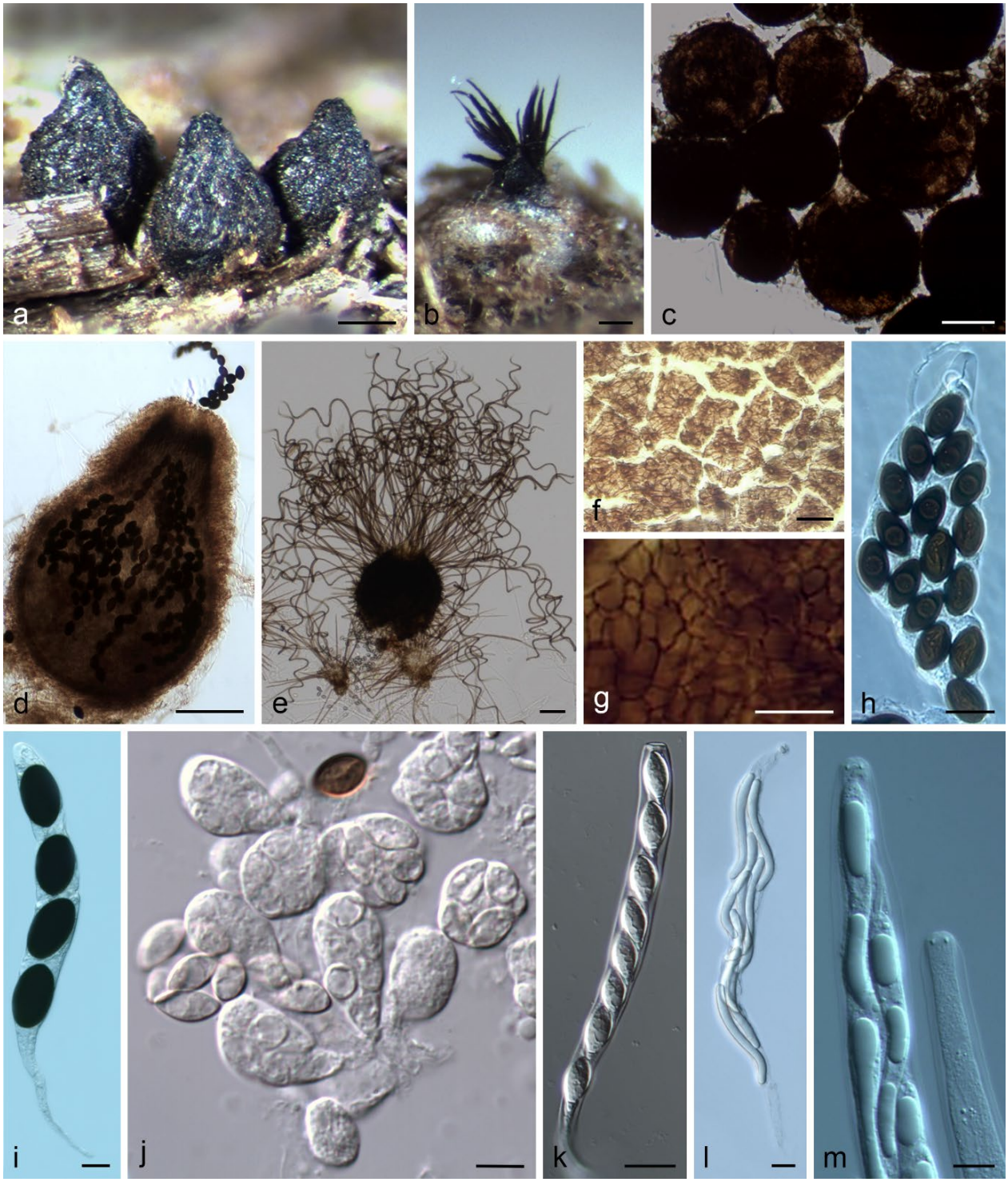


Figure 250 – Morphology of ascomata and asci of the *Sordariales*. a–e Ascomata (a *Areotheca areolata*, b *Triangularia arizonensis*, c *Corynascus fumimontanus*, d *Jugulospora rotula*, e *Amesia hispanica*). f, g Ascomatal wall (f *Podospora costaricensis*, g *Pseudoechria prolifica*). h–m Asci (h *Rhypophila pleiospora*, i *Triangularia arizonensis*, j *Corynascus fumimontanus*, k *Jugulospora rotula*, l *Areotheca areolata*, m *Triangularia striata*). (Pictures a, c, d, f–i, k–m adapted from Marin-

Felix et al. (2020), e adapted from Charria-Girón et al. (2023), c, j adapted from Marin-Felix et al. (2015)). Scale bars: a = 200 µm, b, d = 100 µm, c, e = 50 µm, f, g, j, l, m = 10 µm, h = 25 µm, i = 20 µm, k = 15 µm.

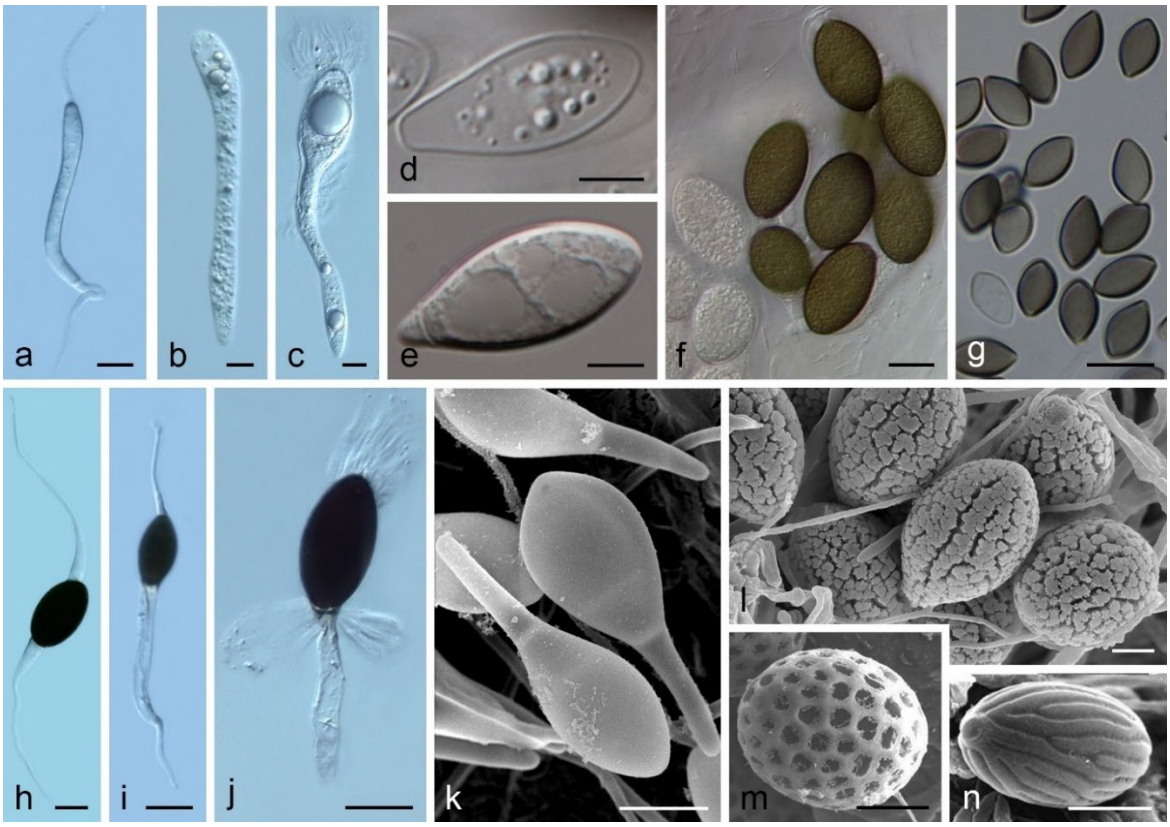


Figure 251 – Ascospore morphology of the *Sordariales*. a–e Immature ascospores (a *Areotheca areolata*. b, c *Rhypophila decipiens*. d, e *Jugulospora rotula*). f–j Mature ascospores (f *Cladorrhinum foecundissimum*. g *Amesia hispanica*. h *Triangularia arizonensis*. i *Areotheca areolata*. j *Rhypophila decipiens*). k–n Ascospore ornamentation (k *Naviculispora terrestris*. l *Jugulospora rotula*. m *Neurospora indica*. n *Neurospora tetrasperma*) (Pictures a–f, h–l adapted from Marin-Felix et al. (2020), g adapted from Charria-Girón et al. (2023), m, n adapted from García et al. (2004)). Scale bars: a–c, g, i, k, m, n = 10 µm, d, e, l = 5 µm, f, h, j = 20 µm.

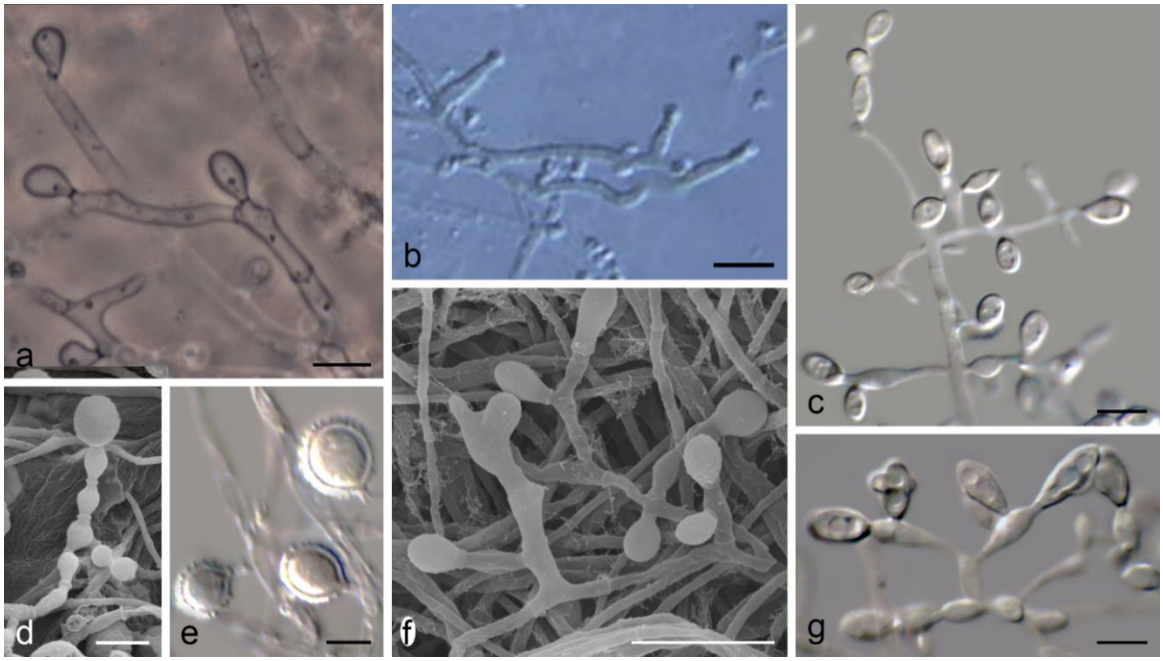


Figure 252 – Asexual morph morphology of the *Sordariales*. a *Naviculispora terrestris*. b *Pseudoschizothecium atropurpureum*. c, g *Thermothelomyces thermophilum*. d *Corynascus sepedonium*. e *Corynascus verrucosus*. f *Myceliophthora lutea* (Pictures adapted from Marin-Felix et al. (2020), b adapted from Miller & Huhndorf (2001), c–g adapted from Marin-Felix et al. (2015)). Scale bars: a, d, e, g = 5 µm, b, c, f = 10 µm.

The main problem in this regard is that living material for many species is not available, which makes it more difficult to derive molecular data for phylogenetic studies. Therefore, it is of utmost importance to recollect material of previously described species to designate as reference material, or even typify when necessary. One of the most significant examples is *Cercophora*, which is one of the largest lasiosphaeriaceous genera and whose species occur in many different lineages throughout the *Sordariales* (Miller & Huhndorf 2004, Kruys et al. 2015). Even though a strain identified as *C. mirabilis*, which is the type species, was placed in the *Schizotheciaceae*, the strain does not sporulate in culture making it impossible to confirm its identity (Marin-Felix et al. 2020, Marin-Felix & Miller 2022). It is necessary to find a suitable epitype to determine the exact taxonomic placement of *Cercophora* so that other *Cercophora* spp. that are located in other lineages can be properly classified. A similar situation is found in *Arnium* since no living material is available for the type species, *A. lanuginosum*. Therefore, it is necessary to recollect the type species to determine the correct taxonomic placement of the genus since several *Arnium* spp. are found scattered throughout *Sordariales* (Kruys et al. 2015). Another recent problem is the confusion surrounding the type species of *Podospora* and *Schizothecium* and the numerous name changes to *Triangularia* for species previously in *Podospora* (Wang et al. 2019b). Although *Podospora* (based on *P. fimiseda* (Ces. & De Not.) Niessl) and *Schizothecium* (based on *S. fimicola* Corda) each have their own type species based on two, distinct specimens, previous authors have erroneously believed these two genera shared the same type species. A proposal to conserve the type of *Podospora* has been offered and, if accepted, will resolve this complex, nomenclatural problem (Vogan et al. 2021).

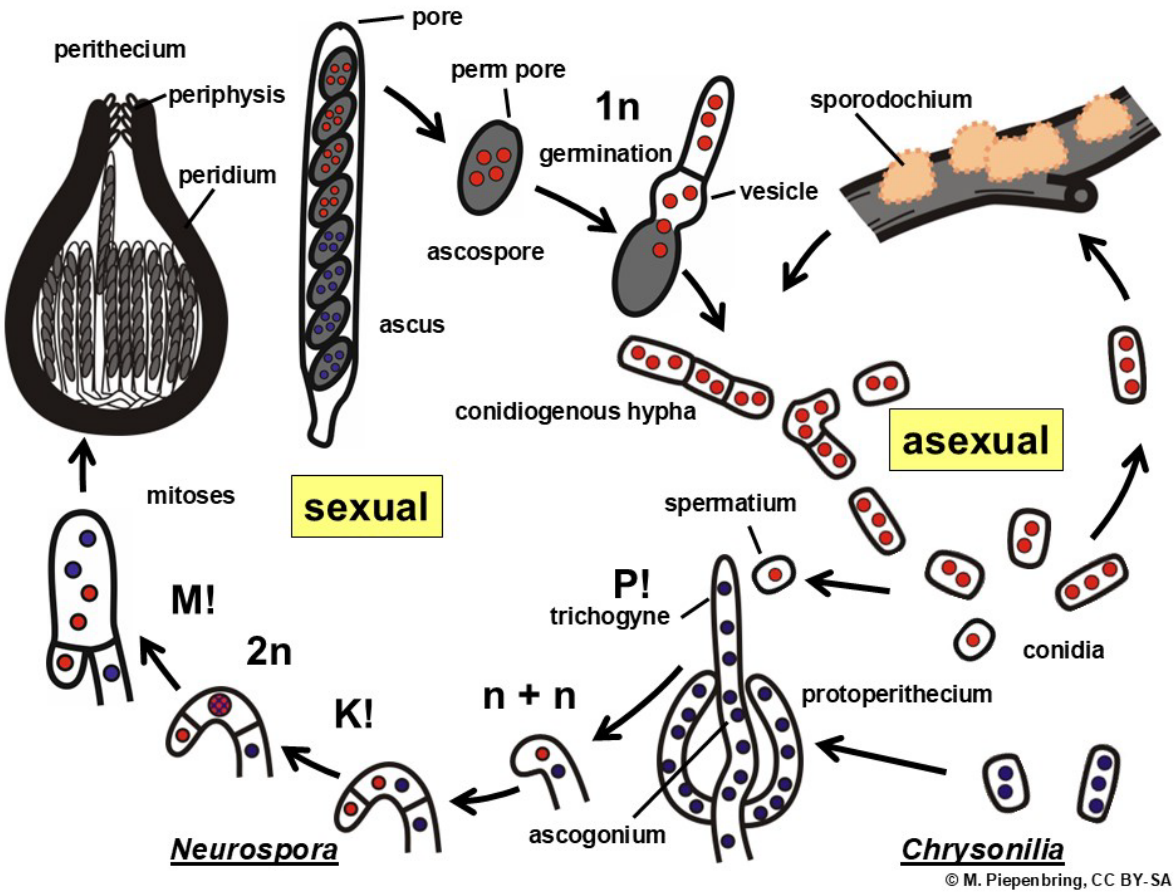


Figure 253 – Sexual and asexual life cycles of *Sordariales* (From Mycological teaching diagrams by Meike Piepenbring (2023)). Abbreviations: 1n = haploid, 2n = diploid, P! = plasmogamy, K! = karyogamy, M! = meiosis. Black and white circles represent haploid nuclei of different mating types, circles of both colors represent diploid nuclei.

Significance

Ecological and economic roles

Members of the *Sordariales* are distributed worldwide and can be found growing on decaying wood, dung, leaf litter and soil (Lundqvist 1972). No members are known to be mycorrhizal and rarely are they found as endophytes. This order is an economically important group since it contains taxa, mostly belonging to *Chaetomiaceae*, that can produce industrial-relevant enzymes and those that can degrade the increasing amount of waste caused by human activity. One of the most interesting examples is the (hemi-)cellulolytic enzymes produced by *Thermothelomyces thermophilus* (syn. *Myceliophthora thermophila*) that have been patented due to their availability to degrade lignocellulolytic plant material (van den Brink et al. 2012, Marin-Felix et al. 2015). Interest is increasing in the degradation and destruction of contaminants because of the high potential of chaetomiaceous taxa to perform these tasks. For example, the ability to degrade PCL (polycaprolactone) and PVC (polyvinyl chloride) by *Chaetomium globosum* has been recently demonstrated (Vivi et al. 2019), which is especially important nowadays since plastic residues are increasing and becoming a global threat.

Chemical diversity

Members of the *Sordariales* have been demonstrated to be prolific producers of active secondary metabolites. Not including *Chaetomiaceae*, 174 compounds have been reported from sordarialean taxa since 2022 (Charria-Girón et al. 2022). *Chaetomiaceae* has been the most studied group for the production of compounds, reporting 191 compounds from 2016 to 2021 (Ibrahim et al. 2021). However, other families have been poorly studied in terms of secondary metabolism, or even neglected as is the case for *Lasiosphaeriaceae* (Charria-Girón et al. 2022). Therefore, it is necessary to study the chemical diversity of these families to corroborate if these harbor the vast chemical diversity found in other families of *Sordariales*.

Some of the most studied compounds produced by taxa belonging to the *Sordariales* are the sordarins. These are antifungal diterpene glycosides that display specific action against elongation factor 2 in protein biosynthesis in fungi (Vicente et al. 2009). Even though some sordarin derivatives underwent preclinical studies, a successful candidate has not yet been found for clinical development. Recently, the chemical diversity of various members of the *Sordariales* has also been demonstrated to be useful for inferring taxonomic relationships. This is especially important taking into account that a large number of taxa remain *incertae sedis*. An example of this is the introduction of the newly described *Pseudorhypophila*. During the reevaluation of the order *Sordariales* by Marin-Felix et al. (2020), a well-supported clade was observed in *Naviculisporaceae* that included the type strains of *Triangularia mangenotii*, *Zopfiella marina*, *Z. pilifera* and *Z. submersa*. The type species of *Triangularia* is located in *Podosporaceae*, whereas the type species of *Zopfiella* nested in *Lasiosphaeriaceae sensu stricto*. However, a new genus to accommodate this lineage was not erected due to the differences in the morphology among its members. Recently, the secondary metabolism of *T. mangenotii* was studied and the same known compound, zopfinol, was isolated from it and *Z. marina* along with other related compounds. Therefore, the new genus, *Pseudorhypophila*, was introduced based on the combination of molecular and chemotaxonomic data (Harms et al. 2021). Similarly, during the evaluation of the compounds produced by different strains of *Jugulospora*, the same new antimicrobial and cytotoxic compounds named xanthoquinodins were observed in all the strains tested, including the type strains of *Apiosordaria globosa* and *Apiosordaria hispanica* (Shao et al. 2020), which were previously synonymized under *Jugulospora rotula* based on molecular and morphological data (Marin-Felix et al. 2020). This synonymy was, therefore, also supported by these chemotaxonomic results.

Other relevant data and future recommendations

Sordariales includes the "fruit flies" of the fungal world, i.e. *Neurospora crassa*, *Podospora anserina* and *Sordaria fimicola*, which have been used extensively as model organisms in genetic research. *Neurospora crassa* is widely known for its ease in molecular genetic manipulation and in constructing multiple deletion strains (Dunlap et al. 2007). *Podospora anserina* has been a workhorse for genetics and molecular biology for over a century being used in thousands of research studies ranging from sexual reproduction to prion biology (e.g., Cummings et al. 1979, Dufour et al. 2000, Espagne et al. 2008). *Sordaria fimicola* is commonly used in genetics courses to study Mendel's law of segregation.

We highly encourage researchers to refrain from introducing new genera or even families in the order if an exhaustive polyphasic study has not been performed due to the difficulty of correctly classifying members even at the generic level. New higher taxa based solely on morphological or molecular data should not be described since the material is lacking for a large number of species. It is essential to recollect sordarialean fungi and generate molecular data to use in phylogenetic studies, which will improve the resolution of many clades.

Finally, the generation of genomic data will allow us to better clarify the taxonomic classification of the lineages that are now in *incertae sedis*. Hitherto, 300 genomes of sordarialean fungi are available at the National Center for Biotechnology Information (NCBI), of which 201 are from members of the *Sordariaceae*, mostly *Neurospora*. Therefore, it is necessary to derive genomic data for other taxa to study the taxonomic relationships of members of this order, as well as to be able to perform studies on the evolution, ecology and biosynthesis of natural products.

Spathulosporales **Kohlm., Mycologia 65(3): 615 (1973)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Incertae sedis*

Introduction

Spathulosporales is a marine fungal order which accommodates two families (*Hispidicarpomycetaceae* and *Spathulosporaceae*) and three genera (*Hispidicarpomyces*, *Retrostium* and *Spathulospora*) (Maharachchikumbura et al. 2016, Hyde et al. 2020d).

History

Spathulosporales was introduced by Kohlmeyer (1973) to accommodate the family *Spathulosporaceae* with the genus *Spathulospora* to encompass four species (*Spathulospora adelpha*, *S. calva*, *S. lanata* and *S. phycophila*) based solely on morphology. *Spathulosporales* shared similar morphology to *Sphaeriales* in having bottle-shaped or subglobose ascocarps, ostiolum with periphyses, inner layers of perithecial wall composed of hyaline, flattened cells, thin-walled, unitunicate, club-shaped or fusiform asci arranged in a hymenium but differs in having simplified thallus structure, and antheridia and trichogynes whereas *Sphaeriales* has true hyphae (Müller & von Arx 1962). Further, *Spathulosporales* have similar morphological characteristics to several members of *Halosphaeriaceae* in having one-celled, appendaged ascospores, the ascogenous tissue is not hyphoid, and asci with thin-walled that are early deliquescing but differ in having antheridia and trichogynes that are absent in *Halosphaeriaceae* (Kohlmeyer 1973). The order also shared similar morphology to the insect parasitic group *Laboulbeniales* in having reduced hyphal growth, sterile perithecial hairs, phialide-like antheridia, spermatia and trichogynes (Kohlmeyer 1973). Both orders are assumed to have originated from a common ancestor, a parasite on red algae. Nakagiri (1993) added the second family, *Hispidicarpomycetaceae* to accommodate *Hispidicarpomyces galaxauricola* that inhabits marine algae *Galaxaura falcata.* Later, Nakagiri & Ito (1997) established the third genus *Retrostium* within the order in the family *Spathulosporaceae. Spathulospora* recovered with *Lulworthiales* in the SSU and LSU DNA sequences obtained from dried herbarium specimens of *S. adelpha* and *S. antarctica* which also raised the question of the phylogenetic position

of *Hispidicarpomycetaceae* (Inderbitzin et al. 2004). Even though *Spathulospora* is morphologically considerably distinct from *Lulworthiales,* they share similar morphology in ascospores with apical chambers containing mucus believed to be involved in ascospore attachment with several members of the latter (Inderbitzin et al. 2004). Maharachchikumbura et al. (2015) accepted the taxonomic placement of *Hispidicarpomycetaceae* within *Spathulosporales*. *Spathulospora* also formed a close phylogenetic relationship to *Lulworthiaceae* in the recent phylogenetic analyses conducted by Hyde et al. (2020d) and is classified under *Sordariomycetes*, *incertae sedis*.

General description

Hispidicarpomyces galaxauricola resembles members of *Spathulospora* in morphology and parasitism on marine red algae (Kohlmeyer 1973, Kohlmeyer & Kohlmeyer 1979). However, *H. galaxauricola* produces true hyphae that grow throughout the algal frond, whereas *Spathulospora* species have reduced-hyphoid structures (Kohlmeyer 1973). Further, intracellular invasion into the algal cell by an infection peg and formation of intracellular crusts are characteristic of *Spathulospora* exhibits only intercellular infection (Nakagiri 1993).

Sexual morph: *Ascomata* superficial, solitary to gregarious, subglobose, ovoid, pyriform, subiculate, coriaceous or leathery, sterile hairs enclosing ascoma, ostiolate, apapillate. *Peridium* composed of three-layers: outer layer with thick-walled, short hyphal projections, brown to dark brown, middle layer of light brown to dark brown, thick-walled hyphal, flattened cells of *textura epidermoidea*, and an inner layer of pale brown, thin-walled, flattened cells of *textura epidermoidea*, lining the whole ascomatal venter. *Paraphyses* septate branched. *Asci* 8-spored, unitunicate, thin-walled, clavate to pyriform, deliquescing early and lacking an apical ring. *Ascospores* hyaline, ellipsoid to elliptic-fusiform, unicellular, lacking appendages or a sheath, overlapping. Asexual morph: Reproductive state of brown hyphae. *Spermodochia* composed of a mass spermatiosphores. *Spermatiosphores* verticilliate, asymmetrical penicilliate-like, brown at the base, paler and hyaline towards the apex. *Stipes* septate, branched, brown at the base. *Spermatia* cylindrical, unicellular, hyaline. *Trichogynes* septate, cylindrical, brown (Fig. 254).

Families included in *Spathulosporales*

Hispidicarpomycetaceae Nakagiri
Spathulosporaceae Kohlm.

Evolution

The morphological characteristics of *Spathulosporales* concurred with the hypothesis of primitive Ascomycetes, which was postulated by Denison & Carroll (1966) that "Ascomycetes evolved from autotrophic marine ancestors with many of the morphological and cytological features of modern *Rhodophyta*.". However, the ecology of the genus contradicts the hypothesis "the primitive Ascomycetes evolved as saprophytes on driftwood in oceans and estuaries .... " as *Spathulosporales* are parasitic on algae (Kohlmeyer 1973).

Justification of order and problems

The phylogenetic studies have shown affinity of *Spathulospora* within *Lulworthiales* (Inderbitzin et al. 2004). In the recent phylogenetic analysis conducted by Hyde et al. (2020d) showed *Spathulospora* close to *Lulworthaiceae*. However, the phylogenetic placement of the order needs detailed investigation based on morphological and phylogenetic analyses of members from type and fresh materials.

Significance

Ecological and economic roles

Members of *Spathulospora* are distributed across the Southern Hemisphere, between Antarctica and the southern regions of the adjacent continents (Kohlmeyer & Kohlmeyer 1975). *Retrostium* and *Hispidicarpomyces* are reported along the Japanese coast (Nakagiri 1993). The members of the order are reported as parasites on marine algae. *Hispidicarpomyces* occurs as biotrophic on the marine alga

Galaxaura falcata (*Rhodophyta*) and *Retrostium* reported on *Amphiroa zonata* (marine *Rhodophyta*), while *Spathulospora* species are parasites on the red algae *Ballia callitricha* and *B. scoparia* (Kohlmeyer 1973).

Chemical diversity

No relevant studies are available for the chemical diversity of *Spathulosporales.*

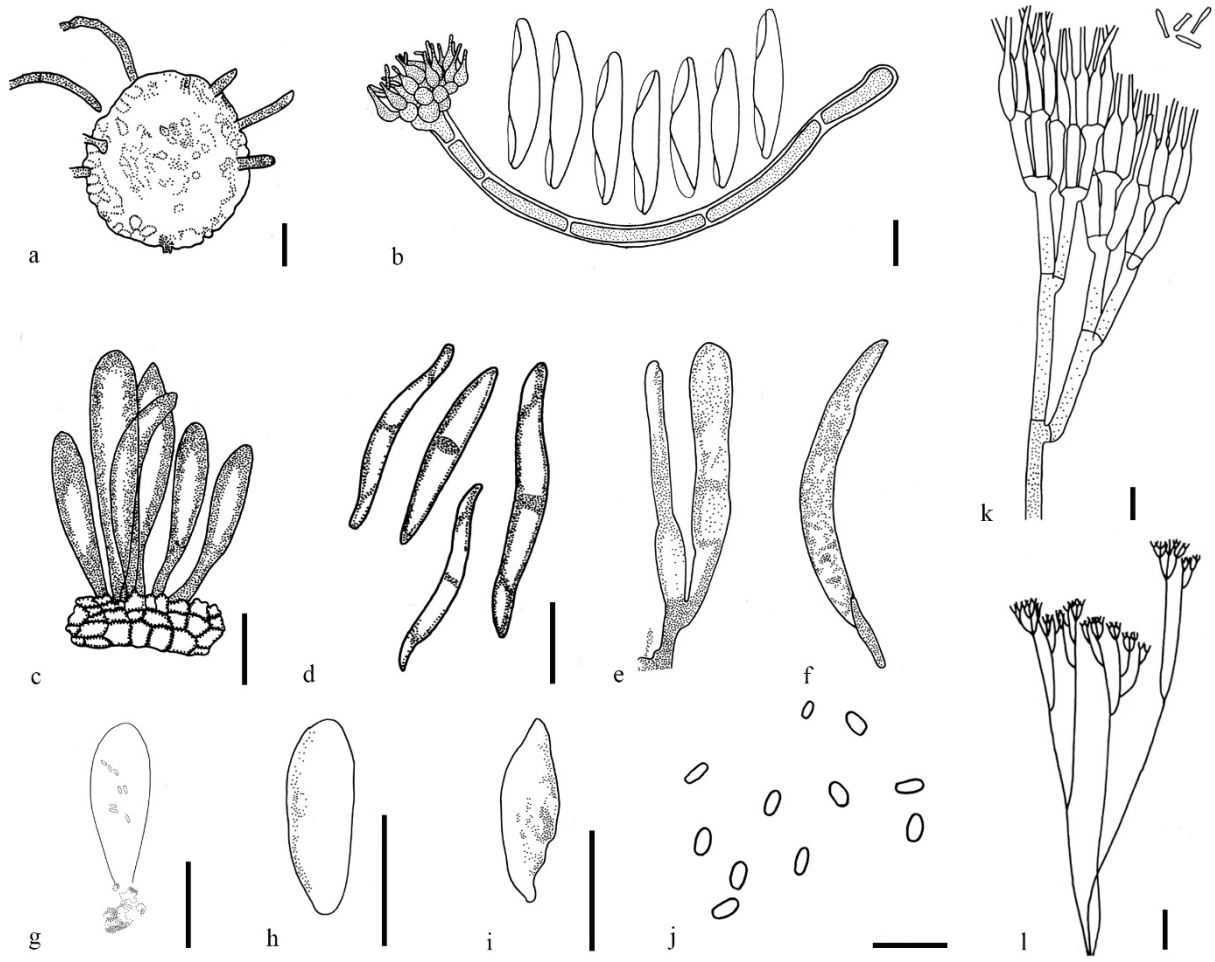


Figure 254 – Sexual and asexual morph of *Spathulosporales*. a Section through ascoma *Spathulospora phycophila*. b perithecial hair with antheridia (*Spathulospora lanata*). c, g Asci (c *Spathulospora lanata*, h *Retrostium amphiroae*). d Ascospores (d *Spathulospora lanata*. h, i *Retrostium amphiroae*). e Ascospore with appressed subterminal appendages (*Spathulospora phycophila*). f Antheridium and abnormal sterile cells (*Spathulospora phycophila*). j Spermatiophores arising from the margin of young ascoma (*Retrostium amphiroae*). k Branching spermatiophores. l Penicillate phialides of spermatiophore and Spermatia (k, l *Hispidicarpomyces galaxauricola*) (redrawn from Kohlmeyer 1973, Nakagiri 1993, Maharachchikumbura et al. 2016, drawn from Kohlmeyer 1973, Hyde et al. 2020d). Scale bars: a, l = 100 µm, b, c, d = 25 µm, g = 20 µm, h, i, k = 10 µm, j = 5 µm.

Other relevant data and future recommendations

So far, only five *Spathulospora* species have been reported whereas a single species has been documented for both *Hispidicarpomyces* and *Retrostium*. However, molecular data are available only for two species, including *S. adelpha* and *S. antarctica* (Inderbitzin et al. 2004) and these sequence data were also obtained from herbarium materials due to the limited distribution of the samples, which renders the recollection of fresh materials. Studies showed the phylogenetic placement of

Spathulospora within *Lulworthiales* (Inderbitzin et al. 2004). Thus, a detailed investigation of the members including the type of material and fresh collection based on molecular data is important to resolve its taxonomy.

Thyridiales **R. Sugita & Kaz. Tanaka, MycoKeys 86: 156 (2022)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Thyridiales was recently introduced for its type family, *Thyridiaceae* based on six genes phylogenetic analysis along with morphological data (Sugita and Tanaka 2022). The taxa are reported in both sexual and coelomycetous and/or hyphomycetous asexual morphs (Sugita & Tanaka 2022) and accommodate two genera namely *Pleurocytospora* and *Thyridium* (Hyde et al. 2024b).

History

Thyridiaceae was introduced for *Thyridium* and *Sinosphaeria* (Yue & Eriksson 1987). *Thyridium* (type *T. vestitum*) was established by Nitschke (1867) to accommodate species with cylindrical, uniseriate, 8-spored asci and muriform, dark-colored, ascospores. Later, *Bivonella* and *Sinosphaeria* were added to *Thyridium* (Eriksson & Yue 1989). *Thyridiaceae* was placed in *Hypocreales* based on the presence of bright pigmentation of stromatic tissues, paraphyses and periphysoids (Eriksson & Yue 1989). Barr (1990b) treated this family under *Xylariales* along with *Valsaria* and *Valsonectria* and stated pigments are not a unique character in *Hypocreales*. However, later studies placed *Valsaria* in *Diaporthales* and *Valsonectria* in *Hypocreales* (Kirk et al. 2008b, Jaklitsch et al. 2015).

Rossman et al. (1999) placed *Balzania*, *Mattirolia* and *Thyronectroidea* in *Thyridiaceae*. However, based on the examination of type species, *Balzania* and *Thyronectroidea* were considered as the synonym of *Mattirolia*. Subsequently, only *Mattirolia* and *Thyridium* were retained under *Thyridiaceae* (Checa et al. 2013). *Mattirolia* was synonymized under *Thyronectria* and the genus recovered in a distant clade to *Thyridiaceae* (Jaklitsch & Voglmayr 2014, Maharachchikumbura et al. 2015). *Pleurocytospora* accommodates three species and the genus was also accepted within *Thyridiaceae* (Maharachchikumbura et al. 2015, Wijayawardene et al. 2018).

The family was placed in *Sordariomycetidae* based on the phylogenetic analyses and later was transferred to a newly established subclass *Diaporthomycetidae* (Maharachchikumbura et al. 2015). The family showed a close phylogenetic relationship to *Annulatascales* and *Myrmecridiales* in the later studies (Hongsanan et al. 2017a, Hyde et al. 2017a, Senanayake et al. 2017a). However, the family differs from both orders in several morphological characters. *Thyridiaceae* differs from *Myrmecridiales* by having pycnidial conidiomata, becoming cup-shaped in the coelomycetous state and micronematous conidiophores with monophialidic conidiogenous cells in the hyphomycetous state, whereas *Myrmecridiales* have brown thick-walled conidiophores with polyblastic conidiogenous cells (Crous et al. 2015a). Members of *Annulatascales* have a relatively massive refractive, well-developed, conspicuous apical ring in the asci (Campbell & Shearer 2004, Dong et al. 2021a) while members of *Thyridiaceae* are compact and inconspicuous. *Phialemoniopsis* was previously placed in *Sordariomycetes*, genera *incertae sedis* (Perdomo et al. 2013) that was later raised to a new family *Phialemoniopsidaceae* in *Diaporthomycetidae* based on molecular clock analysis (Hyde et al. 2021a). *Phialemoniopsidaceae* was synonymized under *Thyridiaceae* due to shared morphological similarities in the asexual morph between *Phialemoniopsis* and *Thyridium* and with phylogeny with the establishment of the new order *Thyridiales* (Sugita & Tanaka 2022).

General description

The taxa of *Thyridium* are mostly reported in their sexual morph while a few species including *T. flavum* and *T. vestitum* produce asexual morph. The sexual and asexual associations have been

reported in the same specimens as well as in the culture studies. *Phialemoniopsis* species have been solely reported based on their asexual morph. Both *Thyridium* and *Phialemoniopsis* have similar morphology in the conidiophores bearing small groups of phialides, hyaline phialidic conidiogenous cells, and ellipsoidal or allantoid, hyaline conidia in both coelomycetous and hyphomycetous states (Sugita & Tanaka 2022).

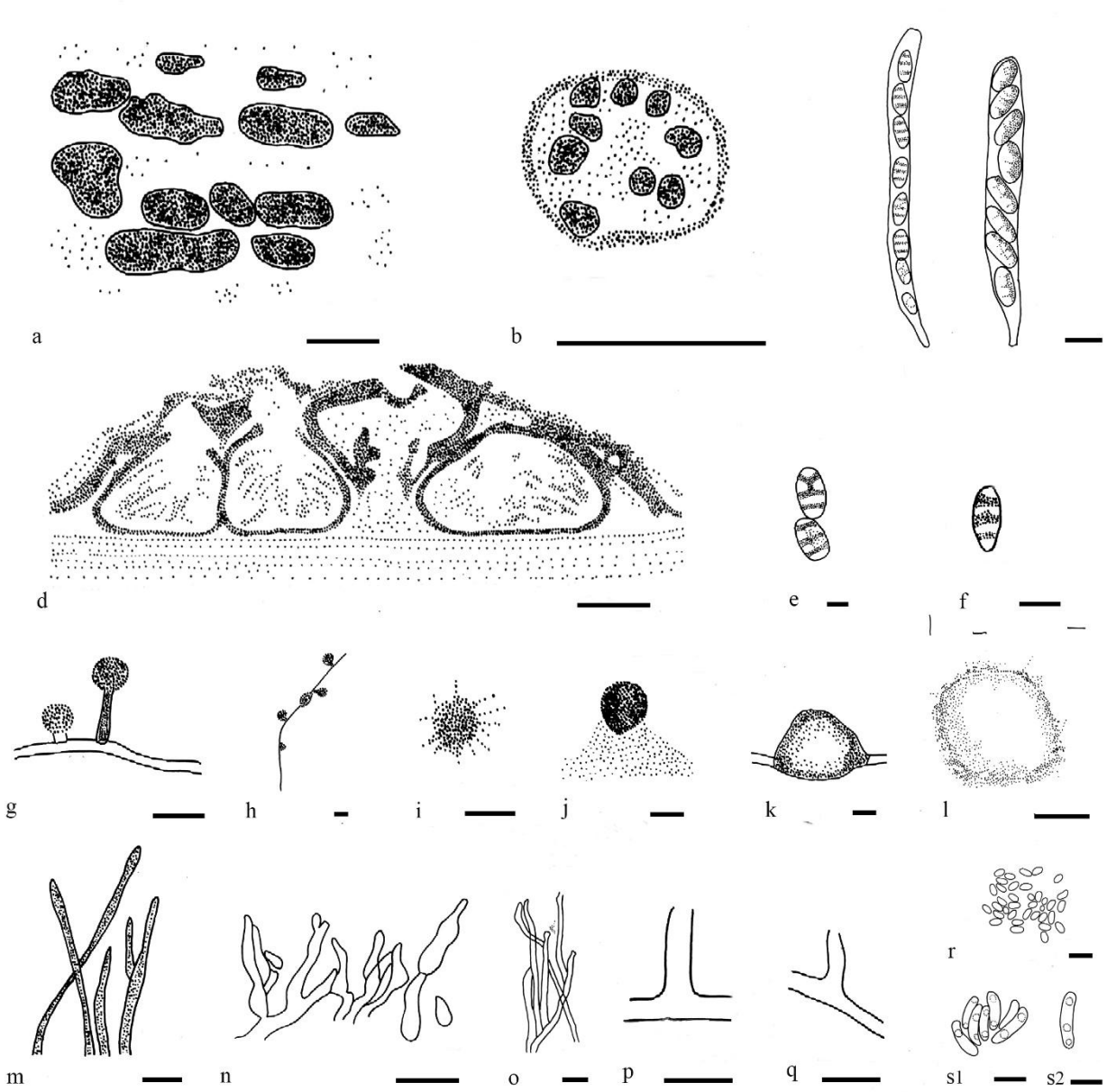


Figure 255 – Morphology of *Thyridiales*. a Appearance of stromata on substrate (*Thyridium flavostromatum*). b Transverse section of appearance of stromata on substrate (*T. pluriloculosum*). c1, c2 (Ascus (c1 *T. pluriloculosum*, c2 *T. flavostromatum*)). d Ascomata in longitudinal section (*T. punctulatum*). e, f Ascospores (e *T. punctulatum*, f *T. pluriloculosum*). g Sporulation in culture (*T. pluriloculosum*). h, p, q Phialides (h *T. flavostromatum,* p *T. pluriloculosum*, q *T. punctulatum*). i, j Conidiomata in culture (i *T. pluriloculosum*, j *T. pluriloculosum*). k slimy head (*T. punctulatum*). l Conidioma in longitudinal section (*T. punctulatum*). m Paraphyses (*T. flavostromatum*). n Conidiophore (*T. flavostromatum*). o Hyphae of conidiomata (*T. punctulatum*) (redrawn from Sugita & Tanaka 2022). Scale bars: a = 1000 µm, b, I, j = 500 µm, c, f, h, k, m = 10 µm, d = 50 µm, e, n, p–s = 5 µm, g = 20 µm, l = 100 µm, o = 200 µm.

Sexual morph: *Ascomata* stromatic. *Stromatal tissue* immersed, becoming erumpent to superficial, soft-textured, reddish brown to brightly pigmented. *Ascomata* immersed in stromata, globose, ostiolate. *Ostioles* periphysate, with short or long papilla or necks, sometimes convergent necks merging into one ostiole. *Peridium* composed of compressed rows of cells, externally brown, internally hyaline. *Paraphyses* filamentous, septate. *Asci* 8-spored, unitunicate, oblong cylindric, apical ring J-. *Ascospores* uniseriate, shades of brown, ellipsoid or biconoid, symmetric, 1-septate or muriform. Asexual morph: Coelomycetous or hyphomycetous, often developing on the edge of sexual morph stroma. *Conidiomata* immersed in stromata, irregular, multilocular and folded inside. *Conidiogenous cells* emerging from the interior of the cavity, bearing one or more conidiogenous cells. *Conidiogenous cells* enteroblastic, phialidic, hyaline. *Conidia* ellipsoidal, aseptate, small, hyaline. Holoblastic sympodial conidia also produced from hyphae. Sometimes ascospores produce primary conidia (adapted from Maharachchikumbura et al. 2015, Hyde et al. 2020d) (Fig. 255).

Families included in *Thyridiales*

Thyridiaceae O.E. Erikss & J.Z. Yue (= *Phialemoniopsidaceae* K.D. Hyde & Hongsanan)

Justification of order and problems

The phylogenetic placement of *Pleurocytospora* remains uncertain due to a lack of molecular data. Sugita & Tanaka (2022) proposed treating the asexual genus *Phialemoniopsis* as a synonym of the sexual genus *Thyridium*. However, Hyde et al. (2021a) noted the lack of morphological data for the holotype material when they established the family *Phialemoniopsidaceae*. Therefore, further fresh collections and a reevaluation of existing species are crucial for improving our understanding of this order.

Significance

Ecological and economic roles

Species of *Thyridium* may have cryptic life cycles and can colonise different host at different reproductive stages. *Thyridium pluriloculosum* was reported in its sexual morph on human nails while the asexual morph was reported on twigs of *Betula maximowicziana* (Perdomo et al. 2013, Sugita & Tanaka 2022). *Thyridium endophyticum* and *T. curvatum* have been isolated from both plants and animals (Gams & McGinnis 1983b, Halleen et al. 2007, Perdomo et al. 2013, Su et al. 2016b). The taxa are reported as endophytes, human pathogens, hemibiotrophs or saprobes and occur on toenails, sinuses, eyes of humans, air, industrial and river water, plant materials, sewage, and soil (Gams & McGinnis 1983b, Halleen et al. 2007, Perdomo et al. 2013, Tsang et al. 2014, Su et al. 2016b, Sugita & Tanaka 2022).

Chemical diversity

No relevant studies are available for the chemical diversity of *Thyridiales*.

***Tirisporellales* Suetrong, E.B.G. Jones & K.L. Pang, Fungal Diversity 73(1): 42 (2015)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Tirisporellales was introduced by Jones et al. (2015) to accommodate a single family *Tirisporellaceae,* with three genera *Bacusphaeria*, *Thailandiomyces* and *Tirisporella*. *Tirisporellaceae* was introduced to accommodate two monotypic genera *Tirisporella* and *Thailandiomyces* (Suetrong et al. 2015a).

History

The generic type *Tirisporella* was introduced to accommodate *T. beccariana* (= *Sphaeria beccariana*). This species was later placed in *Melanomma*, *Gibberidea* and *Tryblidiella*. Jones et al.

(2009) placed this genus within *Pleosporales incertae sedis*. However, Suetrong et al. (2015a) initially provided molecular data and placed it in the newly established family *Tirisporellaceae* along with a saprobic genus *Thailandiomyces*. Subsequently, *Bacusphaeria* was added to this family (Suetrong et al. 2015b). The family formed a sister clade to *Jobellisiaceae* with weak support in the phylogenetic analyses based on SSU and LSU sequence data (Suetrong et al. 2015a) within *Diaporthales*. The family formed a monophyletic clade in the subsequent phylogenetic studies (Hongsanan et al. 2017a, Hyde et al. 2017a) and formed a basal clade to *Diaporthales* in Hyde et al. (2017a). However, the order was treated separately rather than being combined under *Diaporthales* due to their habitat, as the members are primarily reported in freshwater and marine habitats which were not usually found in *Diaporthales* (Zhang et al. 2019b). The order presently accommodates a single family *Tirisporellaceae* with four genera *Bacusphaeria*, *Thailandiomyces* and *Tirisporella* and the newly established genus *Pseudothailandiomyces* (Hyde et al. 2024b).

General description

The taxa are reported in sexual and asexual morphs. Jones et al. (2015) stated the asexual morph of the order as *Craspedodidymum* and phialophora-like. However, more details about the asexual structures are scarce.

Sexual morph: *Ascomata* partially immersed to superficial, globose to subglobose, black, coriaceous to carbonaceous, ostiolate, scattered to gregarious, with necks and periphysate. *Peridium* thick-walled. *Paraphyses* present. *Asci* cylindrical to clavate. *Ascospores* 2–3-seriate, 1–7-septate, fusoid, ellipsoidal to sub-cylindrical, straight to falcate to lunate, hyaline to brown with pale end cells, cell wall smooth or verrucose with or without appendages. Asexual morph: Craspedodidymum and Phialophoralike when present, or undetermined. (adapted from Jones et al. 2015) (Fig. 256).

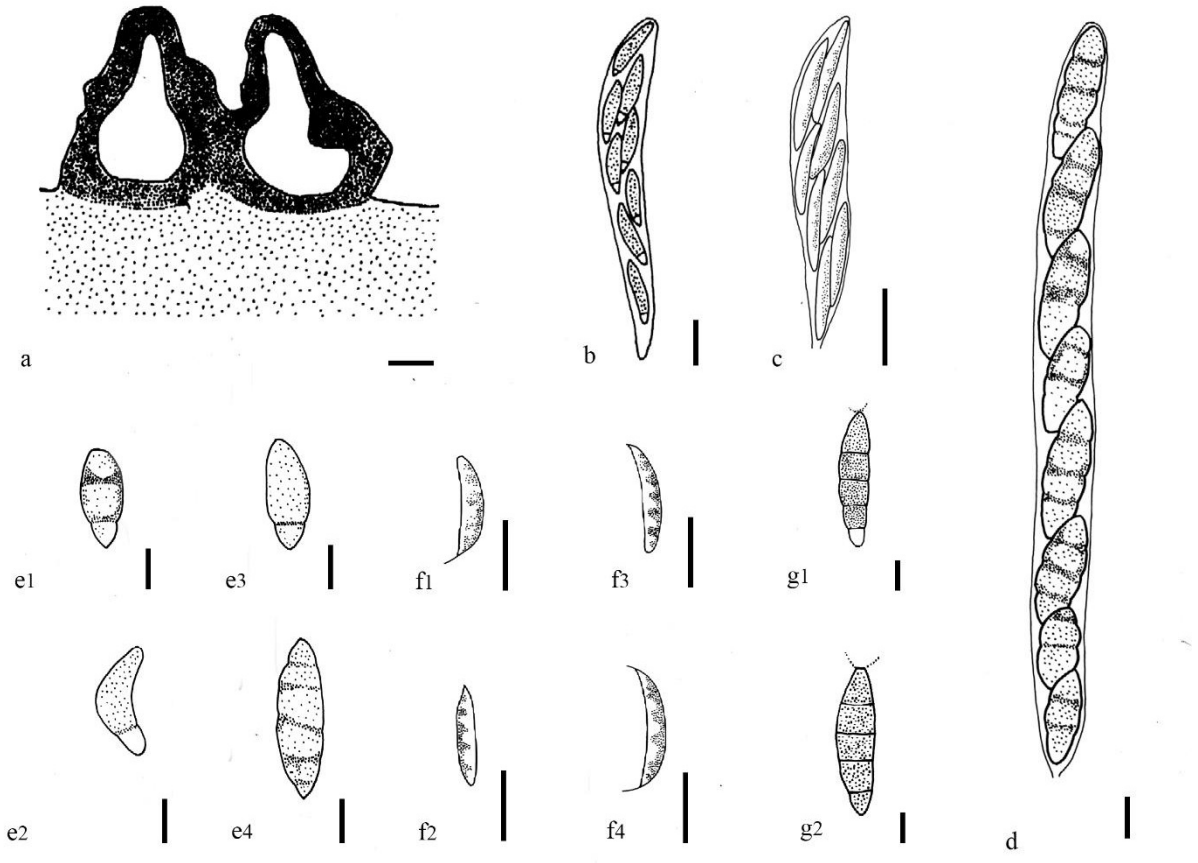


Figure 256 – Morphology of *Tirisporellales*. a Vertical section through *Tirisporella beccariana*. b–d Asci (b *T. beccariana*, c *Thailandiomyces bisetulosus*, d *Bacusphaeria nypae*). e1–g2 Ascospores (e1–e4 *Tirisporella beccariana*, f1–f3 *Thailandiomyces bisetulosus*, g1–g2. *T. beccariana*) (redrawn

from Pinruan et al. 2008, Suetrong et al. 2015a, Abdel-Wahab et al. 2017). Scale bars: a = 500 μm, b = 25 μm, c–d, e1–g2 = 10 μm.

Families included in *Tirisporellales*

Tirisporellaceae Suetrong, E.B.G. Jones & K.L. Pang

Evolution

The divergence time for *Tirisporellales* is estimated as 142 MYA (Hyde et al. 2020d).

Justification of order and problems

The order accommodates four genera and is supported by molecular data.

Significance

Ecological and economic roles

The taxa are reported in freshwater and marine habitats as saprobes (Jones et al. 2015, Suetrong et al. 2015a, b).

***Togniniales* Senan., Maharachch. & K.D. Hyde, Fungal Diversity 72: 220 (2015)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Diaporthomycetidae*

Introduction

Togniniales was introduced to accommodate *Togniniaceae* based on multi-loci phylogenetic analyses (Maharachchikumbura et al. 2015). *Togniniales* as a monotypic order, contains the family *Togniniaceae* and a single genus *Phaeoacremonium* (Index Fungorum 2025). *Togniniaceae* was described by Réblová et al. (2004) based on LSU and SSU sequence data of togninia-like fungus, which presently includes the type genus *Phaeoacremonium*. *Phaeoacremonium* was introduced by Crous et al. (1996). *Togniniales* comprises a single family *Togniniaceae,* which was erected based on phylogenetic analyses, and its similarity to some members of *Calosphaeriaceae* in having perithecial ascomata and clavate, tiny asci with hyaline ascogenous hyphae and cylindrical to allantoid ascospores (Maharachchikumbura et al. 2015, Hyde et al. 2020d). This family is a well-established monophyletic group comprising species with a global distribution and is commonly isolated from rootstocks, stems and branches of diseased woody hosts, and also humans with phaeohyphomycosis (Mostert et al. 2006, Gramaje et al. 2009, Réblová et al. 2015b).

History

Togniniaceae has been referred to as *Calosphaeriales* (Mostert et al. 2003) and *Diaporthales* (Mostert et al. 2006). Maharachchikumbura et al. (2015) accommodated *Togniniaceae* in the new order *Togniniales* based on phylogenetic and morphological distinctiveness. *Togniniaceae* was proposed to accommodate *Togninia* with its *Phaeoacremonium* asexual morphs (Réblová et al. 2004). *Togninia* was introduced by Berlese (1900) with *T. minima* as the type species, and *Togninia* has historically been classified in the *Calosphaeriales* (Barr 1983b, Mostert et al. 2003). Hausner (1992) commented that the asexual morph of *Togninia* has characteristics of *Phialophora* and *Acremonium*, but also does not fit the descriptions of these two genera. Therefore, *Phaeoacremonium* was known to be the asexual morph of *Togninia*.

Togniniaceae comprised both sexual (*Conidiotheca* and *Togninia*) and asexual genera (*Phaeoacremonium*) (Réblová & Mostert 2007). *Conidiotheca* was introduced in *Togniniaceae* by Réblová & Mostert (2007) with *C. tympanoides* as the type species. Huang et al. (2021b) re-examined the type and found that *Conidiotheca* is similar to *Jattaea* (*Calosphaeriaceae*, *Diaporthomycetidae*) and *Pleonectria* (*Nectriaceae*, *Hypocreomycetidae*), so they excluded *Conidiotheca* from *Togniniaceae* and accommodated it in *Sordariomycetes* genera *incertae sedis*. The phylogenetic analysis of the combined LSU and SSU rRNA loci showed that *Togninia* formed a unique cluster

within *Diaporthales* (Réblová et al. 2004). *Diaporthales* and *Calosphaeriales* also appeared to be two of the more closely related groups among the perithecial ascomycetes, indicating that they share very recent common ancestry (Réblová et al. 2004). Two new families were also erected, namely the *Pleurostomataceae* (*Calosphaeriales*), and *Togniniaceae* (*Diaporthales*) (Mostert et al. 2006). Later, *Togniniaceae* formed a distinct clade basal to *Diaporthales* in the subclass *Diaporthomycetidae* and was sister to *Diaporthales* and *Calosphaeriales*. Hence, Maharachchikumbura et al. (2015) excluded *Togniniaceae* from *Diaporthales* and introduced a new order *Togniniales*. Multi-gene analyses showed that *Togniniales* is a distinct order in the subclass *Diaporthomycetidae* (Maharachchikumbura et al. 2015, Réblová et al. 2015b).

General description

Togniniales include both sexual and asexual morphs (Maharachchikumbura et al. 2015). *Phaeoacremonium* is the only genus in *Togniniales*, and its unique morphological characteristics are the key points distinguishing it from closely related genera in the phylogenetic tree (Réblová et al. 2004). *Phaeoacremonium* has long-beaked perithecia of ascomata, octosporous, and basally rounded asci, with ellipsoid to suballantoid to oblong ascospores (Réblová et al. 2004). The asexual morph is reported as mostly pigmented conidiophores, particularly the basal cells, three different types of phialides (Type I, II, and III), with narrow collarette, hyaline, and allantoid conidia (Gams 1996, Mostert et al. 2006, Maharachchikumbura et al. 2015). Among the species of *Phaeoacremonium*, the morphological distinction is complicated by a relatively low degree of variability expressed in the characteristics of conidia, phialides, and conidiophores (Réblová et al. 2015b). The sexual morphs are morphologically similar and the sizes of their asci and ascospores frequently overlap (Réblová et al. 2015b). Therefore, the key morphological features are based primarily on culture characteristics such as growth, colony color, and optimum growth temperature, and are sometimes accompanied by morphological traits (Mostert et al. 2006, Réblová et al. 2015b).

Sexual morph: *Ascomata* lacking stromatic tissues, perithecial, superficial to immersed, astromatic, globose to subglobose, dark, opaque, with 1–3 necks, neck straight or flexuous. *Perithecial wall* fragile to leathery, comprising two layers, the outer layer of thin-walled, brown, pseudoparenchymatous cells of *textura prismatica* to *textura angularis*, the inner layer of non-pigmented flattened cells. *Paraphyses* abundant, broadly cellular, slightly constricted at the septa, branching, slightly tapering apically. *Asci* 8 or poly-sporous, unitunicate, clavate, with sessile bases, occurring on hyaline and branched ascogenous hyphae. *Ascospores* hyaline and unicellular, aseptate, allantoid to suballantoid to ellipsoid. Asexual morph: *Conidiophores* long or short, branched or unbranched, with phialidic conidiogenesis (Normally three types of phialide). *Conidia* hyaline, and aseptate (adapted from Réblová et al. 2004, Maharachchikumbura et al. 2015, Hyde et al. 2020d) (Figs. 257, 258, 259, 260, 261, 262).

Families included in *Togniniales*

Togniniaceae Réblová, L. Mostert, W. Gams & Cro

Evolution

The stem age of *Togniniales* reported as approximately 154 MYA (Chen et al. 2023b).

Justification of the order and problems

The key to *Phaeoacremonium* species published by Mostert et al. (2006) is based primarily on culture characteristics such as growth, colony color, and optimum growth temperature, and are sometimes accompanied by morphological traits. Although the distribution of morphological characteristics of conidia and types I, II, and III phialides are random in the three major clades recovered in *Phaeoacremonium* and cannot be used for their delimitation. Réblová et al. (2015b) showed that these three phylogenetic groups can be characterized by the RNA structural level, distinct topologies of the predicted 2D models of ITS1, ascospore shape and partly ecology and known pathogenicity to humans.

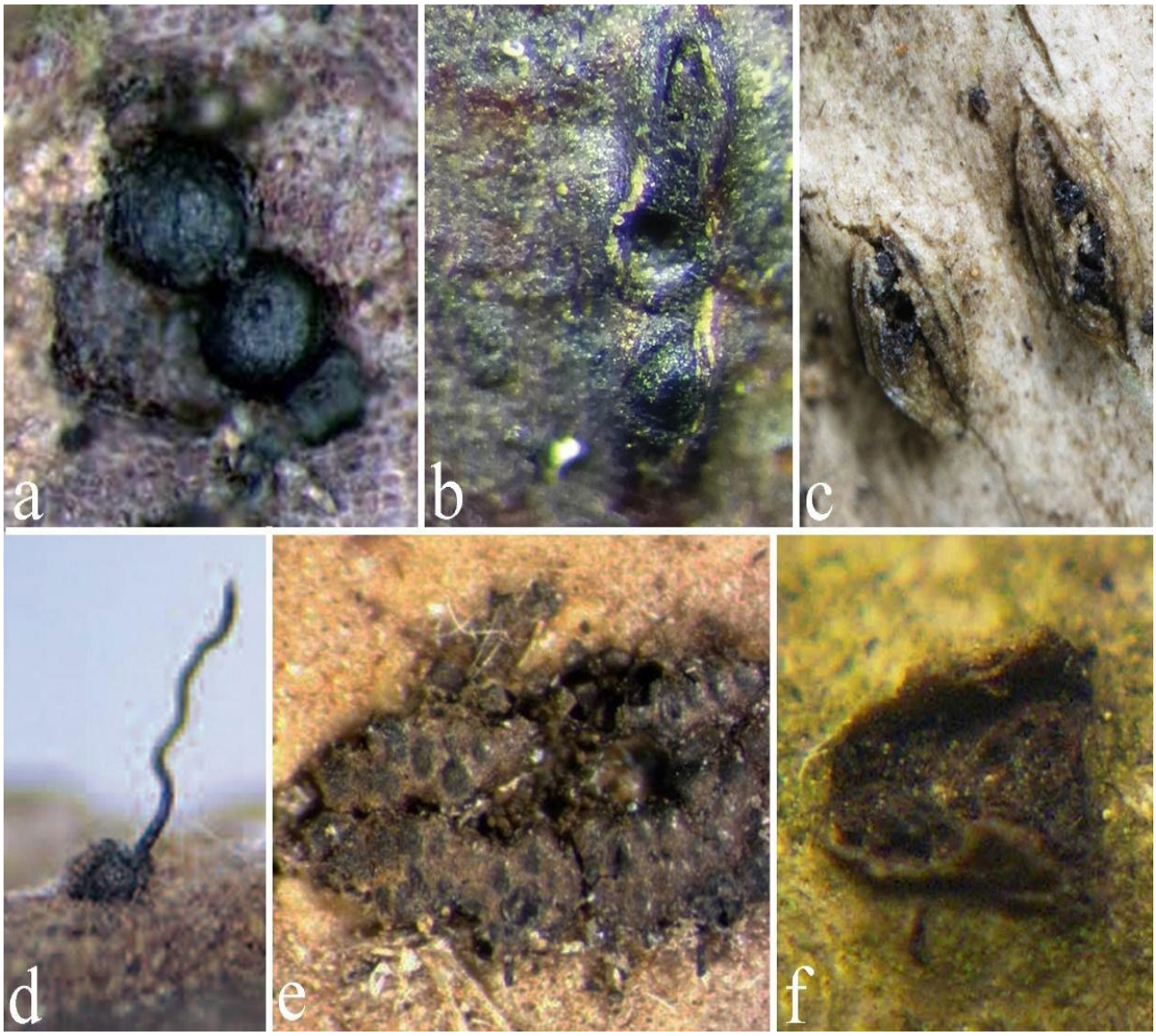


Figure 257 – Fruiting body morphologies of *Togniniales*. a *Phaeoacremonium thailandense*. b *P. croatiense*. c *P. fusiformostromum*. d *P. ovale*. e *P. inconspicuum*. f *P. camporesii*. (Photos were obtained from Huang et al. 2018, Hyde et al. 2020d, Calabon et al. 2021a, Shang et al. 2021, Phukhamsakda et al. 2022).

The sexual genus *Togninia* was experimentally linked to *Phaeoacremonium* with molecular evidence (Réblová 2011). Therefore, *Togninia* was synonymized to *Phaeoacremonium* by Gramaje et al. (2015) as the latter has the most species, and *Phaeoacremonium* is widely used by mycologists, and some *Togninia* species already have names in *Phaeoacremonium*. The molecular identification of *Phaeoacremonium* species has been facilitated by Restriction Fragment Length Polymorphism (RFLP) of the ITS region, PCR-RFLP markers from the ITS and the β-TUB gene, ITS barcode sequences, ITS species-specific primers, and multiple nuclear loci such as calmodulin, ACT and TUB2 (Groenewald et al. 2001, Mostert et al. 2006, Damm et al. 2008b, Gramaje et al. 2009, Réblová et al. 2015b).

Although the ITS region has been used in *Phaeoacremonium* phylogenies (Groenewald et al. 2001, Úrbez-Torres et al. 2014), it has been proven variable in distinguishing several *Phaeoacremonium* species (Groenewald et al. 2001). An emerging problem in *Phaeoacremonium* species-level taxonomy is the lack of distinction between some species using ACT-TUB2 phylogenies (Spies et al. 2018).

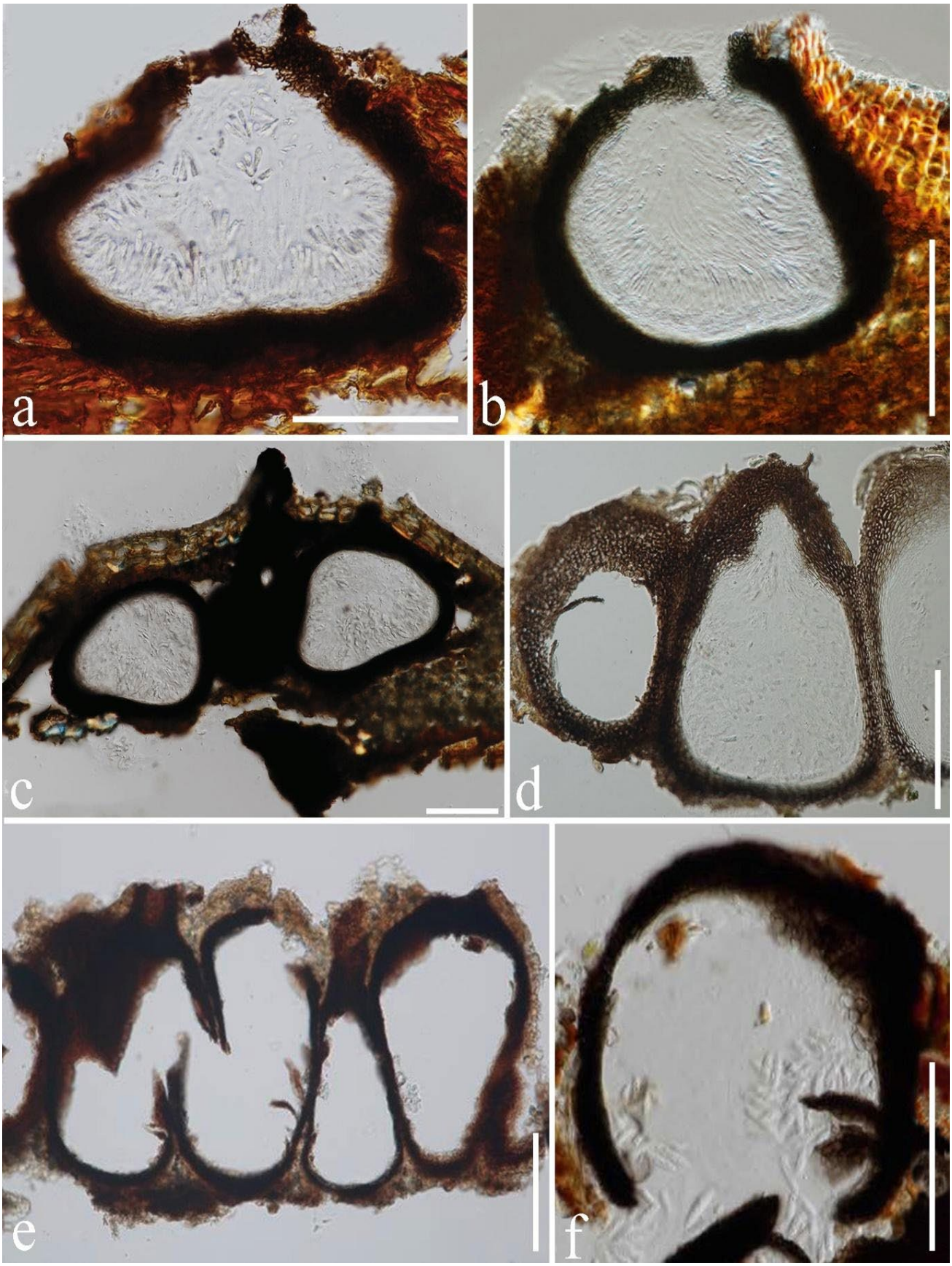


Figure 258 – Ascomata morphologies of *Togniniales.* a *Phaeoacremonium croatiense*. b *P. ovale*. c *P. fusiformostromum*. d *P. camporesii*. e *P. inconspicuum*. f *P. thailandense* (Photos were obtained from Huang et al. 2018, Hyde et al. 2020d, Calabon et al. 2021a, Shang et al. 2021, Phukhamsakda et al. 2022). Scale bars: a–f = 100 µm.

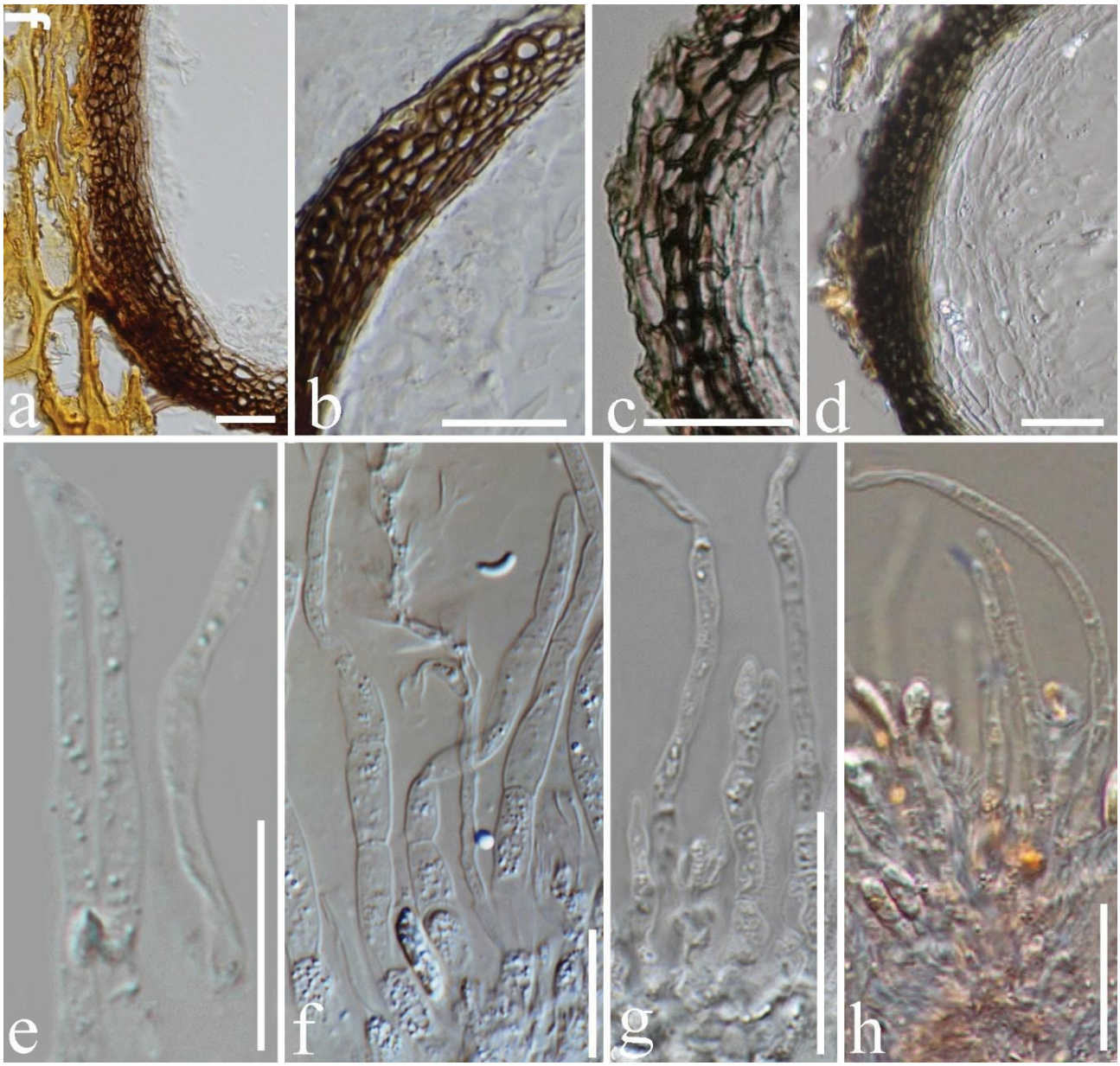


Figure 259 – Peridium and paraphyses morphologies of *Togniniales*. a, e *Phaeoacremonium croatiense*. b, f *P. fusiformostromum*. c, g *P. camporesii*. d, h *P. ovale* (Photos were adapted from Huang et al. 2018, Hyde et al. 2020d, Calabon et al. 2021a, Shang et al. 2021, Phukhamsakda et al. 2022). Scale bars: a–h = 20 µm.

Significance

Ecological and economic roles

Species of *Togniniales* have a worldwide distribution and are well-known pathogens of plants and animals (Kredics et al. 2011, Huang et al. 2018). They can be saprobic, parasitic, or hyperparasitic and play important roles in agriculture, forestry, and medicine (Mostert et al. 2006, Hyde et al. 2020d). *Phaeoacremonium* species have been recorded on monocotyledonous and dicotyledonous hosts (Réblová et al. 2004, Verkley et al. 2014). Many species of *Phaeoacremonium* cause trunk diseases on many plants (e.g., apricot, cherry, olive, poplar, peach, willow, and trees), resulting in severe and widespread tree decline and mortality (Hashemi & Mohammadi 2016, Kazemzadeh et al. 2017, Huang et al. 2018, Hyde et al. 2020d).

Phaeoacremonium minimum is a pathogenic species associated with Petri disease and Esca symptoms in young grapevines worldwide (Halleen et al. 2003, Edwards & Pascoe 2004, Essakhi et al. 2008, Gramaje et al. 2009). *Phaeoacremonium minimum* was also reported as a pathogen causing

subcutaneous lesions on human fingers (Choi et al. 2011, Phukhamsakda et al. 2022). Rooney-Latham et al. (2004, 2005a, b) reported that, in the presence of water, spores in some *Phaeoacremonium* species are forcibly discharged from perithecia through the long neck and exit the ostiole to be dispersed by wind, rain, insects, animals, or humans to colonize other substrates as opportunistic pathogens (Huang et al. 2018, Phukhamsakda et al. 2022).

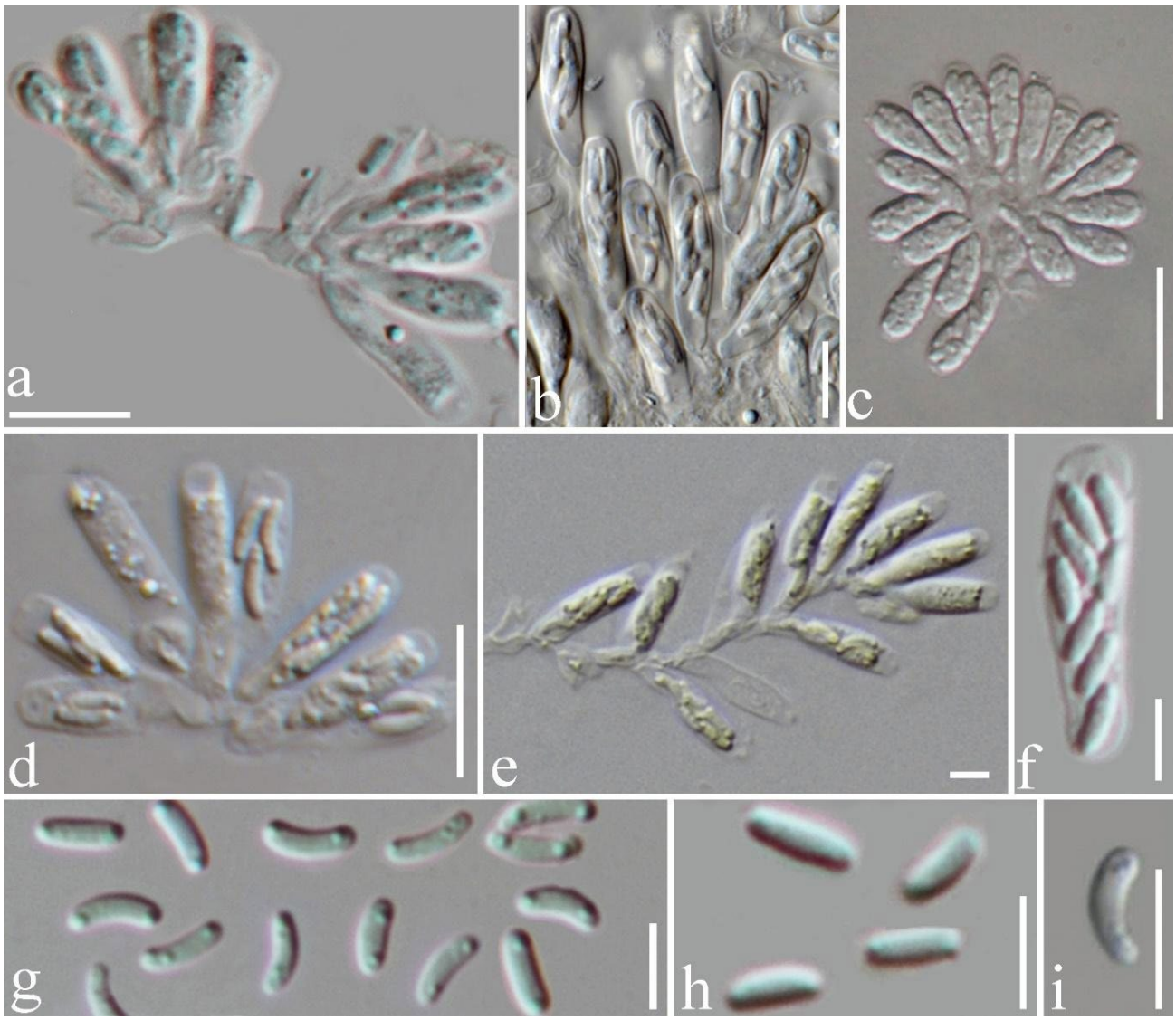


Figure 260 – Asci and ascospore morphologies of *Togniniales*. a, f, h *Phaeoacremonium croatiense*. b, i *P. thailandense*. c *P. ovale*. d *P. camporesii*. e, g *P. fusiformostromum* (Photos were adapted from Huang et al. 2018, Hyde et al. 2020d, Calabon et al. 2021a, Shang et al. 2021, Phukhamsakda et al. 2022). Scale bars: a–e = 10 µm, f–i = 5 µm.

Chemical diversity

Novel bioactive compounds from *Phaeoacremonium* species have been investigated. Lactone derivatives can be produced by *Phaeoacremonium* sp., an endophytic fungus isolated from the leaves of *Senna spectabilis* (Silva et al. 2017). Compounds with antifungal bioactivity against *Aspergillus flavus* and *Fusarium verticillioides* (Reátegui et al. 2006), lactone derivatives with activity against the phytopathogenic fungi (Silva et al. 2017), naphthalenone which is involved in the symptom expression of Esca-effected grapevines (Evidente et al. 2000, Abou-Mansour et al. 2004) and the phytotoxin p-hydoxybenzaldehyde (Tabacchi et al. 2000) have been reported from *Phaeoacremonium* species.

Other relevant data and future recommendations

Phaeoacremonium species were reported as having high diversity worldwide, but their morphology is very similar. Spies et al. (2018) confirmed that climatological factors may not directly explain the high diversity of *Phaeoacremonium* species in some countries, and *Phaeoacremonium* species have broad host ranges and lack host-specificity. Many *Phaeoacremonium* species remain to be discovered when samples from additional hosts and regions are analyzed. Care is needed to prevent misidentifications and the introduction of vague species boundaries as the number of species in this genus increases. In light of the shortcomings of the ACT-TUB2 phylogeny highlighted above, identifying additional phylogenetic markers or techniques to improve the phylogenetic resolution of species should be a priority.

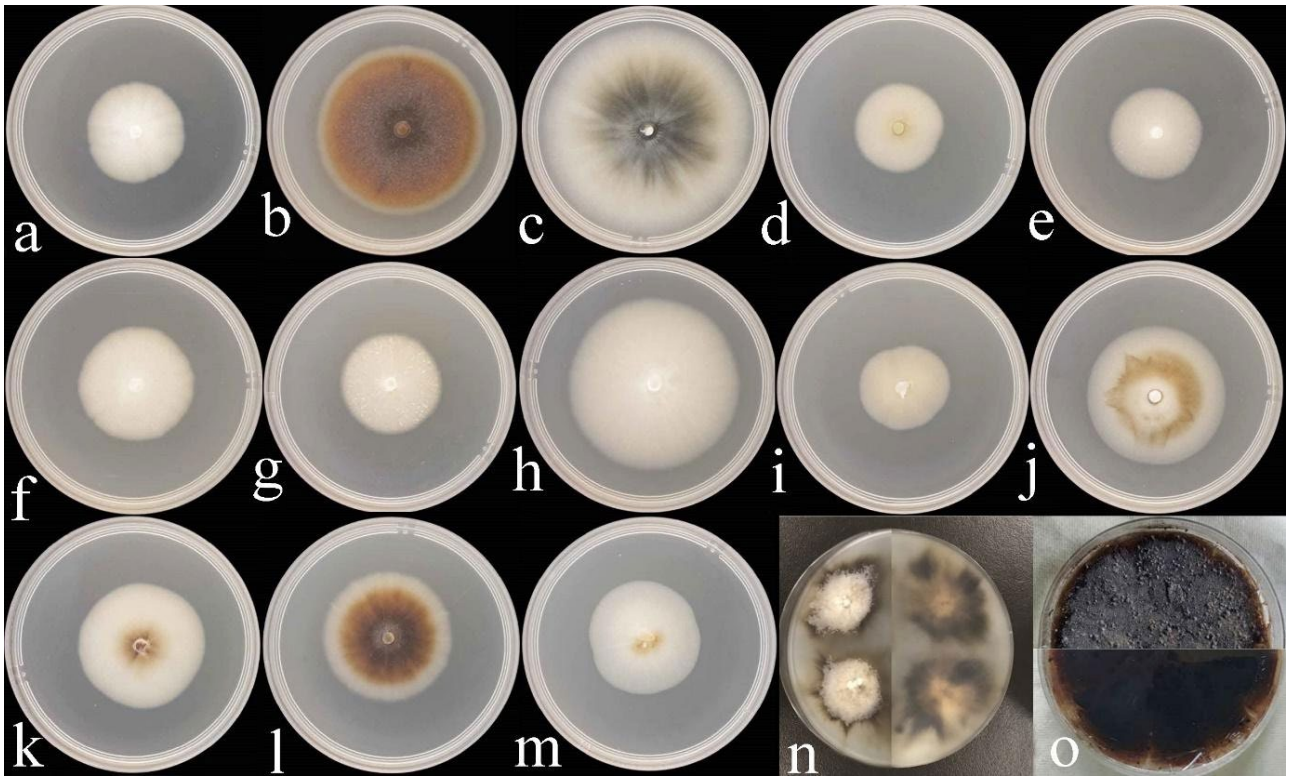


Figure 261 – Colony morphologies (grow on PDA) of *Togniniales*. a *Phaeoacremonium album*. b *P. aureum*. c *P. bibendum*. d *P. gamsii*. e *P. geminum*. f *P. junior*. g *P. longicollarum*. h *P. meliae*. i *P. oleae*. j *P. paululum*. k *P. proliferatum*. l *P. rosicola*. m *P. spadicum*. n *P. ovale*. o *P. chinensis*. (Photos were obtained from Spies et al. 2018, Huang et al. 2018, Senanayake et al. 2023).

Torpedosporales **E.B.G. Jones, Abdel-Wahab & K.L. Pang Fungal Diversity 73(1): 42 (2015)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Hypocreomycetidae*

Introduction

Torpedosporales (*Hypocreomycetidae*, *Sordariomycetes*) is a marine order and its members are saprobes that colonize plant remains in the intertidal zone, e.g., drift and intertidal wood; submerged bark, leaves, roots and wood of mangroves trees; seagrasses and algae. Sakayaroj et al. (2005a), in a study based on the combined phylogenetic analyses of SSU and LSU rDNA sequences, the genera *Swampomyces* and *Torpedospora* formed a new lineage of marine ascomycetes within the subclass *Hypocreomycetidae*, *Sordariomycetes*. Later, Schoch et al. (2007) named that lineage TBM clade (*Torpedospora*/*Bertia*/*Melanospora*). Jones et al. (2014) studied the molecular phylogenetic relationships of the genera *Etheirophora*, *Juncigena*, *Swampomyces*, and *Torpedospora*, along with *Chaetosphaeria chaetosa* and the terrestrial asexual genus *Falcocladium*. The studied taxa formed

four well-supported subclades: 1. *Juncigena* subclade, 2. *Etheirophora* and *Swampomyces sensu stricto* subclade, 3. *Falcocladium* subclade, and, 4. *Torpedospora* subclade. They introduced four new families to accommodate these genera: *Juncigenaceae*, *Etheirophoraceae*, *Falcocladiaceae* and *Torpedosporaceae*, respectively.

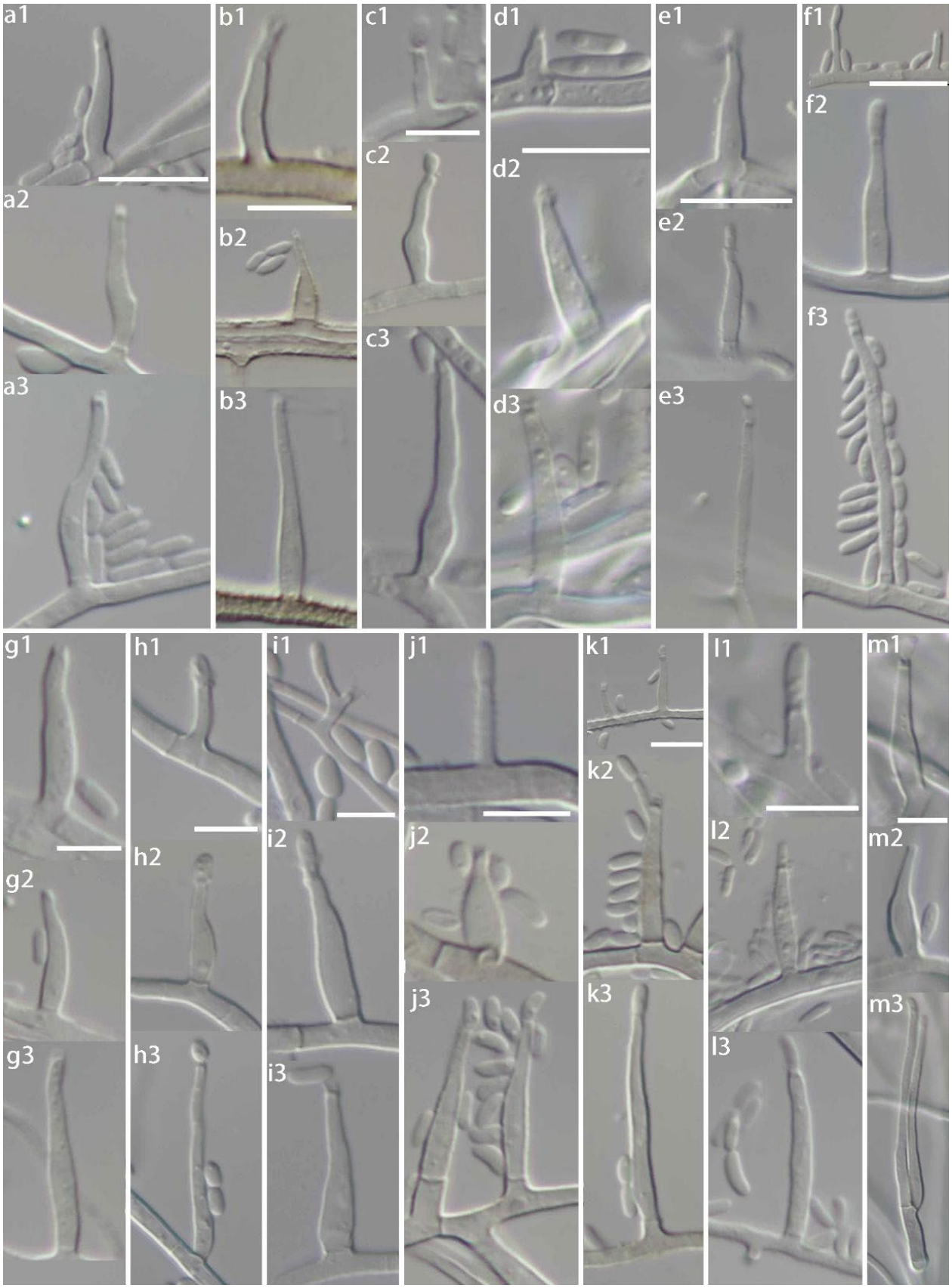


Figure 262 – Different types of phialides and conidia morphologies of *Togniniales*. a1–a3 *Phaeoacremonium album*. b1–b3 *P. aureum*. c1–c3 *P. bibendum*. d1–d3 *P. gamsii*. e1–e3 *P. geminum*. f1–f3 *P. junior*. g1–g3 *P. longicollarum*. h1–h3 *P. meliae*. i1–i3 *P. oleae*. j1–j3 *P. paululum*. k1–k3 *P. proliferatum*. l1–l3 *P. rosicola*. m1–m3 *P. spadicum*. Scale bars: a1–a3, b1–b3, d1–d3, e1–e3, f1–f3, k1–k3, l1–l3 = 10 µm, c1–c3, g1–g3, h1–h3, i1–i3, j1–j3, m1–m3 = 5 µm. (Photos were adapted from Spies et al. 2018, Huang et al. 2018, Senanayake et al. 2023).

Jones et al. (2015) based on the combined phylogenetic analyses of SSU and LSU rDNA sequences introduced the order *Torpedosporales* to accommodate the three families: *Etheirophoraceae*, *Juncigenaceae* and *Torpedosporaceae* that formed a highly supported clade within *Hypocreomycetidae*. *Torpedosporales* formed a sister clade to the orders *Falcocladiales*, *Coronophorales* and *Melanosporales* with high support. The order currently comprises three families, nine genera and 19 species (Hyde et al. 2024b).

The family *Etheirophoraceae* includes the two genera: *Etheirophora* and *Swampomyces* and five species. Members of the family have clypeate, immersed, coriaceous, light colored ascomata with periphysate ostiolar canals. Paraphyses are persistent, numerous, unbranched, narrow, embedded in gel, attached to the top and bottom of the ascomatal venter. Asci are unitunicate, cylindrical to oblong, thin-walled with an apical thickening, persistent. Ascospores are 1-septate, ellipsoidal, with or without appendages. Ascospore appendages when present are bristle-like at one or both ends. There are no reported asexual stages for the species belong to the family (Kohlmeyer & Kohlmeyer 1965, Kohlmeyer & Volkmann-Kohlmeyer 1987b, 1989, Hyde & Nakagiri 1992, Kohlmeyer et al. 1997, Eriksson & Hawksworth 1998, Abdel-Wahab et al. 2001, Eriksson 2006).

Juncigenaceae are represented by five genera: *Elbamycella*, *Fulvocentrum*, *Juncigena*, *Khaleijomyces* and *Marinokulati*, and nine species (Kohlmeyer 1963, Jones et al. 1983b, Kohlmeyer et al. 1997, Abdel-Wahab et al. 2010, 2018, 2019, Jones et al. 2014, Poli et al. 2019, Boonmee et al. 2021). Fungi belong to the family are characterized by small-sized, coriaceous, immersed to superficial ascomata with apricot colored wall and contents. The ostiolar canal is periphysate. Paraphyses are persistent, numerous, unbranched, narrow, embedded in gel, attached to the top and bottom of the ascomatal cavity. Asci are unitunicate, persistent to evanescent, cylindrical, cymbiform, fusiform to clavate, with or without an apical apparatus. Ascospores are ellipsoidal, fusiform to clavate, 3-septate, hyaline to pigmented, with or without sheath, smooth- to rough-walled. The asexual stage are helicoid conidia (Kohlmeyer et al. 1997, Abdel-Wahab et al. 2010).

Torpedosporaceae includes a monotypic genus *Torpedospora* and five species. *Torpedospora* is characterized by immersed or superficial ascomata, hyaline to black, membranous to subcarbonaceous, with periphysate ostiolar canal. Paraphyses are persistent, embedded in gel, attached to the top and the bottom of the ascomatal venter or early deliquescing. Asci are fusiform to broadly clavate or subglobose, thin-walled with or without apical thickening, early deliquescing or persistent. Ascospores are 3-septate, hyaline to apricot in color, cylindrical, ellipsoidal, fusiform, or torpedo-shaped, with or without appendages at one or both ends. The asexual stage when present are irregularly coiled, form a mass of cells and appear muriform, light-brown with basal hyaline cell (Meyers 1957, Kohlmeyer & Kohlmeyer 1979, Abdel-Wahab et al. 2010, 2022, Jones et al. 2014).

History

The first genus to be described under *Torpedosporales* is the type genus *Torpedospora* by Meyers (1957) to accommodate *T. radiata* that was described from yellow pine panels submersed in seawater in Biscayne Bay, Florida, the USA. Three other species were described from intertidal wood namely: *Torpedospora ambispinosa*, *T. mangrovei* and *T. yanbuensis* (Kohlmeyer 1960, Abdel-Wahab et al. 2010, 2022). *Torpedospora mangrovei* is known by its asexual stage only and it was transferred to *Torpedospora* based on its phylogenetic affinities with the genus (Abdel-Wahab et al. 2010, Réblová et al. 2016b). Kohlmeyer (1972) and Kohlmeyer & Kohlmeyer (1979) referred *Torpedospora* to the *Sphaeriales incertae sedis* and did not include it in *Halosphaeriaceae* because does not possess a central pseudoparenchymatous tissue within the centrum and it has paraphyses that grow irregularly inside the ascoma venter and between the asci. Molecular phylogenetics placed

Torpedospora in *Torpedosporaceae* (Sakayaroj et al. 2005a, Jones et al. 2014, Abdel-Wahab et al. 2022).

After the establishment of the order *Torpedosporales* in 2015, several new taxa were described that were affiliated to the order. *Khaleijomyces* was established by Abdel-Wahab et al. (2018) to accommodate *K. marinus* that was described from driftwood in the intertidal zone, Arabian Gulf, Saudi Arabia. A second species, *K. umikazeanus* was recently described from decaying driftwood in the intertidal zone, Yokosuka City, Umikaze Beach, Japan (Boonmee et al. 2021). *Khaleijomyces umikazeanus* has 3-septate, hyaline ascospores, while *K. marinus* has unicellular ascospores that become 1–4-septate and yellow–brown to brown in older specimens. *Elbamycella* is a monotypic genus that was recently described by Poli et al. (2019) to accommodate *E. rosea* that was isolated from the seagrass *Posidonia oceanica* and from the brown alga *Padina pavonica*, in the Mediterranean Sea, Italy. The genus is characterized by cylindrical ascospores with polar appendage and its substrate. Abdel-Wahab et al. (2019) described *Fulvocentrum rubrum* from decaying intertidal wood of *Avicennia marina* from Al-Leith Mangroves, Saudi Arabia. The species is characterized by asci with apical ring and 3–5-septate ascospores that are faint-apricot in color.

General description

All members that belong to *Torpedosporales* are described from marine habitats. Taxa grow as saprobes on decaying wood except *Elbamycella rosea* that was described from decaying seagrass and algae. Members of *Torpedosporales* are diverse in their morphology and have a few characters in common, i.e. apricot color of the ascospores or ascomata, 1 to 3-septate ascospores with (i.e. *Elbamycella*, *Etheirophora*, *Marinokulati* and *Torpedospora*), or without appendages (i.e. *Fulvocentrum*, *Juncigena*, *Khaleijomyces* and *Swampomyces*). Several genera and species of the orders have persistent, narrow, numerous paraphyses that are embedded in gel and attached to the top and bottom of the ascomata cavity. Asci are either widely ellipsoidal to subglobose and deliquesce before ascospore maturity (i.e. *Torpedospora radiata* and *T. ambispinosa*) or cylindrical to clavate and persistent (i.e. the remaining species). Ascospores are one-septate (i.e. *Swampomyces armeniacus* and the three species of *Etheirophora*), 1 to 4-septate (i.e. *Khaleijomyces marinus*) or 3-septate (i.e. the remaining species).

All 18 species of *Torpedosporales* are known by their sexual stage except *Juncigena fruticosae* and *Torpedospora mangrovei* that form helicoid conidia and their sexual stages are unknown (Abdel-Wahab et al. 2010, Réblová et al. 2016b). A third species that forms helicoid conidia is *Juncigena adarca* (Kohlmeyer et al. 1997).

Sexual morph: *Ascomata* perithecioid, immersed or superficial, subglobose, ostiolate, papillate, subcarbonaceous to coriaceous, brown. *Paraphyses* narrow, irregular, persistent or early deliquescing. *Asci* 8-spored, unitunicate, thin-walled, clavate to ellipsoidal, with or without apical apparatus, deliquescing early or persistent, short pedicellate. *Ascospores* cylindrical to ellipsoidal, 1–3-septate, hyaline or apricot in color, with appendages at one or both ends, with equatorial appendages, amorphous material or without appendages. Asexual morph: *Hyphae* septate, branched, hyaline. *Conidiophores* present or obsolete, cylindrical, clavate, septate or aseptate, acrogenous or laterally on the hyphae, hyaline to light-brown. *Conidiogensis* is holoblastic. *Conidia* irregularly helicoid, cells of the conidia are tightly joined and appear muriform, cells of the conidia are more or less of similar size and color, acrogenous, solitary, constricted at the septa, yellow-brown to brown in color. Conidial cells are up to 50 in number (Figs. 263, 264).

Families included in *Torpedosporales*

Etheirophoraceae Rungjindamai, Somrithipol & Suetrong
Juncigenaceae E.B.G. Jones, Abdel-Wahab & K.L. Pang
Torpedosporaceae E.B.G. Jones & K.L. Pang

Justification of order and problems

Torpedosporales represent a well-defined order of marine fungi and include the three families *Etheirophoraceae*, *Juncigenaceae* and *Torpedosporaceae* that form a highly supported clade within

Hypocreomycetidae. The *Torpedosporale*s forms a sister clade to the orders *Coronophorales*, *Falcocladiales*, and *Melanosporales* with high support (Jones et al. 2015, 2019).

Significance

Ecological and economic roles

Torpedosporales fungi are common in the coastal marine habitats both in the open ocean (e.g., *Torpedospora radiata* and *Khaleijomyces* species) and mangroves (e.g., species of *Swampomyces* and *Fulvocentrum*). They play an important role in lignocellulosic biomass breakdown. Species of *Swampomyces* and *Fulvocentrum* are the most common species in the Red Sea and the Arabian Gulf mangroves and it seems they are well-adapted to this harsh environment and play a key stone role in mangrove substrate turnover (Abdel-Wahab 2000, 2001, 2005, 2014, 2019, 2020).

Chemical diversity

There are no physiological studies that have been carried out on any member of *Torpedosporales* and this needs to be covered in the future.

Other relevant data and future recommendations

Members of *Torpedosporales* are very successful saprobic fungi in the marine fungi and play a vital role in organic materials turn over. Species of the genera *Fulvocentrum*, *Swampomyces* and *Torpedospora* are very common in the harsh environment of the Red Sea and the Arabian Gulf mangroves that are characterized by high salinities and temperatures with rare or no input of freshwater and no surrounding vegetation. Species of the three genera are characterized by ascomatal contents that are apricot to bright-colored in mass and this might be a kind or carotenoid pigments that help fungi to tolerate the harsh environment and this needs further investigation. Several new taxa have recently been described that belong to *Torpedosporales* from both tropical and temperate

***Tracyllalales* Crous Persoonia 40: 365 (2018)**

Subphylum *: Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Incertae sedis*

Introduction

Tracyllalales was described by Crous et al. (2018b) to include a single family, *Tracyllaceae* and a genus, *Tracylla*.

History

Tracylla accommodates three species namely *T. spartinae*, *T. aristata*, and *T. eucalypti* and they display differences in their conidial morphology, particularly in relation to the presence or absence of appendages. *Tracylla* was originally established as a subgenus by Saccardo (1895a), and was subsequently raised to a genus by Tassi (1904). The genus is characterized by the species *Tracylla spartinae*, which has been detected on *Spartina patens* along with several other grass species. Its range includes Brazil, Jamaica, Philippines, Sri Lanka, Thailand, and the United States (Nag Raj 1993). *Tracylla aristata* was reported from *Eucalyptus* leaf litter gathered in Australia (Cooke 1891). It was later recorded in New Zealand and South Africa (Crous & Van der Linde 1993) and growing on *Hakea dactyloides* (Nag Raj 1993). *Tracylla eucalypti* was found on the leaves of *Eucalyptus urophylla* in Colombia (Crous et al. 2018b). Intriguingly, *T. eucalypti*, despite its lack of conidial appendages, groups with *Tracylla aristata*. The latter was initially described from *Eucalyptus* leaf litter collected in Australia (Nag Raj 1993). Hernandez-Restrepo (2016), positioned *T. aristata* within the *Sordariomycetidae incertae sedis*, based on LSU and ITS sequence data. This classification followed the discovery of a new species of *Tracylla* from the leaves of the *Eucalyptus urophylla* (a member of the *Myrtaceae* family) in Colombia. Crous et al. (2018b) proposed the new order *Tracyllalales* based on combined phylogeny (ITS, LSU, SSU).

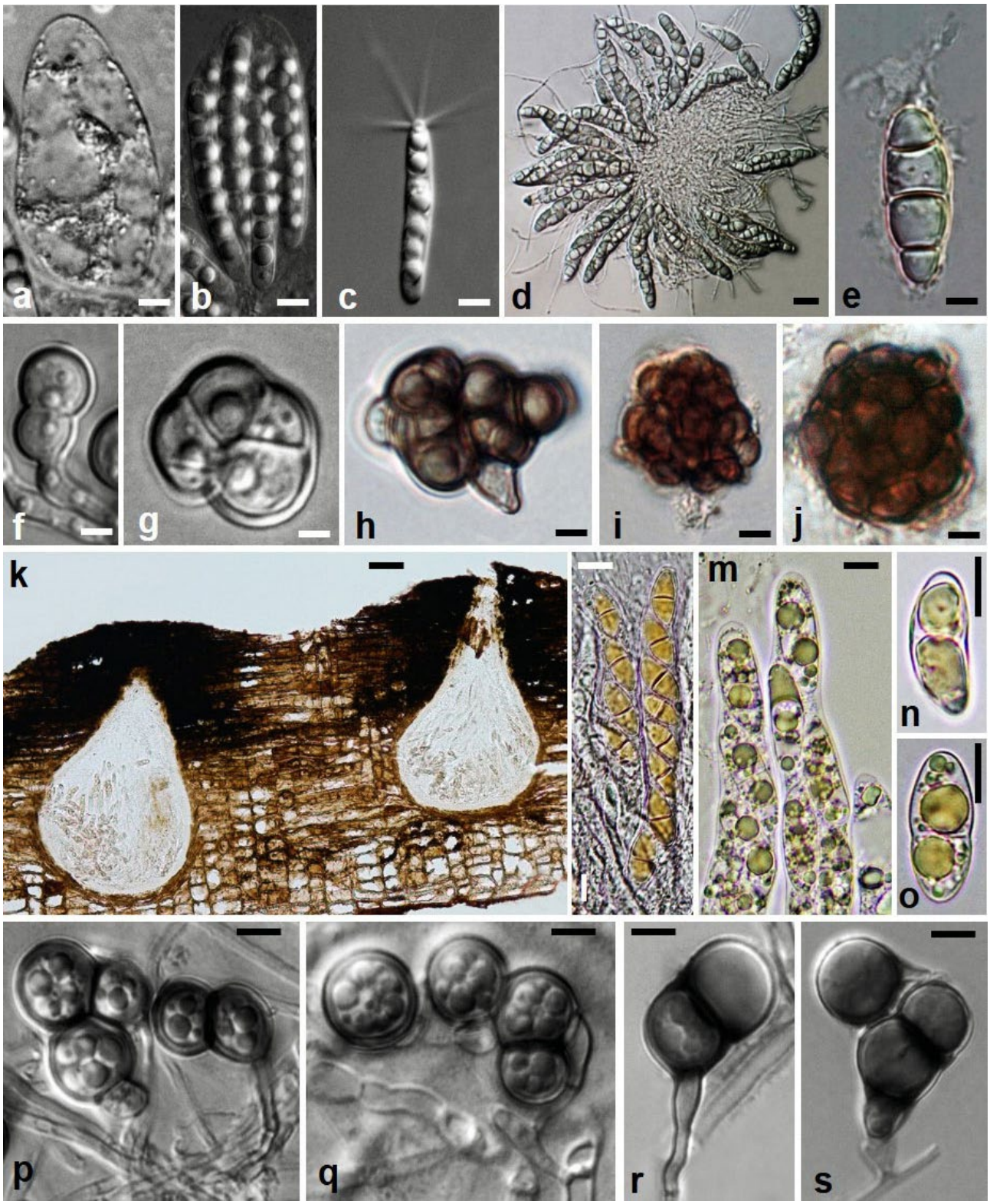


Figure 263 – Representatives of *Torpedosporales*. a–c *Torpedospora radiata*. a Immature ascus. b Mature ascus. c Ascospore with appendages. d–e *T. yanbuensis*. d Variously-shaped asci and paraphyses. e Ascospore with amorphous polar appendages. f–j *T. mangrovei*. Conidia at different stages of development. f–h Conidia from culture. i–j Conidia from natural wood. k–o *Swampomyces armeniacus*. k Vertical section through ascomata. l–m Variously-shaped asci and paraphyses. n–o Variously-shaped ascospores. p–s *Juncigena fruticosae*. Conidia at different stages of development. Scale bars: a–d, i–j, k–o = 5 µm, e–f = 100 µm, e–f = 10 µm, k = 100 µm, l–o = 10 µm, p–s = 5 µm.

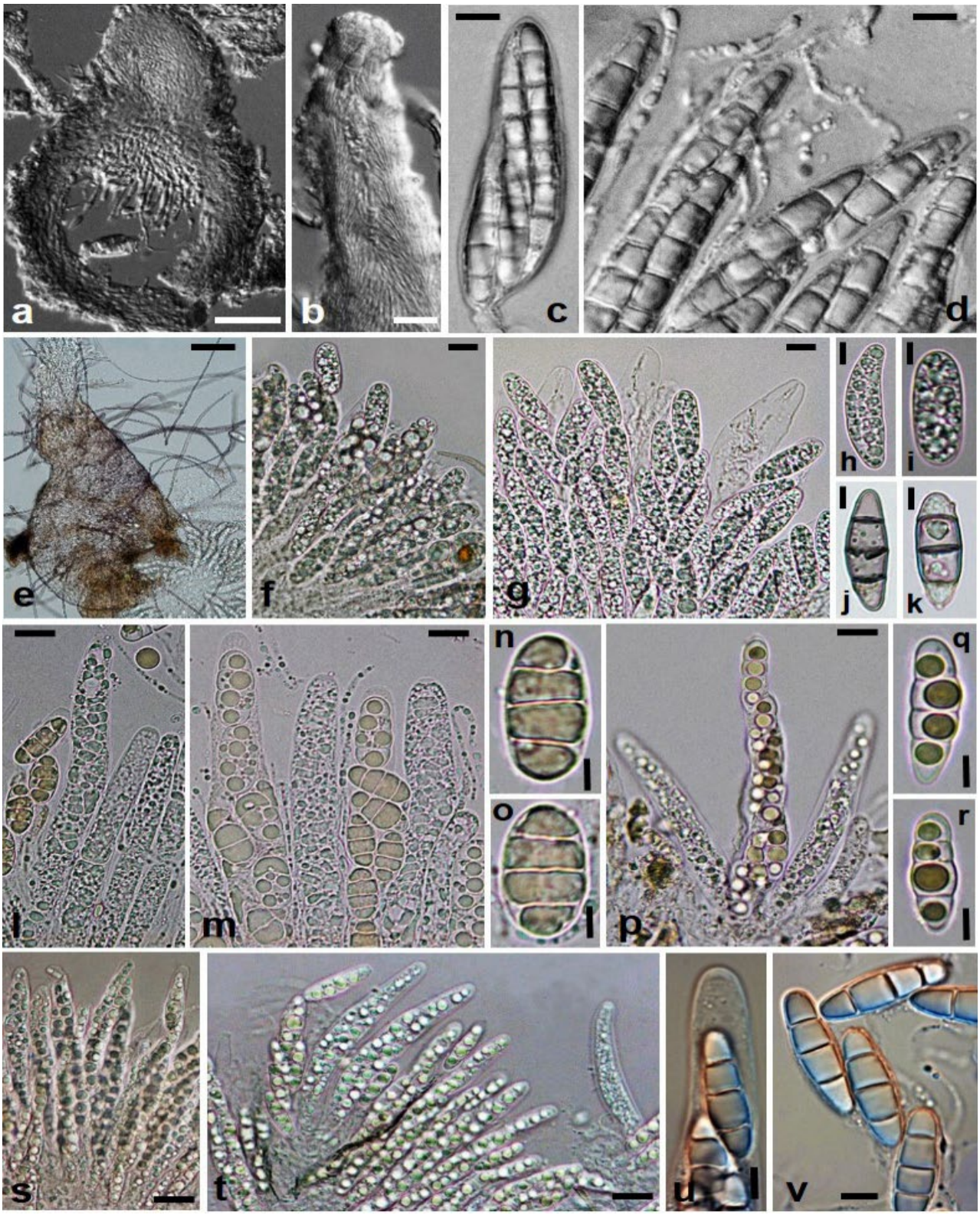


Figure 264 – Representatives of *Torpedosporales*. a–d *Khaleijomyces umikazeanus*. a Vertical section through ascoma. b Magnified part of the neck shows periphyses. c Mature ascus. d Ascal tips and paraphyses. e–k *Khaleijomyces marinus*. e Squash of an ascoma and asci mounted in seawater. f–g Variously-shaped asci. h–k Variously-shaped ascospores. l–o *Fulvocentrum aegyptiacum*. l–m Variously-shaped asci and paraphyses. n–o Variously-shaped ascospores. p–r *F. clavatisporum*. p Asci at different stages of maturity. q–r Variously-shaped ascospores. s–v *F. rubrum*. s–t Variously-shaped asci. u Magnified apical part of an ascus. v Variously-shaped ascospores and paraphyses. Scale bars: a, e = 50 μm, b–d, f–g, l–m, p, s–t = 10 μm, h–k, n–o, q–r, u–v = 5 μm.

habitats and this show that members of the orders are successful marine fungi colonizing dead organic materials in a wide range of habitats.

General description

Sexual morph: Undetermined. Asexual morph: *Pycnothyria* superficial on leaves, round, brown, with central column of cells; ostiole lacking, margin of catenate, darker brown cells. *Conidiophores* reduced to conidiogenous cells arising from a central columella, doliiform to ellipsoid, hyaline, smooth, with a single conidiogenous locus, phialidic. *Conidia* solitary hyaline, aseptate, smooth, guttulate, falcate to naviculate or ellipsoid, apex subobtusely rounded, base truncate; with or without unbranched polar appendages, not delimited by septa (Fig. 265).

Families included in *Tracyllalales*

Tracyllaceae Crous

Evolution

Crous et al. (2018b) found that the clades of *Tracyllalales* and *Chaetosphaeriales* were close. However, Hyde et al. (2020d) found low statistical support for this position. The divergence time for *Tracyllalales* has been estimated as 154 MYA (Hyde et al. 2020d).

Justification of order and problems

Tracyllalales presently includes two genera (*Neotracylla* and *Tracylla*) and are supported with morphological characteristics and molecular data.

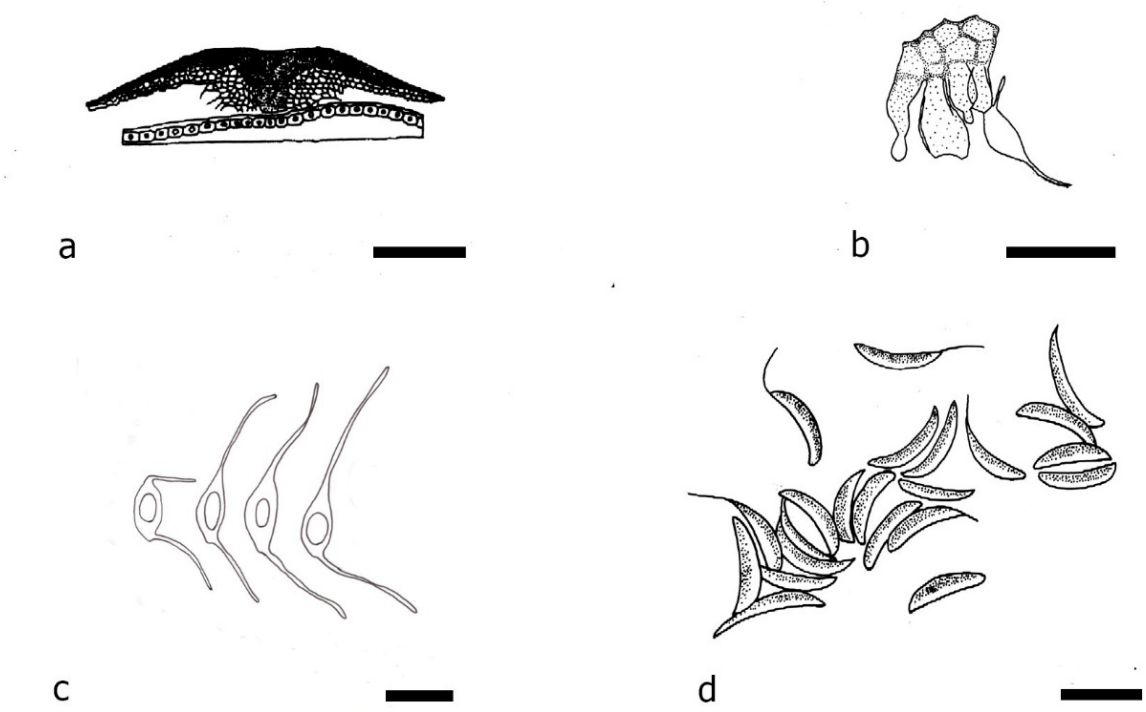


Figure 265 – Morphology of *Tracyllalales* (*Tracylla spartinae*). a Cross section of conidiomata. b Conidiogenous cells and conidia. c Conidia. d Conidia of *Tracylla aristata* (redrawn from Nag Raj 1993, drawn from Hernandez-Restrepo et al. 2016). Scale bars: a = 50 µm, b, c = 20 µm, d = 10 µm.

Significance

Ecological and economic roles

The taxa of *Tracyllaceae* can be found in various ecological roles, including as endophytes, saprobes, or pathogens on the leaves of both grasses and trees (Crous et al. 2018b). As endophytes, they establish symbiotic relationships with plants, residing harmlessly within their tissues and providing benefits including enhanced stress tolerance, improved nutrient uptake, and protection

against threats (Crous et al. 2018b). *Tracyllalales* can alternatively act as saprobes, playing an important role in decomposing organic matter (Crous & Van der Linde 1993). Understanding the ecological roles of *Tracyllalales* could have economic applications. In agriculture, specific strains can be utilized to improve crop health and productivity through their endophytic properties (https://www.sordariomycetes.org/tracyllalales-/tracyllaceae/tracylla/accessed July 29, 2023), leading to increased yields and reduced reliance on chemical inputs (Gutierrez et al. 2012, Rustamova et al. 2020).

***Vermiculariopsiellales* Hern.-Restr., J. Mena, Gené & Crous, Studies in Mycology 86: 91 (2017)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Sordariomycetidae*

Introduction

Vermiculariopsiellales was introduced by Hernández-Restrepo et al. (2017) to accommodate the newly introduced family *Vermiculariopsiellaceae* based on phylogenetic analysis. Currently, *Vermiculariopsiellales* includes a solitary family, *Vermiculariopsiellaceae*, with five genera, *Chloridiopsiella*, *Chloridiopsis*, *Tubulicolla*, *Stephanophorella*, *Vermiculariopsiella* and *Vermiculariopsis* (Hernández-Restrepo et al. 2017, Réblová et al. 2021a, 2021d, Réblová & Nekvindová 2023, Hyde et al. 2024b). The taxonomic assignment of *Vermiculariopsiellales* to the class *Sordariomycetes* was established by Hernández-Restrepo et al. (2017).

History

Vermiculariopsiella was introduced by Bender (1932) and Hernández-Restrepo et al. (2017) introduced a new order *Vermiculariopsiellales* and new family *Vermiculariopsiellaceae* for this genus based on phylogenetic analysis. *Vermiculariopsiella* was emended by Hernández-Restrepo et al. (2022) and only six species were accepted and the generic boundary was narrowed for species with setose sporodochial conidiomata with simple setae. *Stephanophorella*, a *Zanclospora*-like genus, was introduced by Réblová et al. (2021a) and placed within *Vermiculariopsiellales*. Réblová et al. (2021d) established a new genus *Tubulicolla* to accommodate *Dictyochaeta cylindrospora*, and this genus was placed within *Vermiculariopsiellales* based on multi-gene phylogenetic analysis. Réblová & Nekvindová (2023) introduced two genera, *Chloridiopsiella* and *Chloridiopsis* and included within *Vermiculariopsiellales*.

General description

Sexual morph: Undetermined. Asexual morph: hyphomycetous. *Conidiomata* sporodochial, setose. *Setae* branched or unbranched when present. *Conidiophores* macronematous, densely packed in a palisade. *Conidiogenous cells* monophialidic, discrete. *Conidia* grouped in dry masses, unicellular or septate. *Stroma* present or absent (adapted from Hernández-Restrepo et al. 2017) (Fig. 266).

Families included in *Vermiculariopsiellales*

Vermiculariopsiellaceae Hern.-Restr, J. Mena, Gené & Crous

Justification of order and problems

Morphologically, species within the order *Vermiculariopsiellales* exhibit considerable resemblance to those found in *Chloridium*, *Gyrothrix* and *Zanclospora* and other closely related genera, posing a challenge in their differentiation based solely on morphological characteristics.

Significance

Ecological and economic roles

Vermiculariopsiellales species primarily demonstrate saprobic behavior on plants. Functioning as decomposers and recyclers, species within *Vermiculariopsiellales* play a crucial role in nutrient cycling, contributing to ecological balance.

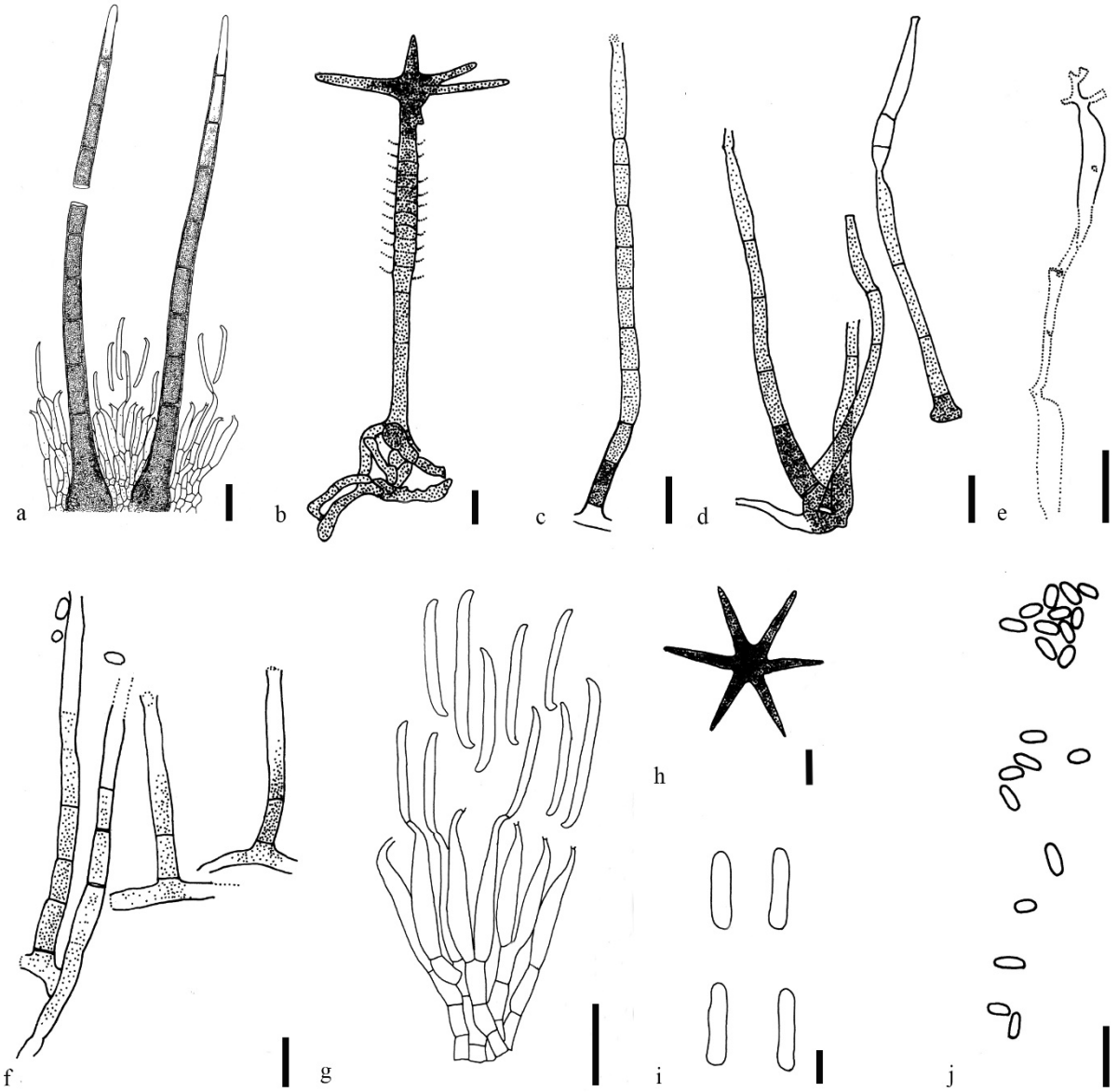


Figure 266 – Asexual morphology of *Vermiculariopsiellales*. a Conidiophores, conidiogenous cells and conidia (*Vermiculariopsiella immersa*). b–f Conidiophores (b *Stephanophorella stellata*, c *Chloridiopsiella preussii*, d *Chloridiopsis constrictospora*, e *Tubulicolla cylindrospora*, f *Chloridiopsiella preussii*). g Sporodochia with setae (*Vermiculariopsiella immersa*). h Branches arranged in a stellate fashion (*Stephanophorella stellata*). i, j Conidia (i *Chloridiopsis constrictospora*, j Conidia *Chloridiopsis syzygii*) (drawn from Réblová et al. 2021a, Réblová & Nekvindová 2023, Redrawn from Hyde et al. 2020d). Scale bars: a–j = 10 µm, b = 20 µm.

Chemical diversity

Comprehensive investigations into the chemical productions within *Vermiculariopsiellales* remains unexplored. This underscores the need for further research, especially in light of the growing number of reported species within this order.

Other relevant data and future recommendations

The history of *Vermiculariopsiella* serves as a compelling illustration of the enhanced precision in fungal taxonomy achieved through molecular data analysis (Hernández-Restrepo et al. 2017, 2022).

Xenodactylariales **D.F. Bao, K.D. Hyde & Z.L. Luo, Fungal Diversity 121: 71 (2023)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Incertae sedis*

Introduction

Xenodactylariales is a monophyletic order that accommodates a single family *Xenodactylariaceae*, a genus *Xenodactylaria* and a species *Xenodactylaria thailandica* (Bao et al. 2023).

History

Xenodactylariales was introduced to accommodate a monotypic family *Xenodactylariaceae* that was introduced by Crous et al. (2018a). The family was established to accommodate a single genus *Xenodactylaria* and a species *Xenodactylaria thailandica* that was isolated as an endophytic fungus from leaves of an unidentified vine in Thailand. The genus formed a close phylogenetic clade to *Purpureocillium* (*Ophiocordycipitaceae*) and *Simplicillium* (*Cordycipitaceae*) within *Hypocreales* when it was introduced but placed in *Myrmecridiales* in the subclass *Diaporthomycetidae* (Crous et al. 2018a).

However, the family formed a close clade to *Torpedosporales* and clustered within *Hypocreomycetidae* in the phylogenetic analyses conducted by Hyde et al. (2020d). Hyde et al. (2021a) revised the subclass *Diaporthomycetidae,* focusing on freshwater fungi and found that *Xenodactylariaceae* clustered outside of *Diaporthomycetidae* in the phylogenetic analyses and suggested excluding this family. Consequently, the family formed a distinct clade close to *Torpedosporales* within *Hypocreomycetidae* in the phylogenetic analyses conducted by Bao et al. (2023). Based on phylogenetic analyses, time divergence estimates and morphological evidence, a new order *Xenodactylariales* was introduced to accommodate *Xenodactylariaceae*.

General description

The family accommodate a single species *Xenodactylaria thailandica* which was only reported in its asexual morph. The species showed morphological similarity to *Dactylaria* as well as *Cylindrosympodium* but differed in having hyaline conidia that occur in short chains (Crous et al. 2018a).

Sexual morph: Not observed. Asexual morph: *Mycelium* consists of smooth, hyaline, branched, septate, hyphae. *Conidiophores* reduced to conidiogenous cells on hyphae, erect to fexuous, hyaline, smooth-walled, with one to several denticulate apical loci. *Conidia* occur in branched chains, hyaline, smooth- walled, subcylindrical, septate (adapted from Crous et al. 2018a) (Fig. 267).

Families included in *Xenodactylariales*

Xenodactylariaceae Crous

Evolution

The stem age for *Xenodactylariales* is reported as 211 MYA (Hyde et al 2021a).

Justification of order and problems

Xenodactylariales formed a close phylogenetic clade to *Torpedosporales*. However, the former has subcylindrical, hyaline, septate conidia that are in branched chains, whereas the latter has solitary and helicoid conidia. Further, members of *Torpedosporales,* such as *Juncigenaceae* have single,

brown, helicoid conidia and *Torpedosporaceae* has solitary, irregularly helicoid and muriform (Hyde et al. 2020d).

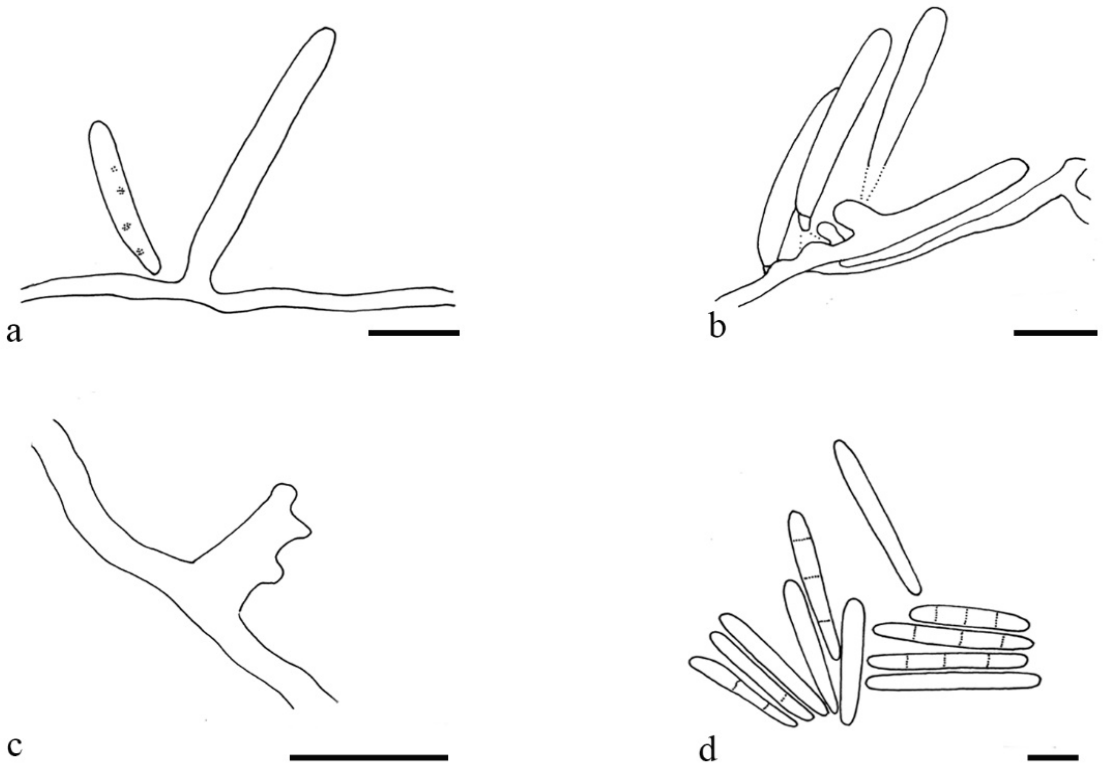


Figure 267 – Asexual morphology of *Xenodactylariales*. a–d Morphology of conidiogenous cells and conidia (*Xenodactylaria thailandica*) (drawn from Crous et al. 2018a). Scale bars: a–d = 10 µm.

Significance

Ecological and economic roles

The order is only reported from Thailand in leaves of an unidentified vine as an endophyte from terrestrial habitats (Crous et al. 2018a).

Chemical diversity

No relevant studies are available on the chemical diversity of *Xenodactylariales.*

Other relevant data and future recommendations

The order is established based on evolutionary and phylogenetic analyses conducted by Bao et al. (2023) without studying the holotype specimen which showed a close phylogenetic relationship *Torpedosporales*. Crous et al. (2018a) discussed the morphological similarities to *Dactylaria* which was previously placed in *Magnaporthales* and is presently accepted under *Helotiales incertae sedis* (Wijayawardene et al. 2022a). The ITS sequences showed high similarities to *Fusarium venenatum* and *F. sambucinum*. Thus, studying the holotype material with further new collections can provide a better taxonomic understanding of *Xenodactylariales* as well as closely related groups.

Xenospadicoidales **Hern.-Restr., J. Mena & Gene, Studies in Mycology 86: 91. (2017).**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Sordariomycetidae*

Introduction

Xenospadicoidales was established with the single family *Xenospadicoidaceae* to encompass two monotypic dematiaceous hyphomycete genera, *Xenospadicoides* and *Pseudodiplococcium*, based on partial LSU sequence data (Hernández-Restrepo et al. 2017). Currently, the order comprises six genera, *Calyptosphaeria*, *Lentomitella*, *Spadicoides* and *Torrentispora* (Réblová et al. 2018), *Gangliostilbe* (Lad et al. 2022) and *Neospadicoides* (Luo et al. 2019b). *Spadicoides,* including its synonyms *Xenospadicoides* and *Pseudodiplococcium*, serves as the type genus of the family. While *Lentomitella* and *Spadicoides* are holomorphic genera, the asexual morphs of *Calyptosphaeria* and *Torrentispora* have never been determined, and *Gangliostilbe* and *Neospadicoides* are known to reproduce only asexually. A noteworthy characteristic of this family is the variability in the mode of conidiogenesis, which includes tretic, holoblastic, holoblastic-denticulate, and sometimes holoblastic with a 'gangliar' mechanism. Members of *Xenospadicoidales* are commonly found in both terrestrial and freshwater environments, particularly on decaying wood, bark and other plant material, and are distributed across temperate, subtropical and tropical regions.

History

The taxonomic history of this order traces its origin to the discovery of *Helminthosporium binum* [as '*Helmisporium*'] by Corda (1854), collected on wood in the Czech Republic. The species was placed in *Massarinaceae*, *Pleosporales*. Later, Hughes (1958) introduced the genus *Spadicoides*, typified by *S. bina* [as '*binum*']. Shenoy et al. (2010) conducted a study involving two available strains of *Spadicoides*: *S. bina* (CBS 113708), which was positioned as a sister to *Cordana pauciseptata* within the *Cordanales*, and *Spadicoides atra* (CBS 489.77), identified as a sister to *Lentomitella* (Réblová 2006, Réblová et al. 2018). Regrettably, it appears that Shenoy et al. (2010) did not confirm the identity of the *Spadicoides bina* strain. Hernández-Restrepo et al. (2017) incorporated these findings and separated *S. atra* from *Spadicoides*, placing it in the newly introduced genus *Xenospadicoides*, with *Spadicoides atra* serving as a designated type species of the genus, while proposing the new order *Xenospadicoidales*. Réblová et al. (2018) conducted a revision of the initial material from which the culture CBS 113708 of *Spadicoides bina* was derived, as well as the dried culture, leading to the discovery that the fungus is actually *C. pauciseptata*. Phylogenetic analyses, which included the recently obtained strain of *S. bina* (CBS 137794), along with *X. atra* (CBS 489.77), confirmed the congeneric relationship between *Spadicoides* and *Xenospadicoides* (Réblová et al. 2018). In the same study, Réblová et al. (2018) also merged *Pseudodiplococcium* into synonymy under *Spadicoides*, drawing on both morphological and molecular evidence. This aligns with the initial concept outlined by Hughes (1958), which placed significant emphasis on the development of simple and branched conidiophores as the primary diagnostic criterion for distinguishing *Spadicoides* from similar *Diplococcium* (Grove 1885). In contrast, the formation of single and occasionally catenate conidia (in short chains) were considered less pivotal than the characteristics of conidiophores.

Based on previously published ITS, LSU, SSU, and RPB2 sequence data of *Lentomitella cirrhosa* (ICMP 15131) and *L. crinigera* (CBS 131481) (Réblová 2006, Réblová et al. 2016b), Zhang et al. (2017a) introduced the new family *Lentomitellaceae*. Due to insufficient sampling in both studies (Hernández-Restrepo et al. 2017, Zhang et al. 2017a), the relationships of *Lentomitella* with other genera have not been established; either members of *Lentomitella* or *Spadicoides* were not present in the same phylogenetic analysis and the relationship between *Lentomitella* and similar *Torrentispora* (as *Pseudoannulatascus biatriisporus* and *Fusoidispora aquatica*) lacked statistical support.

Réblová et al. (2018) revised the concept of *Xenospadicoidales*, synonymized *Lentomitellaceae* with *Xenospadicoidaceae* based on molecular phylogenetic evidence and the principle of priority and established the current circumscription of the order. In their phylogeny, the authors assessed 38 combined sequences from ITS, LSU, SSU, ACT1, RPB2 and TUB2 for 24 species belonging to four accepted genera, namely *Calyptosphaeria*, *Lentomitella*, *Spadicoides* (including its synonyms *Xenospadicoides* and *Pseudodiplococcium*) and *Torrentispora* (including its synonyms

Pseudoannulatascus and *Fusoidispora*). The taxonomic history of *Lentomitella* is closely intertwined with the genus *Ceratostomella* (Saccardo 1878), which is a diverse and polyphyletic group of morphologically similar, but phylogenetically distantly related fungi (Réblová 2006, 2011, Huhndorf & Fernández 2005, Huhndorf et al. 2008, 2009, Réblová & Štěpánek 2009, de Beer et al. 2013a, b, 2014, Réblová et al. 2015b).

Two other genera were added to *Xenospadicoidales*. Luo et al. (2019b) introduced *Neospadicoides* based on *N. lignicola*, whose species thrive on submerged wood. The establishment of *Neospadicoides* as an independent lineage was substantiated by combining sequence data from LSU, SSU, RPB2 and TEF1α. Distinguishing between *Neospadicoides* and closely related *Spadicoides* has proven challenging. This difficulty arises due to the heterogeneity of conidiogenous cells observed in three species recognized by Luo et al. (2019b). Apart from *N. yunnanensis* and *N. aquatica*, which exhibit characteristics that do not align with the type species *N. lignicola*, *Neospadicoides* is characterized by holoblastic conidiogenous cells. These cells are typically terminal, discrete, sometimes on short branches, and produce septate, asymmetrical conidia (Bao et al. 2021, Hyde et al. 2021b, Fryar & Catcheside 2023, Yang et al. 2023b). Recently, Lad et al. (2022), in their establishment of the phylogeny of *Gangliostilbe indica* (Vittal 1975) using ITS and LSU sequence data, assigned the genus to *Xenospadicoidaceae*. This led to an amendment of the circumscription of the order to accommodate this asexual synnematous dematiaceous hyphomycete with holoblastic gangliar conidiogenesis.

General description

Members of *Xenospadicoidales* are easily identifiable by their astromatic, dark perithecial ascomata featuring a central, cylindrical, or rostrate neck, which may or may not have sulcations at the tip. The ascomata are immersed, often partially erumpent, and occasionally become superficial. Typically, their necks penetrate the substrate while their venters remain submerged. The ascomatal wall usually comprises two layers, although in some species, there is an additional superficial colored layer that can stain the surrounding substrate. The hamathecium consists of septate, tapering, partially disintegrating paraphyses. The asci are unitunicate, persistent, cylindrical or cylindrical-clavate, with a distinct inamyloid apical ring, they are stipitate or the stipe is absent and the base is bluntly rounded. The asci contain eight ascospores. The ascospores are hyaline or pale brown prior to discharge, aseptate or with several transverse septa, mostly ellipsoidal to fusiform, sometimes flattened on one side, smooth-walled or ornamented, typically with a delayed formation of septa.

The asexual morphs are dematiaceous hyphomycetes that form effuse colonies and are characterized by macronematous, mononematous or synnematous conidiophores, which can be branched or unbranched. Conidiogenous cells display significant variability. The conidiogenesis has been interpreted as tretic and holoblastic in *Neospadicoides*. According to the protologues and accompanying photographs provided by Luo et al. (2019b) for three *Neospadicoides* species, the conidiogenous cells exhibit remarkable heterogeneity, displaying a range of characteristics. This heterogeneity is unusual within a single genus, particularly in the absence of a synasexual morph. The conidiogenous cells of *N. lignicola* are holoblastic (terminal and discrete), conidia taper towards the base and have a basal scar. On the other hand, *N. aquatica* forms conidiophores with frequently percurrently elongating conidiogenous cells which remain active along the whole length of the conidiophore and become intercalary, and conidia have a basal frill suggesting rhexolytic secession. The third species, *N. yunnanensis*, described by Luo et al. (2019b), has enteroblastic mono- and polytretic conidiogenous cells that are terminal, intercalary and discrete. Four additional species assigned to the genus (Bao et al. 2021, Hyde et al. 2021b, Fryar & Catcheside 2023, Yang et al. 2023b) display the same conidiogenesis mode as *N. lignicola*, featuring holoblastic conidiogenous cells that are either terminal or discrete, occasionally on short branches.

The conidiogenesis is tretic in *Spadicoides* (Hughes 1958, Goh & Hyde 1996, Seifert et al. 2011, Réblová et al. 2018); the genus is associated with the selenosporella-like synasexual morph producing holoblastic conidia on minute denticles, and the conidiogenous cells elongate sympodially. The sexual-asexual relationships have been experimentally verified for *S. bina*, *S. fuscolutea* and *S.*

hyalostoma (Réblová et al. 2018). The phaeoisaria-like asexual morph, characterized by holoblastic conidia produced on a sympodially extending rachis or on a terminal cluster of denticles, has been experimentally verified as a part of the life cycle of the genus *Lentomitella*. *Gangliostilbe* exhibits holoblastic 'gangliar' conidiogenesis, characterised by the absence of constriction between the denticle and conidium. Conidia are hyaline or brown, aseptate or with one to several transverse septa, and their shape varies. Other members of the order produce mostly sterile mycelium in axenic culture, but their ascospores often do not germinate *in vitro*.

While elucidating the evolutionary relatedness of genera in *Xenospadicoidales*, Réblová et al. (2018) observed that the phylogenetic tree topology was consistent with ascospore morphology and conidiogenesis shared by members of this order. The morphology of ascospores, and to some extent also of the ascomatal neck, are the primary diagnostic features to distinguish genera in the *Xenospadicoidales*. In *Calyptosphaeria* the ascospores are dull brown prior to discharge, smooth-walled, ellipsoidal to fusiform with a tendency to collapse within the asci, while the ascomatal neck is sulcate or rarely roughened without sulcations. In *Lentomitella* the ascospores are hyaline, longitudinally striate, ellipsoidal or ellipsoidal-fusiform, and the neck is sulcate. In *Torrentispora* the ascospores are hyaline, smooth-walled or occasionally with a fibrillar sheath, distinctly thick-walled, fusiform or elongated fusiform, rarely cymbiform, and the neck is smooth or roughened without sulcations. *Spadicoides* produces hyaline, ellipsoidal to ovoid ascospores. In species with verruculose ascospore wall, the ascomatal neck is partly light fulvous to subhyaline without sulcations (as in *S. hyalostoma*). However, if the ascospores have smooth walls, the ascomatal neck is dark and sulcate (as in *S. bina*, *S. fuscolutea*). In all genera except in *Lentomitella* a delayed formation of septa was observed in ascospores, either within or outside the asci. In contrast, *Lentomitella* produces ascospores that are 1-septate early in ontogeny, but exhibit a delayed formation of the second and third septum. In addition to the ascospore and ascomatal neck morphology, the apical ring also appears to have taxonomic value (Réblová et al. 2018). In all genera it is distinct, refractive, but differs in size. The relatively smallest apical ring occurs in *Lentomitella* (2.5–3 × 1.5–2 μm, width × height) and *Spadicoides* (2–3.5 × 1.5–2 μm), medium-sized apical rings occur in *Calyptosphaeria* (3–5 × 2.5–4.5 μm) and the largest apical rings are present in members of *Torrentispora* (4–8 × 3.5–4.5 μm) (Réblová et al. 2018).

Sexual morph: *Ascomata* perithecial, astromatic, venter immersed, partially erumpent, occasionally becoming superficial. *Neck* cylindrical or rostrate with or without sulcations. *Ostiole* periphysate. *Hamathecium* composed of paraphyses. *Ascomatal wall* 2-layered, occasionally with a third superficial colored layer. *Asci* unitunicate, cylindrical to cylindrical clavate, stipitate or stipe is absent, with a distinct, inamyloid apical ring, 8-spored. *Ascospores* hyaline or pale brown prior to discharge, aseptate or septate, variable in shape. Asexual morph: Dematiaceous hyphomycetes producing effuse colonies. *Conidiophores* macronematous, mononematous or synnematous, branched or unbranched. *Conidiogenous cells* terminal or integrated, sometimes sympodially elongating, conidiogenesis tretic, holoblastic-denticulate or holoblastic 'gangliar'. *Conidia* hyaline or brown, aseptate or with 1–several transverse septa, variable in shape, single or adhering in short chains. Chlamydospores absent (Figs. 268, 269, 270).

Families included in *Xenospadicoidales*

Xenospadicoidaceae Hern.-Restr., J. Mena & Gené

Evolution

Xenospadicoidales form a robust clade nested in the *Sordariomycetidae* (*Sordariomycetes*). The order shares relationships with other fungal groups, such as *Atractosporales*, *Barbatosphaeriaceae*, *Myrmecridiales*, *Ophiostomatales*, *Papulosaceae*, *Rhamphoriales*, *Sporidesmiaceae* and numerous *incertae sedis* genera, which predominantly exhibit holoblastic conidiogenesis, particularly holoblastic-denticulate. Nonetheless, it is worth noting that within this order, two members, *Spadicoides* and *Neospadicoides* (only *N. yunnanensis*), produce conidia on polytretic conidiogenous cells, representing a unique and rare mode of conidiogenesis within the

Sordariomycetes. In the same class, a similar conidial ontogeny has been described for the morphologically similar *Diplococcium*, which is affiliated with *Helminthosphaeria* in *Helminthosphaeriaceae* (Samuels et al. 1997, Réblová 1999c). *Diplococcium* and *Spadicoides* exhibit the same trend of co-occurring two asexual morphs with different modes of conidiogenesis, such as tretic associated with holoblastic-denticulate conidiogenesis (as a selenosporella-like synasexual morph) in the life cycle of a single organism (Wang & Sutton 1998, Réblová et al. 2018). Unlike *Spadicoides*, *Diplococcium* is a polyphyletic genus (Shenoy et al. 2010).

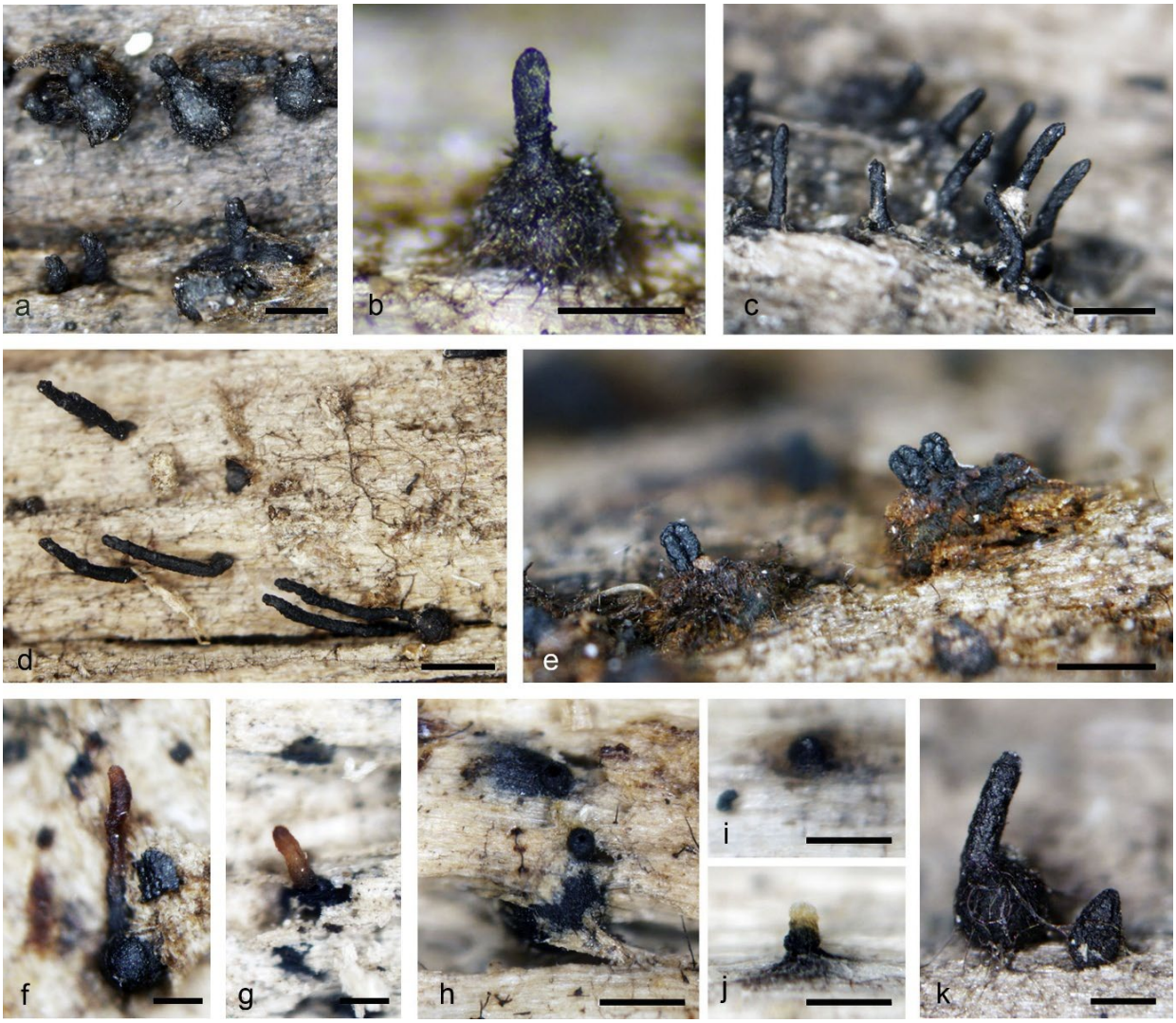


Figure 268 – Ascomata morphology of *Xenospadicoidales*. a *Calyptosphaeria tenebrosa*. b *Calyptosphaeria subdenudata*. c *Lentomitella vestita*. d *Lentomitella striatella*. e *Spadicoides fuscolutea*. f, g *Spadicoides hyalostoma*. h, i, j *Torrentispora fibrosa*. k *Torrentispora dubia*. (adapted from Réblová et al. 2018). Scale bars: a, b, c, d, e = 500 µm, f, g, h, I, j, k = 250 µm.

Justification of order and problems

The classification of *Xenospadicoidales*, which comprises six genera exhibiting similar sexual morphs, is consistently supported by a combination of morphological and molecular sequence data from ribosomal and protein-coding genes (Réblová et al. 2018, Luo et al. 2019b, Lad et al. 2022). Réblová et al. (2018) proposed that the ceratostomella-like phenotype (characterized by ascomata with a protruding rostrate neck and often immersed venter, ellipsoidal hyaline or pigmented ascospores, and cylindrical asci with a distinct inamyloid apical ring) represents an ecological adaptation. Consequently, such phenotype independently evolved multiple times within the

Sordariomycetes. However, *Helminthosphaeriaceae*, which are characterized by the same rare mode of tretic conidiogenesis, have different sexual morphology and are distantly related.



Figure 269 – Asci and ascospores of *Xenospadicoidales*. a, b *Calyptosphaeria tenebrosa*. c, d, e, f. *Calyptosphaeria subdenudata*. g *Lentomitella vestita*. h *Lentomitella striatella*. i, j *Spadicoides*

fuscolutea. k. *Spadicoides hyalostoma*. l *Torrentispora fibrosa*. m, n *Torrentispora dubia* (adapted from Réblová et al. 2018). Scale bars: a, b, c, d, e, f, g, h = 10 µm, i = 20 µm, j, k, l, m, n = 10 µm.



Figure 270 – Asexual morphology of *Xenospadicoidales*. a, b *Spadicoides fuscolutea.* c, d. *Spadicoides hyalostoma*. e, f *Spadicoides bina*. g, h, i, j *Lentomitella* sp. k, l, m, n, o *Neospadicoides lignicola*. p, q, r, s *Gangliostilbe indica* (adapted from Réblová et al. 2018, Luo et al. 2019b). Scale bars: a–f = 10 µm, g–j = 5 µm, k, l = 50 µm, m = 30 µm, n, o = 20 µm, p–s = 10 µm.

Significance

Ecological and economic roles

Members of *Xenospadicoidales* are distributed across temperate, subtropical and tropical zones, although some species are specific to particular regions. Generally, they are saprobic in nature and associated with decaying processes in freshwater and terrestrial habitats. As a result, they play a significant role in ecosystems by facilitating the recycling of nutrients. Consequently, there is likely no need for quarantine assessment unless it is determined that these fungi represent plant pathogens.

In terrestrial habitats, these fungi typically thrive on wood in advanced stages of decay; the wood is usually soft, soaked with water or lying on the ground, and in some cases, it may be partially buried in soil. They are abundant in natural stands where harvesting is restricted and fallen trunks and large branches are commonly present on the ground and naturally decomposing. Species of *Calyptosphaeria* are primarily found on decaying wood and bark in terrestrial biotopes, with occasional reports from freshwater environments, in tropical and temperate regions of the Southern and Northern Hemispheres. Similarly, species of *Lentomitella* are commonly found on decaying wood and bark within terrestrial habitats in temperate zones of both Hemispheres. They are widely distributed on hardwoods, occasionally found on wood from fruit trees (*L. conoidea*, Feltgen 1903) or on senescent flower heads of *Protea lepidocarpodendron* (*Lentomitella unipretoriae*, Marincowitz et al. 2008a). Some species, like *L. crinigera*, exhibit a clear preference for coniferous wood (Réblová et al. 2018). Members of *Spadicoides* thrive on decaying wood or plant remnants (Hughes 1958, Ellis 1963, 1971b, Wang 1976, Holubová-Jechová 1982, Réblová et al. 2018). Species of *Torrentispora* are primarily found in freshwater habitats from subtropical, tropical and temperate zones (Hyde et al. 2000, Fryar & Hyde 2004, Barbosa et al. 2013). *Torrentispora fibrosa* was originally collected on submerged wood in streams in Hong Kong, China, where the climate is subtropical but tends to become temperate for nearly half of the year (Hyde et al. 2000, Ho et al. 2001). Other collections have been reported from Florida, USA (Raja et al. 2003), but no states north of Florida (Shearer 1993, 2001). Réblová et al. (2018) introduced *T. calembola* and *T. novae-zelandiae* from terrestrial habitats from temperate zones of Europe and New Zealand.

Chemical diversity

There have been no known biochemical studies conducted on members of *Xenospadicoidales*, nor have there been any studies exploring their industrial applications. It is recommended that these genera be further assessed to uncover their chemical diversity and the potential presence of novel compounds.

Other relevant data and future recommendations

Xenospadicoidales are important components of biodiversity and play a role in the decomposition of plant material. Species of *Calyptosphaeria*, *Lentomitella* and *Torrentispora* that consistently produce sexual morphs, typically develop inconspicuous colonies consisting of ascomata that are immersed in wood, often with only their necks protruding. They are virtually invisible to most people and challenging to locate even for a trained observer. Because of their inconspicuous nature, there is significant potential for discovering new species within this group. The presence of diagnostic traits, including characteristics of ascospores (such as septation, ornamentation, and color) and ascomata (with special emphasis on the neck anatomy), greatly aids in the identification of these three genera that possess well-documented sexual morphs. Conversely, *Neospadicoides*, *Spadicoides*, and *Gangliostilbe* are relatively straightforward to locate and distinguish due to their conspicuous dark effuse colonies on substrates and the distinctive morphological features exhibited by their conidiophores, conidiogenous cells, and conidia.

The primary challenge within this group of fungi is the absence of living cultures. Continued research, with a specific focus on the cultivation of these genera and the establishment of axenic cultures derived from ascospores, has the potential to unveil previously undiscovered asexual morphs. This effort will be instrumental in advancing our understanding of *Xenospadicoidales*. In addition, due to the significant variability observed in the asexual morphs, it is reasonable to anticipate the discovery of additional hyphomycetous genera that are closely related to or belong within the *Xenospadicoidales*. Very little is known about their possible endophytic activity and the presence of bioactive chemical compounds. Special attention should also be directed towards evaluating the diagnostic significance of branched versus simple conidiophores and single versus shortly catenate conidia, particularly in members of *Spadicoides* and *Neospadicoides*. Several species, including *S. grovei*, *S. obovata*, and *S. xylogena* (Hughes 1958, Ellis 1963), display traits that are typical of *Neospadicoides*.

Xylariales **Nannf., Nova Acta Regiae Societatis Scientiarum Upsaliensis Ser. 4 8(no. 2): 66 (1932)**

Subphylum : *Pezizomycotina*
Class : *Sordariomycetes*
Subclass : *Xylariomycetidae*

Introduction

Xylariales is one of the largest orders of *Ascomycota*, introduced by Nannfeldt (1932), and belongs to the subclass *Xylariomycetidae* and class *Sordariomycetes* (Hyde et al. 2020b). Many *Xylariales* produce conspicuous fruiting bodies (stromata) and are known as "macromycetes" (Helaly et al. 2018). *Xylariales* members are characterized by perithecial stromata, usually dark-colored and thick-walled ascomata with true paraphyses, periphysate and papillate ostioles, eight-spored unitunicate asci, often with amyloid J+ apical apparatus (rings) and pigmented ascospores (Smith et al. 2003, Maharachchikumbura et al. 2016, Hyde et al. 2020b).

Xylariales consists of coprophilous saprobes, pathogens and endophytic fungi. Saprobes generally occur on wood and other plant debris. Wood decomposers are important for forest ecosystems (Stadler 2011, Hyde et al. 2020d). Members in *Xylariales* are known as soft-rot fungi, while also grouped as the white-rot fungi because of their ability to degrade lignin (Bucher et al. 2004b, Raju et al. 2022). Some species are important plant pathogens in terrestrial habitats such as *Biscogniauxia* (Nugent et al. 2005), *Dematophora* (Wittstein et al. 2020), *Entoleuca* (Ostry & Anderson 2009), *Hypoxylon* (Stadler 2011) and *Kretzschmaria* (da Luz Morales et al. 2021). Also, some species of *Xylariales* are endophytes, acting as mycobionts (lignicolous) and endolichens (U'Ren et al. 2016, Oh et al. 2020, Dissanayake et al. 2021b). Moreover, some species are typically encountered on dung or related to insect vectors (Stadler 2011, Pažoutová et al. 2013, Wendt et al. 2018).

Some *Xylariales* species, especially endophytes as well as lignicolous and endolichenic taxa, were reported as secondary metabolites producers (Calcott et al. 2018, Oh et al. 2020, Becker & Stadler 2021). These secondary metabolites have shown antibacterial, antifungal, cytotoxic, antimalarial, anti-inflammatory, anti-neuroinflammatory, immunosuppressive and herbicidal activities and are used in medicine and agriculture (Biasetto et al. 2019, Chen et al. 2019, Intaraudom et al. 2019, Wang et al. 2019a, Chen et al. 2020a, b, Noppawan et al. 2020, Wittstein et al. 2020Patjana et al. 2021). Franco et al. (2022) reported that diverse secondary metabolite gene clusters that may facilitate symbiosis with phylogenetically diverse hosts.

The secondary metabolite production in these taxa is unique or specific for certain groups, and secondary metabolite profiles were demonstrated as important species-specific characters and have phylogenetic significance (Stadler 2011). Therefore, metabolite profiles are used as an additional tool to support classical morphology and molecular phylogenetic approaches (Helaly et al. 2018). Polyphasic studies using chemotaxonomic, molecular phylogenetics and morphological data have led to numerous changes in the classification of *Xylariales*.

Presently, *Xylariales* comprises 22 families and over 2,400 species assigned to 194 genera (Wendt et al. 2018, Voglmayr et al. 2019a, Hyde et al. 2020b, d, Sun et al. 2021b, Hernández-Restrepo et al. 2022, Sugita et al. 2022, Wijayawardene et al. 2022a). However, the xylariaceous taxa have shown a polyphyletic topology and require further verification (Wendt et al. 2018, Konta et al. 2020).

History

Nannfeldt (1932) established *Xylariales* in *Sordariomycetes*. Xylariaceous taxa have been recognized to comprise a homogenous evolutionary lineage based on its ascal and ascospore morphology (Rogers 1979), which was later accommodated as the only order in the subclass *Xylariomycetidae*, introduced by Eriksson & Winka (1997). Initially, *Xylariales* was classified mainly based on morphology (Müller et al. 1962, Wehmeyer 1975, Barr 1990b). With the adoption of molecular technologies for species identifications, the *Xylariales* classification changed drastically

(Smith et al. 2003, Eriksson et al. 2003b). Smith et al. (2003) introduced seven families in this order based on LSU and SSU rDNA phylogeny, while Lumbsch & Huhndorf (2010) accepted six families, and Senanayake et al. (2015) resurrected *Amphisphaeriales* in *Xylariomycetidae* using ITS and LSU phylogeny and accepted six families for *Amphisphaeriales* and eleven for *Xylariales*, together with morphological evidence. However, Maharachchikumbura et al. (2016) considered *Amphisphaeriales* as a synonym of *Xylariales* because of the poor phylogenetic support in the LSU, SSU, TEF and RPB2-based phylogeny. Also, they synonymized *Graphostromataceae* with *Xylariaceae* and accepted 22 families for *Xylariales* (Maharachchikumbura et al. 2016). Simultaneously, Jaklitsch et al. (2016b) transferred *Requienellaceae* to *Xylariales* based on morphology and ITS and LSU-based phylogeny, which previously was classified in *Melanommatales* in the class *Loculoascomycetes* (Liew et al. 2000). Subsequently, Perera et al. (2017) introduced *Delonicicolales* to accommodate *Delonicicolaceae* in *Xylariomycetidae* as the third order, using morphology and LSU, SSU and RPB2-based phylogeny. Later, *Clypeophysalosporaceae* was introduced into *Xylariales* based on ITS and LSU data (Giraldo et al. 2017).

Xylariaceae was divided into two major sections (*Xylarioideae* and *Hypoxyloideae* subfamilies), based on their respective asexual morphs, the genera related to *Xylaria* with geniculosporium-like asexual morphs and the genera related to *Hypoxylon* with nodulisporium-like asexual morphs (Daranagama et al. 2015, Maharachchikumbura et al. 2015, 2016, Senanayake et al. 2015). Later, Wendt et al. (2018) introduced *Xylarioideae* and *Hypoxyloideae* subfamilies in separate families. Hyde et al. (2020d) revised the families of *Sordariomycetes* using morphology and multi-gene analysis (LSU, ITS, RPB2 and TEF1 sequence data) and accepted 15 families. Marasinghe et al. (2019) transferred *Iodosphaeriaceae* from *Amphisphaeriaceae* to the *Xylariales* with *Iodosphaeria* as the type genus. In subsequent studies, several new families were introduced using the morphological data and phylogenetic analysis, such as *Barrmaeliaceae* (Voglmayr et al. 2019a), *Hypoxylaceae* (Wendt et al. 2018), *Fasciatisporaceae* (Hyde et al. 2020b), *Spirodecosporaceae* (Sugita et al. 2022), and *Vamsapriyaceae* (Sun et al. 2021b). Sun et al. (2021b) introduced two genera *Podosporium* and *Tretophragmia* into the novel family *Vamsapriyaceae*. Wijayawardene et al. (2022a) listed 20 families under *Xylariales*. The genera *Circinotrichum*, *Gyrothrix* and *Vermiculariopsiella* had a complex taxonomy and have generally been confused in the past. Both *Circinotrichum* and *Gyrothrix* have polyblastic conidiogenous cells, while *Vermiculariopsiella* has phialidic conidiogenous cells. *Circinotrichum* produces simple setae, *Gyrothrix* produces branched setae and *Vermiculariopsiella* produces both simple and branched setae (Hernández-Restrepo et al. 2022). Morphological and phylogenetic analyses based on the ITS, LSU, and RPB2 sequences showed that *Circinotrichum* and *Gyrothrix* are polyphyletic and placed in *Coniocessiaceae* and *Gyrothricaceae*, respectively. *Gyrothricaceae* was introduced to accommodate *Gyrothrix*, *Xenoanthostomella*, and the newly introduced *Neogyrothrix*, *Pseudocircinotrichum* and *Pseudoceratocladium*. The new genus *Pirozynskiomyces* was introduced into *Coniocessiaceae* (Hernández-Restrepo et al. 2022). The genus *Vermiculariopsiella* was emended to include species with setose sporodochia with simple setae, which belongs to order *Vermiculariopsiellales* and the family *Vermiculariopsiellaceae*. Also, *Vermiculariopsis* was resurrected and includes setose fungi (Hernández-Restrepo et al. 2022), while Crous et al. (2018a) suggested to retain *Vermiculariopsis* as the older name over *Vermiculariopsiella*.

Hernández-Restrepo et al. (2022) resurrected the genus *Peglionia* in the family *Microdochiaceae*. Cedeño-Sanchez et al. (2023a) considered *Barrmaeliaceae* synonymous with *Induratiaceae* and accommodated the genera *Emarcea* and *Muscodor* in the *Xylariaceae*. Also, the new genus *Parahypoxylon* was introduced using a polyphasic approach, considering morphology, multi-gene phylogeny and chemotaxonomy (Cedeño-Sanchez et al. 2023b). *Alloeutypa* was introduced into *Diatrypaceae* using morphological features and molecular evidence (Ma et al. 2023a). Therefore, *Xylariales* comprises 22 families as mentioned in the introduction (Daranagama et al. 2018, Wendt et al. 2018, Voglmayr et al. 2019a, Hyde et al. 2020b, d, Sun et al. 2021b, Hernández-Restrepo et al. 2022, Sugita et al. 2022, Wijayawardene et al. 2022a).

General description

Xylariales taxa produce both conspicuous and inconspicuous stromata, of which many are "macromycetes" and produce conspicuous fruiting bodies (Helaly et al. 2018). Stromata are variable in size and shape, and are mostly dark (Hyde et al. 2020d). *Clypeosphaeriaceae* taxa produce a pseudoclypeus, which is black and comprises both host and fungal tissues (Hyde et al. 2020d). Metabolite profiles of stromata are often complementary to those of mycelial cultures (Helaly et al. 2018). Most *Xylariales* have a persistent hamathecium. Ascomata are usually perithecial, dark-colored and thick-walled with true paraphyses and periphysate ostioles. However, the ascomata color is variable and is seen as whitish, greyish to black. The interior of ascomata is sometimes zonate or filled with a liquid, as in the family *Hypoxylaceae*. Paraphyses develop from a hymenial layer, which is apically free (Barr 1990b, Hawksworth et al. 1995). Asci are mostly unitunicate and eight-spored with a J+, apical ring when stained in the Melzer's reagent or with apical thickening. Sometimes asci are with J- or J+ annulus (ring), such as in *Barrmaeliaceae*, *Clypeosphaeriaceae*, *Diatrypaceae*, and *Hypoxylaceae*. Asci of some taxa turn slightly reddish in Congo Red as in *Requienellaceae*. The ascospores are usually pigmented, 1–2-celled, and often with germ slits (Maharachchikumbura et al. 2016, Hyde et al. 2020b). Anamorphs of *Xylariales* taxa are mostly hyphomycetous, with holoblastic conidial production (Rogers 1979, Whalley 1996), some are coelomycetous, as *Diatrypaceae* (Konta et al. 2020). Among these, are libertella-like, phomopsis-like, geniculosporium-like and nodulisporium-like anamorphs (Phookamsak et al. 2019, Dayarathne et al. 2020).

Sexual morph: *Stromata* are eustromatic or pseudostromatic, dark colored, more or less well-developed, or sometimes reduced or lacking, variable in size, shape and color, erect, glomerate, pulvinate, discoid, effused-pulvinate, hemispherical, spherical, peltate applanate or effuse-pulvinate, ostiolate, arising singly or aggregated into groups, with one to several ascomata, mostly with extractable stromal pigments, unipartite or bipartite, sometimes with carbonaceous outer layer. *Ascomata* are variable in size and shape, immersed to erumpent or superficial, perithecial, bottle-shaped, spherical, globose-subglobose, coriaceous or elongate cylindrical-pyriform, solitary or aggregated. *Ostioles* are inconspicuous or strongly erumpent, flattened or papillate to conical, umbilicate or at the same level as the stromal surface, with or without discs. *Paraphyses* are hyaline, filamentous, septate, embedded in a gelatinous matrix. *Asci* are 4–8-spored or sometimes polysporous, unitunicate, cylindrical to clavate to pyriform, fusiform or globose, pedicellate-apedicellate, apically rounded, with or without J+ or J-, apical ring stained in Melzer's reagent, or with apical thickening. *Ascospores* are unicellular or septate, uniseriate-biseriate, variously-shaped, sphaerical, ellipsoidal, subglobose, reniform, oval, straight, spiral or sigmoid, allantoid or ellipsoid, yellow to black, mostly dark, with or without germ slits or germ pores, sometimes surrounded by a gelatinous sheath. *Perispore* is dehiscent or lacking, smooth or with patterns. Asexual morph: hyphomycetous or coelomycetous, libertella-like, phomopsis-like, geniculosporium-like, nodulisporium-like, periconiella-like or xylocladium-like. *Conidiomata* are pycnidial, acervuli, sporodochial. *Conidiophores* are micronematous, macronematous, synnematous or sympodially proliferating, hyaline to light brown, smooth to finely verruculose, simple or branched. *Conidiogenous cells* are polyphialidic, polyblastic, sympodial, cylindrical, usually hyaline, one to several on each branch of the conidiophore, and have a swollen apex. *Conidia* are solitary, aggregating in slimy mass, unicellular or septate, hyaline to pale brown, with pointed ends, roughened or smooth, elongate fusiform, falcate, lunate, ellipsoidal, obclavate, clavate. *Chlamydospores* are present or absent (adapted from Wendt et al. 2018, Daranagama et al. 2018, Hyde et al. 2020d) (Figs. 271, 272, 273, 274).

Families included in *Xylariales*

Anungitiomycetaceae Crous
Barrmaeliaceae Voglmayr & Jaklitsch
Cainiaceae J.C. Krug
Clypeosphaeriaceae G. Winter
Coniocessiaceae Asgari & Zare

Diatrypaceae Nitschke
Fasciatisporaceae S.N. Zhang, K.D. Hyde & J.K. Liu
Gyrotrichaceae Hern.-Restr. & Crous
Graphostromataceae M.E. Barr, J.D. Rogers & Y.M. Ju
Hansfordiaceae Crous
Hypoxylaceae DC.
Lopadostomataceae Daranag. & K.D. Hyde
Microdochiaceae Hern.-Restr., Crous & J.Z. Groenew.
Nothodactylariaceae Crous
Pallidoperidiaceae R. Sugita & Kaz. Tanaka
Polystigmataceae Höhn. ex Nannf.
Requienellaceae Boise
Spirodecosporaceae R. Sugita & Kaz. Tanaka
Vamsapriyaceae Y.R. Sun, Yong Wang bis & K.D. Hyde
Xyladictyochaetaceae Crous & Hern.-Restr
Xylariaceae Tul. & C. Tul. (= *Clypeosphaeriaceae* G. Winter; = *Induratiaceae* Samarak., Thongbai, K.D. Hyde & M. Stadler)
Zygosporiaceae J.F. Li, Phook. & K.D. Hyde

Xylariales genera *incertae sedis*
Adomia S. Schatz
Alloanthostomella Daranag., Camporesi & K.D. Hyde
Anthostomella Sacc.
Anungitea B. Sutton
Ascotrichella Valldos. & Guarro
Basifimbria Subram. & Lodha
Bicellulospora W.L. Li, R.R. Liang & Jian K. Liu
Biporispora J.D. Rogers, Y.M. Ju & Cand.
Castellaniomyces Senan., Camporesi & K.D. Hyde
Catenuliconidia N.G. Liu & K.D. Hyde
Chaenocarpus Rebent.
Circinotrichum Nees
Cryptostroma P.H. Greg. & S. Waller
Cyanopulvis J. Fröhl. & K.D. Hyde
Diamantinia A.N. Mill., Læssøe & Huhndorf
Gigantospora B.S. Lu & K.D. Hyde
Guayaquilia R.F. Castañeda, Magdana, D. Sosa & Hern.-Restr.
Guestia G.J.D. Sm. & K.D. Hyde
Hadrotrichum Fuckel
Haploanthostomella Konta & K.D. Hyde
Idriellopsis Hern.-Restr. & Crous
Kirstenboschia Quaedvl., Verkley & Crous
Lanceispora Nakagiri, Okane, Tad. Ito & Katum.
Lasiobertia Sivan.
Magnostiolata Samarak. & K.D. Hyde
Natonodosa Heredia, R.F. Castañeda & D.W. Li
Neoanthostomella D.Q. Dai & K.D. Hyde
Neobarrmaelia Crous
Neoidriella Hern.-Restr. & Crous
Neoleptodontidium Crous & Jurjević
Neotrichosphaeria Crous & Carnegie
Nipicola K.D. Hyde



Figure 271 – Stromatal morphology in *Xylariales*. a Cross section through stroma in *Engleromyces goetzei*. b Cross section through stroma in *Annulohypoxylon truncatum*. c *Entonaema liquescens*. d, e *Hypoxylon fragiforme*. f Longitudinal section through ascomata of *Allocryptovalsa sichuanensis*. g Cross section through sroma in *Diatrype disciformis*. h *Camillea leprieurii*. i *Jackrogersella minutella*. j *Xylaria Karsticola*. k *Camillea tinctor*. (Photos credits to Daranagama et al. 2018, Samarakoon et al. 2022, Karimi et al. 2023). Scale bars: a, b, c = 1000 µm, d, e = 2000 µm, f = 200 µm, g = 500 µm, h = 10 µm, i, h = 1000 µm.

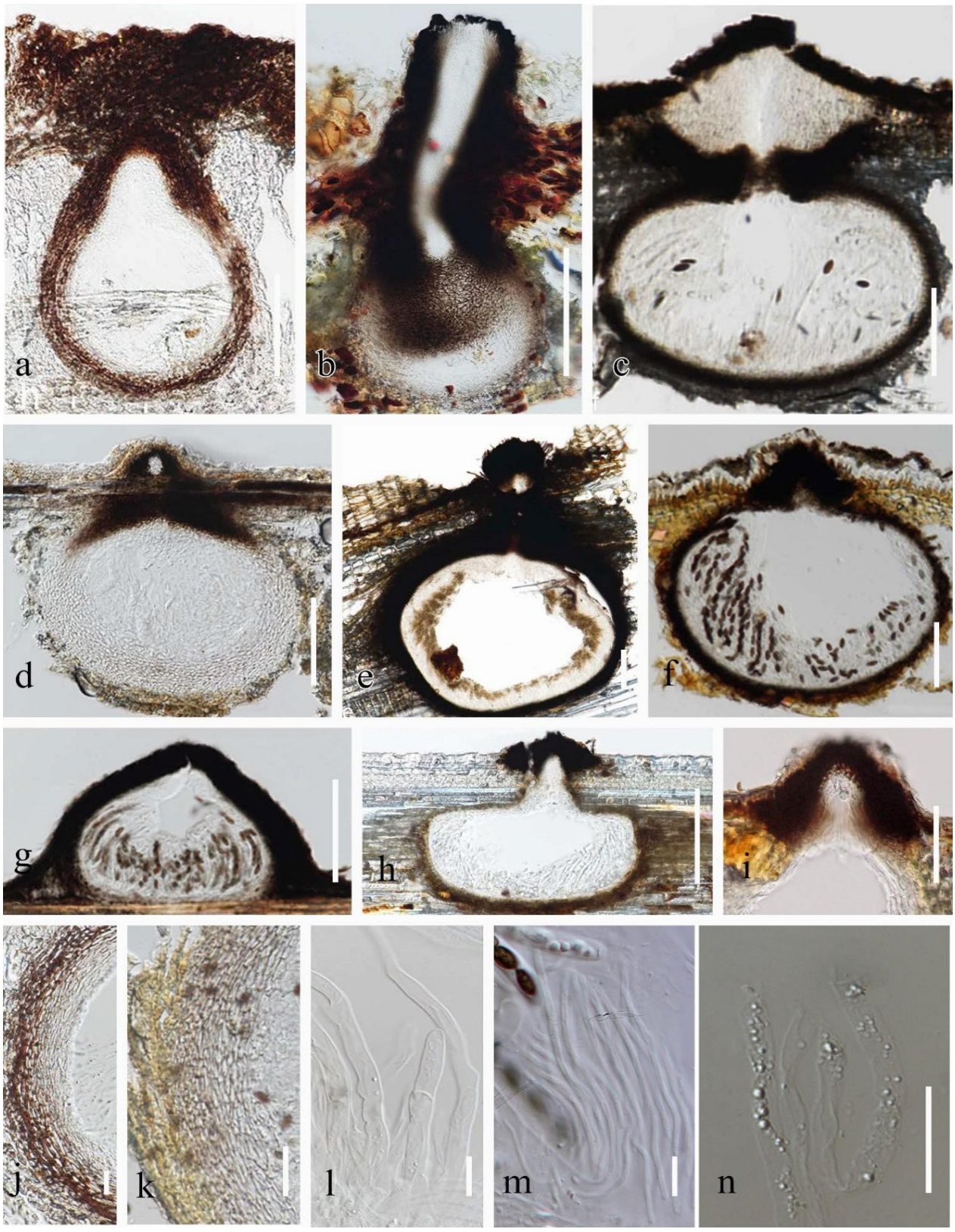


Figure 272 – Ascomata, peridium and paraphyses morphology of *Xylariales*. a–i Ascomatal morphologies: a *Eutypa camelliae*. b *Melanostictus longiostiolatus*. c *Magnostiolata mucida*. d *Hypocopra zeae*. e *Peroneutypa leucaenae*. f *Occultitheca rosae*. g *Xenoanthostomella chromolaenae*. h *Vamsapriya mucosa*. i *Emarcea castanopsidicola*. j–k *Peridium morphologies*: j *Eutypa camelliae*. k *Hypocopra zeae*. l–n Paraphyses morphologies: l *Acrocordiella photiniicola*. m *Xylaria* sp. n *Jackrogersella minutella* (Photos adapted from Daranagama et al. 2018, Samarakoon

et al. 2022, Karimi et al. 2023). Scale bars: a, b = 200 µm, c−h = 200 µm, i = 50 µm, j, k = 20 µm, l−n= 10 µm.

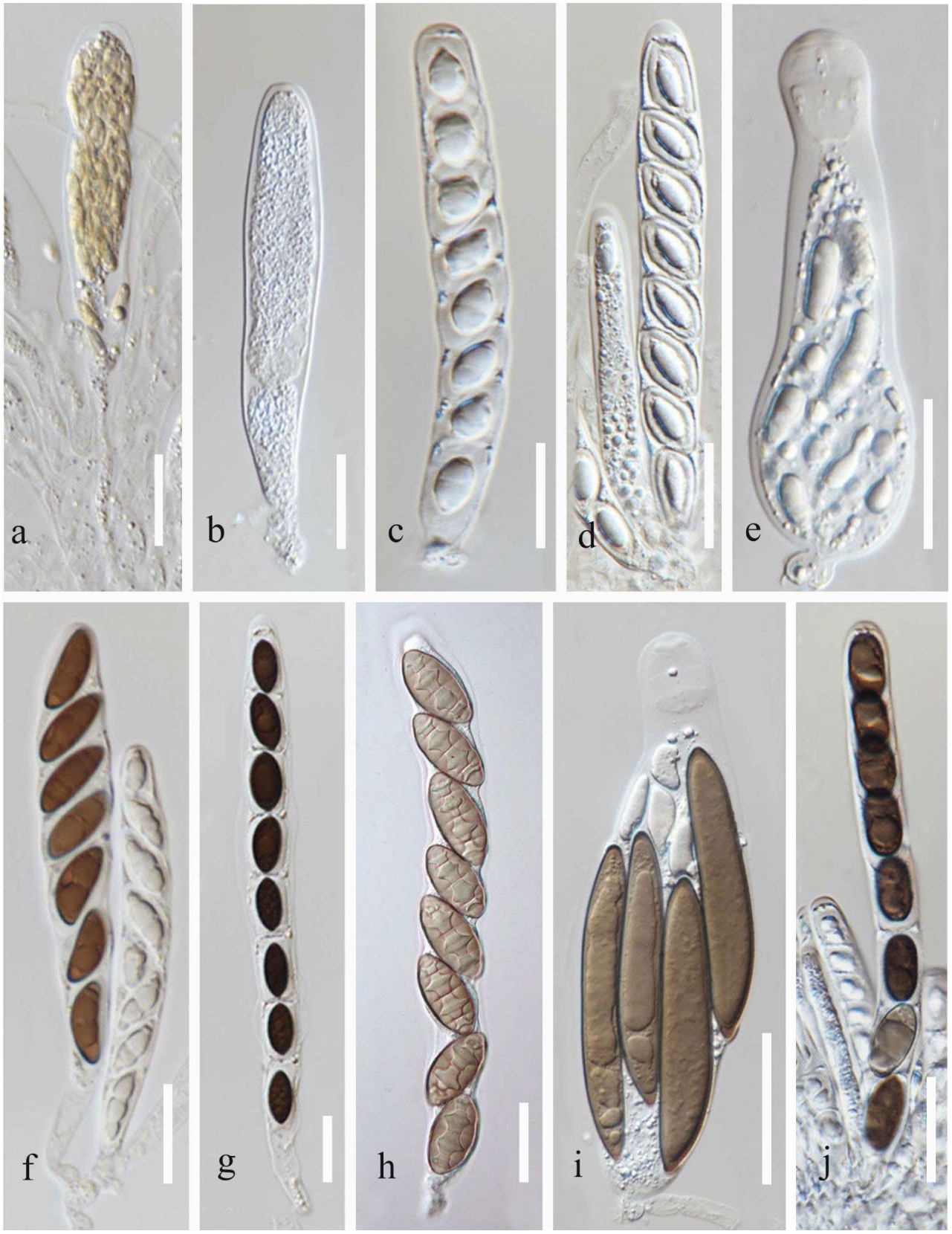


Figure 273 – Ascal morphology in *Xylariales.* a *Allocryptovalsa sichuanensis*. b *Acrocordiella photiniicola*. c *Nigropunctata bambusicola*. d *Magnostiolata mucida*. e *Rosellinia markhamiae,* f *Neoanthostomella bambusicola*. g *Magnostiolata mucida*. h *Acrocordiella photiniicola*. i *Rosellinia*

markhamiae. j *Nigropunctata bambusicola*. (Photos adapted from Konta et al. 2016, Samarakoon et al. 2022). Scale bars: a, b, f, g, h = 20 µm, c, j = 10 µm, e, i = 50 µm.

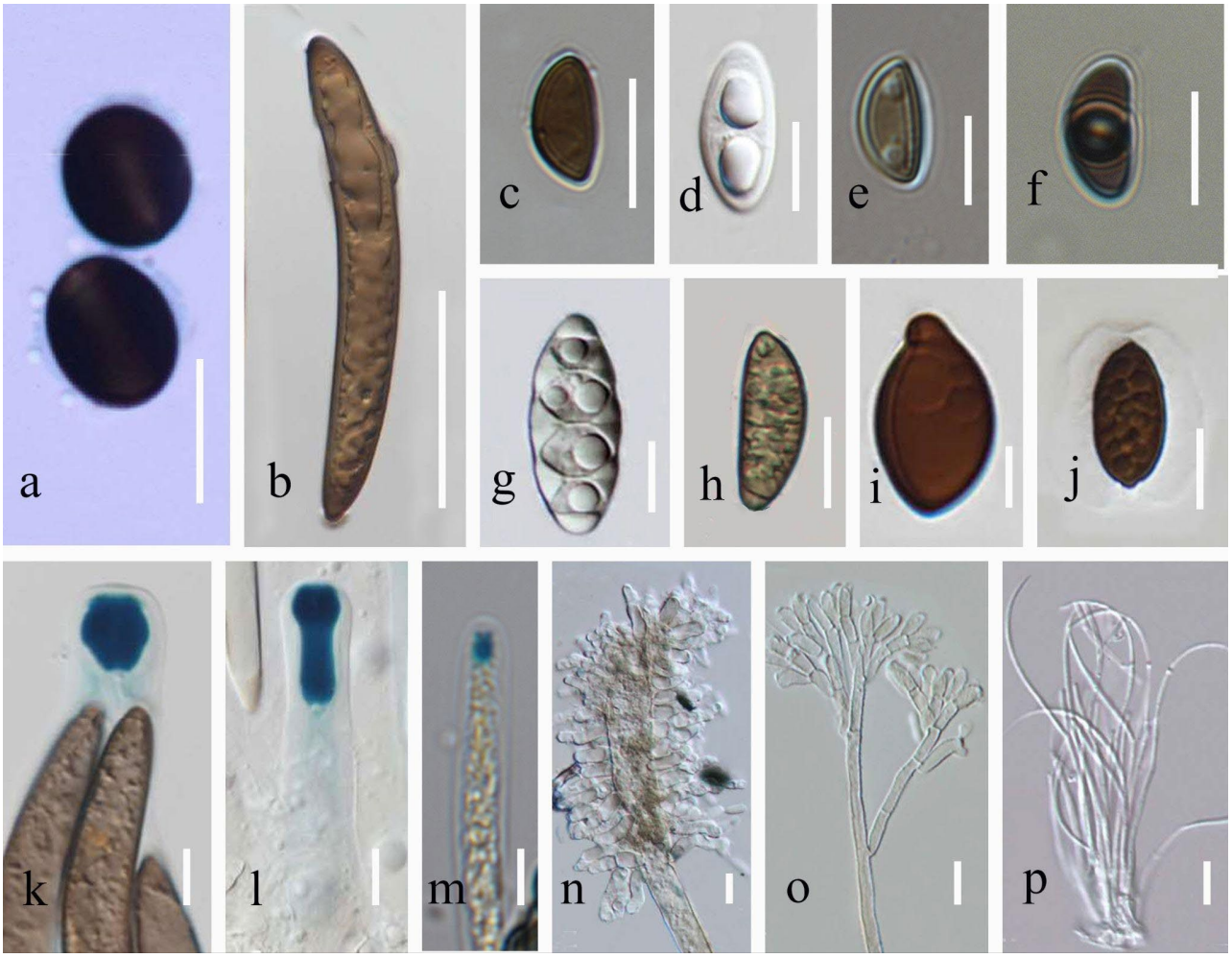


Figure 274 – Ascospores, apical ring and asexual-morphs morphology of *Xylariales*. a–j Ascospore morphologies: a *Biscogniauxia marginata*. b *Rosellinia markhamiae*. c, e, f *Xylaria* spp. d, g *Acrocordiella photiniicola*. h *Rosellinia aquila*. i *Nemania paraphysata*. j *Magnostiolata mucida*. k–m Apical ring morphologies: k, l *Rosellinia markhamiae*. m *Xylaria* spp. n–p Asexual morph morphologies: n *Camillea tinctor*, o *Biscogniauxia magna*, p *Eutypa camelliae* (Photos adapted from Konta et al. 2016, Daranagama et al. 2018, Samarakoon et al. 2022, Karimi et al. 2023). Scale bars: a = 20 µm, b = 50 µm, c, d, e, f, g, h, j, k, l, n, o, p = 10 µm, i, m = 5 µm.

Occultitheca J.D. Rogers & Y.M. Ju
Ophiorosellinia J.D. Rogers, A. Hidalgo, F.A. Fernández & Huhndorf
Palmicola K.D. Hyde
Pandanicola K.D. Hyde
Paraidriella Hern.-Restr. & Crous
Paramphisphaeria F.A. Fernández, J.D. Rogers, Y.M. Ju, Huhndorf & L. Umaña
Paucithecium Lloyd
Pidoplitchkoviella Kiril.
Polyancora Voglmayr & Yule
Polyscytalum Riess
Poroleprieuria M.C. González, Hanlin, Ulloa & Elv. Aguirre
Pseudoanthostomella Daranag., Camporesi & K.D. Hyde
Pseudophloeospora Crous & R.G. Shivas
Pulmosphaeria Joanne E. Taylor, K.D. Hyde & E.B.G. Jones

Pyriformiascoma Daranag., Camporesi & K.D. Hyde
Roselymyces Fiuza, C.R. Silva, R.F. Castañeda & Gusmão
Sabalicola K.D. Hyde
Sporidesmina Subram. & Bhat
Striatodecospora D.Q. Zhou, K.D. Hyde & B.S. Lu
Stromatoneurospora S.C. Jong & E.E. Davis
Subanthostomella S.N. Zhang, K.D. Hyde & Jian K. Liu
Surculiseries Okane
Synnemadiella Crous & M.J. Wingf.
Tristratiperidium Daranag., Camporesi & K.D. Hyde
Xylocrea Möller
Yuea O.E. Erikss.

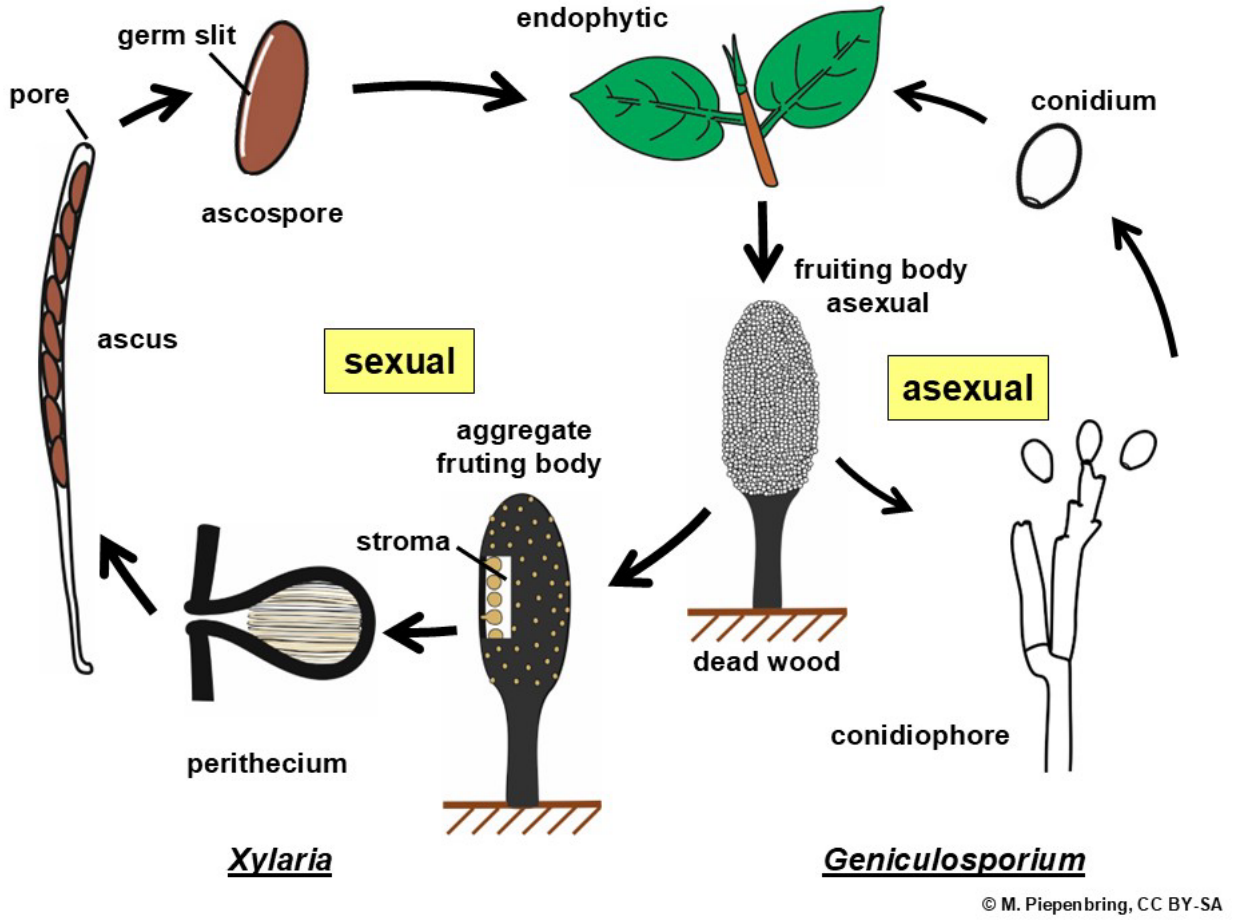


Figure 275 – Sexual and asexual life cycles of *Xylariales* (From Mycological teaching diagrams by Meike Piepenbring (2023)). Abbreviations: 1n = haploid, 2n = diploid, P! = plasmogamy, K! = karyogamy, M! = meiosis. Black and white circles represent haploid nuclei of different mating types, circles of both colors represent diploid nuclei.

Evolution

Earlier *Xylariomycetidae* have evolved around 159 (124–193) MYA and the divergence between *Amphisphaeriales* and *Xylariales* occurred approximately 150.5 MYA during the rapid diversification in the early Mesozoic era (Samarakoon et al. 2022). The rapid diversification of angiosperms during the Cretaceous period likely influenced the diversification of xylarialean taxa, giving rise to several independent lineages (Samarakoon et al. 2022).

Numerous researchers have postulated a hypothesis regarding the evolutionary transition of fungi from aquatic to terrestrial environments. According to this theory, fungal endophytes are believed to represent the ancestral lifestyle, which later underwent further evolution leading to the development of saprobes and pathogens (Krings et al. 2012, Lutzoni et al. 2018, Samarakoon et al. 2022, Bhunjun et al. 2024). The transition from an endophytic to a saprobic lifestyle is evident in certain *Xylariales* taxa, as observed in instances where they appear on freshly fallen branches as well as branches attached to the host tree (Whalley 1996). Astromatic xylarialean taxa evolved from endophytes and further diversified into stromatic forms, adapting to various environmental conditions. It is also believed that the endophytes originate from spores that come from saprobes (Promputtha et al. 2007, Zhou et al. 2018). The spore origin of endophytes is supported by the substantial genetic diversity observed in *X. cubensis* endophytic isolates found on leaves of the Brazilian rainforest palm (Rodrigues et al. 1993). Some saprobic *Oxydothis* and *Linocarpon* taxa produce hyaline appressoria (Konta et al. 2016, 2017), which is considered as the ancestral character of endophytic *Ascomycota* (Chethana et al. 2021a, b). Based on the evidence produced from previous research, it is suggested that early xylarialean fungi likely had an endophytic lifestyle, giving rise to simple anthostomella-like ascomata on the surface of the host (Rogers 2000, Phillips et al. 2019). Over time, other stromatic forms evolved as a response to different environmental conditions (Samarakoon et al. 2022). The development of stromatic structures may have been linked to successful parasitism and saprotrophism (Rogers 1979), with Samarakoon et al. (2022) proposing that stromata development might be related to moisture conservation. Furthermore, stromatic forms have been found to produce a variety of chemical compounds, as reported by Becker & Stadler (2021), which could serve the purpose of deterring insects. Samarakoon et al. (2022) further mentioned that these stromatic forms likely developed insecticidal chemicals as a means of protection against insects and other predators. Through ancestral character analysis, it has been revealed that the divergence of ascomata types predominantly occurred during the Cretaceous period, between 66 and 145 MYA (Samarakoon et al. 2022).

According to Rogers (2000), it is suggested that truly xylariaceous fungi, characterized by aseptate ascospores with a germ slit, evolved from dark-colored fungi with one septate ascospores lacking a germ slit. Additionally, Samarakoon et al. (2022) proposed that an independent evolution may have occurred from aseptate to septate ascospores in response to rapid diversification (Samarakoon et al. 2022). Through ancestral character analysis, Samarakoon et al. (2022) stated that the ascospore germ slit appeared exclusively in *Xylariales* during the Cretaceous period, around 95 to 156 MYA. Therefore, the genus *Collodiscula* with its two-celled ascospores was suggested as the primitive xylarialean taxon, and the genus *Astrocystis* was identified as its closest relative (Ju & Rogers 1990). According to the hypothesis of Samarakoon et al. (2022), the ancestral *Xylariomycetidae* probably featured astromatic, clypeate ascomata with aseptate, hyaline ascospores lacking a germ slit, which likely evolved through interactions with plant-fungal endophytes.

Justification of order and problems

The taxonomic placements of many genera in *Xylariales* are controversial, and these taxa are considered genera *incertae sedis* due to uncertain morphologies (sexual or asexual) and lack of molecular data (Daranagama et al. 2018, Wendt et al. 2018, Hyde et al. 2020b). Wijayawardene et al. 2022a) listed 57 genera under *Xylariales* genera *incertae sedis*, of which most of these genera have only a single collection.

Hypocopra species inhabit dung, while *Hypocopra zeae* is saprobic on a dead culm of *Zea mays* and is the only species described from plant substrates. This species is similar to xylariaceous taxa based on morphological characteristics such as immersed ascomata under a clypeus, septate, hyaline paraphyses, 8-spored, unitunicate, cylindrical asci with a J+, apical ring and uniseriate, brown ascospores with a short germ slit. Also, *H. zeae* is similar to *H. rostrata* (99%), *Podosordaria muli* (89%) and *Stromatoneurospora phoenix* (92%) using the LSU, ITS and RPB2 sequences (Samarakoon et al. 2022). Furthermore, there are few *Hypocopra* species and only *Stromatoneurospora phoenix* with molecular data (Becker et al. 2020b). Therefore, the phylogenetic

placement could be altered with the investigation of new sequence data and more collections are needed (Samarakoon et al. 2022).

Hypoxylon, typified by *H. fragiforme*, is clustered in a relatively small clade with *H. howeanum*, *H. ticinense* and *H. rickii* in the recently established phylogenies (Wendt et al. 2018, Lambert et al. 2021), which shows that *Hypoxylon*, in the current sense, is heterogeneous and paraphyletic. Song et al. (2022) also showed that *Hypoxylon* is a polyphyletic genus using phylogenetic analyses. Their studies also showed that the species of *Hypoxylon* were distributed in six separate clades, and any apparent correlation in morphological features with the distribution of species in the phylogenetic trees was not observed. Therefore, the phylogenetic tree showed that the classification of *Hypoxylon* is confusing. They also suggested that more collections, more gene sequences, new taxonomic features, and the application of polyphasic taxonomic approaches using morphological (asexual and sexual), phylogenetic and chemotaxonomic data are needed in the further studies (Song et al. 2022). However, Wibberg et al. (2021) performed a phylogenomic analysis and provide a stable phylogeny for *Hypoxylaceae*, which can also be adapted for *Xylariales* in the future.

Significance

Ecological and economic roles

These taxa consist of coprophilous saprobes, lignicolous (mycobionts or lichen-forming fungi), endolichenic and endophytic fungi, which have potential ecological and industrial applications. Several taxa of *Xylariales*, such as *Daldinia*, *Nemania*, *Hypocopra*, *Podosordaria*, *Poronia* and *Wawelia*, are important in forestry and plant ecology as wood decomposers (coprophilous saprobes) worldwide and are involved in the biodegradation of xenobiotics (Whalley 1996, Stadler 2011, Hyde et al. 2020d). These fungi mostly colonize dead and decaying wood of angiospermous plants and are considered soft-rot fungi mainly because of their ability to degrade lignin, and their ability to degrade cellulose has also been reported (Merrill et al. 1964, Wei et al. 1992). Some xylarialean taxa are mycobionts (lichen-forming fungi), such as *Acrocordiella*, *Burrowsia*, *Parapyrenis* and *Requienella*. These taxa play important roles in ecosystems, providing habitats and food for other animals (birds, ants, snails and mites), aiding soil formation and participating in nutrient cycling (Jackson 2015). They also include secondary metabolites producers (Calcott et al. 2018).

Several genera in *Xylariales* have shown high potential for producing bioactive secondary metabolites by endophytic, lichens and endolichenic fungi, which are used as pharmaceuticals and agrochemicals (Calcott et al. 2018, Oh et al. 2020, Becker & Stadler 2021). These beneficial compounds have shown antibacterial (Hein et al. 1998, Kralj et al. 2006, Arunrattiyakorn et al. 2018, Intaraudom et al. 2019, Liang et al. 2019, Wittstein et al. 2020), antifungal (Schneider et al. 1995, 1996, Burgess et al. 2017, Xu et al. 2017, Intaraudom et al. 2019), cytotoxic (McCloskey et al. 2017, Wang et al. 2019a, Noppawan et al. 2020, Patjana et al. 2021), antimalarial (Intaraudom et al. 2019), anti-inflammatory (Arunrattiyakorn et al. 2018, Chen et al. 2019, Patjana et al. 2021), anti-neuroinflammatory (Chang et al. 2017a, Patjana et al. 2021), immunosuppressive (Chen et al. 2020a,b), and herbicidal (Biasetto et al. 2019, Han et al. 2019) properties, and are used in medical and agriculture industries.

Several important plant parasites have been reported in this order, of which *Dematophora* is the most severe pathogen on trees or agricultural plants (Wittstein et al. 2020). Other pathogenic genera include *Biscogniauxia* (Nugent 2005), *Entoleuca* (Ostry & Anderson 2009), *Hypoxylon* (Stadler 2011) and *Kretzschmaria* (da Luz Morales et al. 2021). Therefore, genera of *Xylariales* are important in terms of their economic and environmental value due to their various lifestyles as saprobes, pathogens, endophytes and lichen-forming fungi (Hyde et al. 2020d).

Chemical diversity

Secondary metabolites are produced by many genera in *Xylariales* in their mycelial cultures and stromata. These compounds are categorized into cytochalasans (a class of hybrid polyketide non-ribosomal peptide), terpenoids, hybrid-terpenoids, non-ribosomal peptides, polyketides, benzenoids, lactones and azaphilones, and are used as pharmaceuticals and agrochemicals (Becker & Stadler

2021). Also, enzymes are essential for biotechnological applications. *Kretzschmaria zonata*, a plant pathogenic fungus, showed great potential for enzyme production. The fungus produced a wide variety of enzymes, such as xylanases, endoglucanases, pectinases, β-glucosidases and hemicellulases (da Luz Morales et al. 2021). Stadler (2011) reported that secondary metabolite production in xylarialean taxa was correlated with molecular data and demonstrated that secondary metabolite profiles are important species-specific characters and have phylogenetic significance. For example, azaphilone pigments are exclusively found in *Hypoxylaceae* (Cedeño-Sanchez et al. 2023a). Different secondary metabolites of this order and their bioactivities are summarized in Table 1.

Table 1 Secondary metabolites and their bioactivities of *Xylariales.*

Species	Chemical compounds	Class of chemical compounds	Bioactivity	Reference
Amphirosellinia nigrospora	Coriloxin	Cyclohexenone derivative	Antimicrobial	Nguyen et al. (2019)
***Annulohypoxylon* sp.**	Hypoxylide Viridistratins A–C	Polyketide Benzenoid	Cytotoxic Antimicrobial	Liu et al. (2018b), Becker et al. (2020a)
***Biscogniauxia* sp.**	Nigriterpene A, 10 xylariterpenoid, Isocoumarin orthosporin, Daldinin C, 7'dechloro-5'-hydroxygriseofulvin, Daldinone D, Sch-642305, Curtachalasin A, Cytochalasin E, Epoxycytochalasins Z8, Z8 isomer, and Z17	Terpenoids and polyketide	Cytotoxic	Pedra et al. (2023)
***Daldinia* sp.**	Botryane-type sesquiterpenoids and Sacchalasins Daldinin Daldiquinone	Polyketide-nonribosomal Peptide Polyketide-nonribosomal Peptide Naphthoquinone	Anti-HIV Cytotoxic Cytotoxic	Qin et al. (2006), Trung et al. (2019), Kamauchi et al. (2018)
***Dematophora* sp.**	Dematophoranes A and B	Isopimarene diterpenoid	Antibacterial and cytotoxic	Wittstein et al. (2020)
***Hypoxylon* sp.**	Rickenyls A-E, Fendlerinines A–D, Fendlerinines E–F Fendlerals A-B and Hypoxyside Hybridorubrins A-D	Terphenyl Terpenoid Azaphilone Diterpene Benzenoid α-pyrones Polyketide-nonribosomal peptide	Antimicrobial, antioxidative, cytotoxic and Anti-malaria Antibacterial Antiparasitic Antimicrobial Cytotoxic	Kuhnert et al. (2015), Intaraudom et al. (2019), Becker et al. (2021), Bills et al. (2012),

	Nodulisporic acid Viridistratins A–C Hypotiens A –D Pseudofuscochalasin A and daldinin F		Antibacterial and Cytotoxic	Becker et al. (2020a), Yuan et al. (2019), Lambert et al. (2021)
Muscodor albus	1-butanol, 3-methyl-, acetate	Ester	Antimicrobial	Strobel et al. (2001)
***Nemania* sp.**	Nemenonediol A and B, Botryane-type sesquiterpenoids, 19,20-epoxycytochalasin C and D, and 18-deoxy-19,20-epoxycytochalasin C	Terpenoid Polyketide-nonribosomal peptide	Cytotoxic Antiplasmodial, cytotoxic and antibacterial	Medina et al. (2019), Kumarihamy et al. (2019)
***Rosellinia* sp.**	Jammosporin A Cytochalasin E and $\Delta^{6,12}$-cytochalasin E	Polyketide-nonribosomal peptide Polyketide-nonribosomal peptide	Cytotoxic Cytotoxic	Sharma et al. (2018), Pourmoghaddam et al. (2022)
Stromatoneurospora phoenix	Phoenixilanes A-B and Punctaporonin B	Sesquiterpenoid	Cytotoxic (Phoenixilanes B)	Becker et al. (2020b)
***Xylaria* sp.**	Cytochalasin C and D Cytochalasin P1 Demethylincisterol A3 and chaxine C Hydroxydecandrin G Nigriterpenes A–F Xylareremophil Xylarinoditerpenes A–R Xylarilongipins A-B xylapeptide A–B E1011 Fimbriethers B, E and G Xylarianin A Penixylarins C Xylarodons A and B β-mangostin 6-ethyl-7,8-dihydroxy-4Hchromen-4-one	Polyketide-nonribosomal peptide Terpenoid Terpenoid Terpenoid Terpenoid Terpenoid Terpenoid Cyclic pentapeptides Polyketides Benzenoid Oxydibenzenoid Benzenoid Hexaketide Xanthone Polyketides Pyranone Pyranone Alkaloid Alkaloid	Herbicide, cytotoxic Cytotoxic Cytotoxic Herbicide Anti-neuroinflammatory Antibacterial Immunosuppressive Immunosuppressive Antibacterial Cytotoxic Anti-inflammatory Cytotoxic Antimicrobial Cytotoxic Anti-inflammatory, antibacterial, antimalarial, and ntimycobacterial	Biasetto et al. (2019), Chen et al. (2017b), McCloskey et al. (2017), Han et al. (2019), Chang et al. (2017a), Liang et al. (2019), Chen et al. (2020a), Chen et al. (2020b), Xu et al. (2017), Ai et al. (2018), Chen et al. (2019), Zhang et al. (2018b), Yu et al. (2019),

	and 3,4-dihydro-5,7,8-trihydroxy-3-methyl-isocoumarin Xylariahgins A –F Xylaropyranones B -C Xylaridines A –B Xylaridines C–D	Anti-inflammatory Cytotoxic Cytotoxic Antimicrobial and Cytotoxic Antimicrobial and Cytotoxic	Guo et al. (2019), Arunrattiyakorn et al. (2018), Patjana et al. (2021), Chen et al. (2018), Guo et al. (2018), Li et al. (2019a), Li et al. (2019b)

Other relevant data and future recommendations

Some species of *Xylariales* are endolichenic fungi, which live in the lichen thallus (Arnold et al. 2009), and have high diversity in tropical or subtropical regions (Oh et al. 2020). Suryanarayanan & Thirunavukkarasu (2017) suggested that endolichenic fungi influence the physiology of lichens and promote the biological function of host lichens in the ecosystems. While the relationship between endolichenic fungi and lichens is unclear (Suryanarayanan & Thirunavukkarasu 2017), Oh et al. (2020) stated that the distribution pattern and biodiversity of endolichenic fungi are essential for understanding the ecology and physiology of lichens and the maintenance of ecosystem sustainability against global climate change. Therefore, they suggested analyzing various lichen species in more environments for more expansion of the diversity and ecology of endolichenic fungi (Oh et al. 2020).

Also, fossils can give complete information about evolution, but the fossil *Xylariales* are extremely rare. There is only a little information about fossils of *Xylariales*, although fruiting bodies and spores were found on the leaves of *Dacrycarpus* (Wu et al. 2021) and in ancient carbonized specimens (Surup et al. 2018). Studies of fossils will expand our understanding of the evolution of *Xylariales* in the future (Maslova et al. 2021). Schmitt et al. (2009) hypothesised that ancestral character state reconstruction can play a vital role in a better understanding of morphological character evolution. Many researchers studied the ancestral character state reconstruction in xylarialean taxa using morphological data of ascospores and appressoria (Chethana et al. 2021b), lifestyles and geographical and host distributions (Pichova et al. 2018, Zhu et al. 2019). However, no information is available on the study of the ancestral character state reconstruction using molecular data (Samarakoon et al. 2022).

Samarakoon et al. (2022) stated that the pseudo-stromatic character found in some diatrypaceous fungi may have an intermediate astromatic and stromatic development and needs more characterizations to examine unknown sexual morphs. According to Samarakoon et al. (2022), the early *Ascomycota* likely have been endophytes and then evolved as saprobes, however, it is unknown how the endophytic species arise as saprobes. Many researchers reported evidence that it is possibly due to the spore origin of endophytes (Rodrigues et al. 1993) and wind-borne xylariaceous fungal spores (Ju et al. 2018). Therefore, Ju et al. (2018) suggested using the efficiency of modern molecular techniques for tracing infections and propagules.

Samarakoon et al. (2022) suggested introducing higher ranks for xylarioid taxa because the criteria for taxonomic classification were altered using molecular data. Therefore, it showed that stalk-like or well-developed stromata could not be used to place all taxa in *Xylariales*. Also, the classification of xylarialean taxa will not be based on stromatic variations in the future, but it will be based on the type of ring, the color of the ascospores, and the presence or absence and the type of germ slit. Daranagama et al. (2018) stated that *Xylaria* may comprise several thousands of species, with the majority not described formally because this genus has never been subjected to a world monograph using modern methodology. Wibberg et al. (2021) sequenced the whole genomes of 13

members of *Hypoxylaceae* and addressed the issues of generic and species delimitation based on phylogenomic reconstructions using amino acid sequences and genomic comparisons. These methods can also be used to define family, generic and species delimitation in *Xylariales*. Therefore, future research can be focused on re-evaluating *Xylariales* using polyphyletic approaches, combining morphology, phylogenetics, phylogenomics and genomic comparisons to produce reliable and stable taxonomy for the order.

***Xylobotryomycetes* Voglmayr & Jaklitsch, Persoonia 42: 41 (2018)**
***Xylobotryales* Voglmayr & Jaklitsch, Persoonia 42: 41 (2019)**

Subphylum : *Pezizomycotina*
Class : *Xylobotryomycetes*

Introduction

Based on the phenotypic differences, coupled with phylogenetic analyses of a combined SSU, LSU, mtSSU, RPB1, RPB2 DNA matrix, the new class *Xylobotryomycetes* was erected to accommodate the single new order *Xylobotryales* with two new families *Xylobotryaceae* and *Cirrosporiaceae* described by Voglmayr et al. (2019b). *Xylobotryales* members are saprobic or maybe parasitic on wood or bark (Voglmayr et al. 2019b).

History

In the primary description of *Xylobotryum*, in 1895a, Patouillard & Lagerheim observed similarities to *Kretzschmaria* and *Xylaria*, and it was accommodated in the heterogeneous, poorly described family *Sphaeriaceae* (Saccardo 1895b, Gäumann 1964, Müller 1973), whereas *Xylobotryum* was placed in *Xylariaceae* by Lindau (1897b). Möller (1901) erected the genus *Trachyxylaria* for *T. phaeodidyma* (the synonym of *Xylobotryum portentosum*), within *Xylariaceae*, while Smith (1901) stated *Xyloceras elliottii* as another synonym of *Xylobotryum portentosum*. Lloyd (1920) combined the generic type *Xylobotryum andinum* in *Thamnomyces* (*Xylariaceae*) based on stromata which is similar in branching pattern but admitted *Xylobotryum* for *X. portentosum* and *X. rickii* (Lloyd 1925). Miller (1949) removed *Xylobotryum* from *Xylariaceae* because of bicellular ascospores and lack of a xylariaceous apical apparatus in the asci, but did not suggest a substitute classification. Acknowledging essential distinct morphological characteristics, and contemplating the similarities to *Xylaria* to be superficial the genus was placed in *Diatrypaceae* (*Xylariales*, *Sordariomycetes*) (Müller & von Arx 1962, Dennis 1970). Rossman (1976) did not assigned *Xylobotryum* to a family, but based on her observations of unitunicate asci and true unbranched paraphyses, she presumed a pyrenomycetous affinity. Based on fissitunicate ascus dehiscence, Rogerson et al. (1990) accommodated *Xylobotryum* in *Pleosporales* (*Loculoascomycetes* = *Dothideomycetes*). *Xylobotryum* was tentatively classified within the *Didymosphaeriaceae*, *Dothideomycetes* based on asci and 1-septate ascospores and it was considered similar to *Didymosphaeria*, but highlighting its unique stipitate stromata in the family (Barr 1987b, 1990a). It was hypothesized that *Xylobotryum* might be affiliated with *Hypsostromataceae* (*Dothideomycetes*) (Huhndorf 1994). This genus was not allocated to a family or order after precise morphological investigation and pure culture, but uncertainly considered affinities of loculoascomycetes, based on the light functional bitunicate asci and the stromal nature of the ascoma (Ju & Rogers 1994). Eriksson & Hawksworth (1988) and Kirk et al. (2008a), accommodated *Xylobotryum* in *Dothideales* and *Dothideomycetes* genera *incertae sedis*, respectively.

Réblová & Seifert (2012), revealed a phylogenetic position of *Cirrosporium* as a sister clade to *Mycocaliciales* within *Eurotiomycetes* with low support in their phylogenetic results of a multi-gene sequence matrix. They concluded that *Cirrosporium* may warrant placement in a family and order of its own. However, they did not describe them due to their separate phylogenetic position. *Xylobotryaceae* is the type family in *Xylobotryales*. It is typified by *Xylobotryum andinum,* which is characterized by not being thickened at the apex, a crown, and asci with a pore and two-celled ascospores. *Xylobotryum* is a curious genus that is broadly distributed worldwide and found in

tropical and subtropical regions (Rossman 1976, Ju & Rogers 1994). Members of *Xylobotryum* have dark carbonaceous stromata which are similar to *Xylaria* species, however, they have naked perithecia and two-celled ascospores (Trierveiler-Pereira et al. 2008). *Xylobotryum rickii* was described as a new species which closely resembles *X. portentosum*, but has much larger ascospores (Müller & von Arx 1962). *Xylobotryum rickii* was investigated by Rossman (1976), a species which was precisely xylariaceous, because of having an amyloid ascus apex and dark-brown ascospores with distinguished germ slits. *Xylobotryum coralloides* was introduced from New South Wales (Petrak 1950). After investigating the isotype, the species was considered valid (Chaves-Batista & Silva-Maia 1958). Subsequently, it was synonymized with *X. andinum* (Müller & von Arx 1962). Hawksworth (1980b) synonymized *X. caespitosum* under *Chaenothecopsis caespitosa*. Réblová & Seifert (2012), isolated *Cirrosporium novae-zelandiae*, from wood and bark on a trunk of *Dacrydium cupressinum* (*Podocarpaceae*) in New Zealand. Compound microscopic and environmental scanning electron microscopic examinations showed the details of the unusual meristem arthric conidium ontogeny existing in the protologue. A multi-locus phylogeny showed that it is phylogenetically related to *Eurotiomycetes* and it was recovered in a long branch as sister to *Mycocaliciales* of *Mycocaliciomycetidae*. *Cirrosporium* morphologically resembles those members of *Mycocaliciales*. However, the lack of known anamorphs in this order does not provide any further explanation of possible relationships. The rare and widespread ontogenetic pattern of arthritic meristem is polyphyletic and occurs in completely separate groups of *Ascomycota* and *Basidiomycota* anamorphs. Their position has been ambiguous within *Ascomycota*, but recent molecular evidence supported their placement in *Xylobotryales* (Voglmayr et al. 2019b).

General description

The taxa are reported as sexual and asexual morphs except *Xylobotryum* whose asexual morph is unknown (Eriksson & Hawksworth 1995, Lumbsch & Huhndorf 2007, 2010).

Sexual morph: Stromatic. *Stromata* large, stipitate, upright, branched or unbranched, bearing superficial ascomata. *Ascomata* perithecioid, sessile or stipitate, ostiolate. *Ostioles* periphysate. *Paraphyses* filiform, free at ends. *Asci* bitunicate, fissitunicate, with an apical ring at apex. *Ascospores* brown, two-celled, with longitudinal germ slits. Asexual morph: *Pycnidial* unilocular, cylindrical, comprising a sterile basal part and a fertile upper part with an apical ostiole. *Conidiogenous cells* forming a meristem, producing pigmented, septate arthroconidia (Voglmayr et al. 2019b) (Figs. 276, 277, 278).

Families included in *Xylobotryales*

Cirrosporiaceae Voglmayr & Jaklitsch
Xylobotryaceae Voglmayr & Jaklitsch

Evolution

Voglmayr et al. (2019b) confirmed the placement of the *Xylobotryum-Cirrosporium* clade basal to the entire *Eurotiomycetes* and sister to the *Dothideomycetes-Arthoniomycetes* clade based on multigene phylogenetic tree. When it comes to morphology, the characters such as longitudinal germ slit in *Xylobotryum* and meristem arthroconidia in *Cirrosporium* are polyphyletic and occur in several classes of *Ascomycota*. For instance, longitudinal germ slits in brown ascospores are common in some *Sordariomycetes*, *Dothideomycetes* and *Leotiomycetes* families (Jaklitsch et al. 2014, 2016a). Meristem arthroconidia also arise in *Leotiomycetes* and other genera of uncertain affinities (Réblová & Seifert 2012). However, the phylogenetic support and some unique morphological characteristics of *Xylobotryum* and *Cirrosporium* supported the classification of these genera into a new class, *Xylobotryomycetes.*

Justification of order and problems

The close phylogenetic relationship between *Xylobotryum* and *Cirrosporium* was unexpected. Considering the differences of morphological character combinations between these two genera, it was doubtful that these two genera are only distinct at the generic level, but classified as two

dissimilar families *Cirrosporiaceae* and *Xylobotryaceae* within *Xylobotryales* (Voglmayr et al. 2019b).



Figure 276 – a–f Morphology of *Xylobotryum portentosum* stromata *in situ* (Adapted from Trierveiler-Pereira & Baltazar 2022).

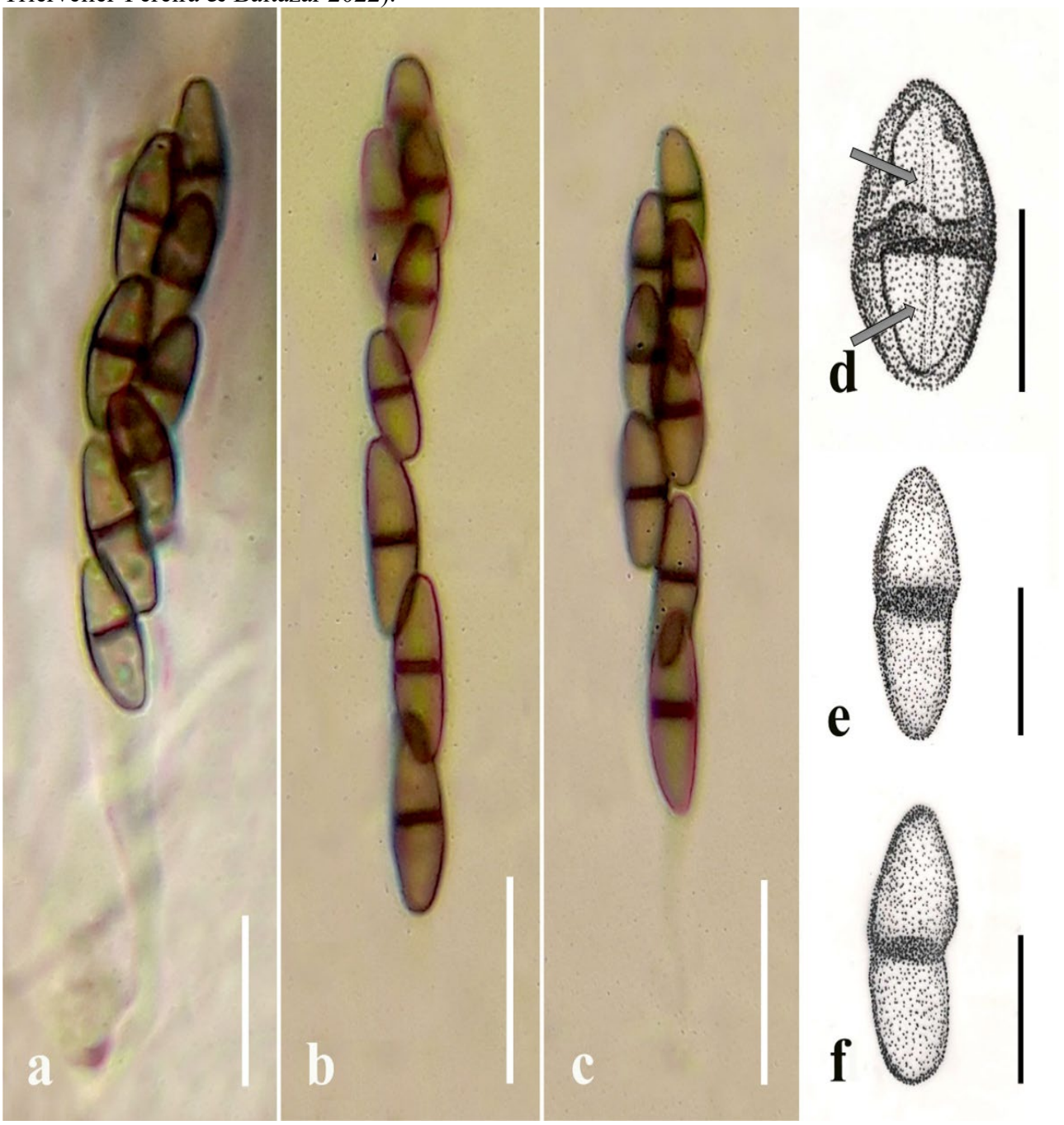


Figure 277 – Asci and ascospores of *Xylobotryum portentosum*. a–c Asci. d Mature ascospore indicating faint longitudinal germ slits with arrows. e, f Ascospores (adapted from Trierveiler-Pereira & Baltazar 2022, redrawn from Voglmayr et al. 2019b). Scale bars: a–c = 10 µm, d–f = 5 µm.

Significance

Ecological and economic importance

Both genera in this order are saprobic. *Xylobotryum* is widely distributed in warm tropical and subtropical regions (Müller & von Arx 1962, Rossman 1976, Ju & Rogers 1994) including Brazil, Chile, Colombia, Costa Rica, Dominica, Ecuador, French Guiana, Guadeloupe, Guyana, Jamaica, Martinique, Nicaragua, Panama, Peru, and Puerto Rico (Voglmayr et al. 2019b). *Cirrosporium* was collected from two locations in New Zealand; Westland National Park, Lake Matheson, on the bark of fallen *Weinmannia racemosa*, and Tai Poutini National Park, Westland, on decaying wood and bark of *Dacrydium cupressinum* (Réblová & Seifert 2012).

Chemical diversity

Relevant studies are not available for the chemical diversity of *Xylobotryales*.

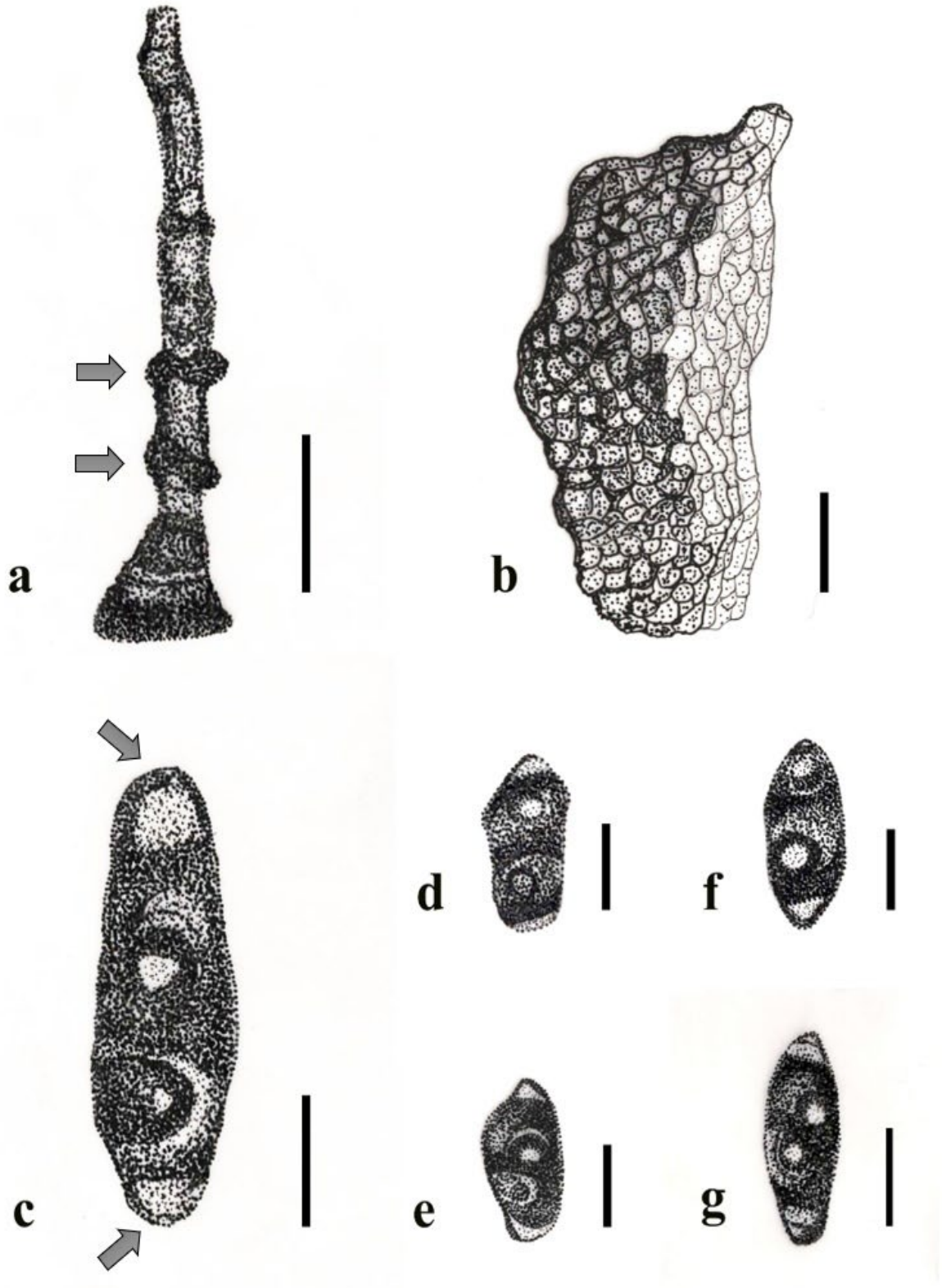


Figure 278 – Morphology of *Cirrosporium novae-zelandiae*. a Conidioma grown in the culture (arrows show sterile hyphae growing in ring-like formations on the outer conidiomata wall). b Section of the pycnidium. c–g Conidia (Arrows show a circular pore-like structure in both end cells) (redrawn from Réblová & Seifert 2012). Scale bars: a = 1 mm, b= 50 μm, c–g = 5 μm.

Other relevant data and future recommendations

Based on the results of Voglmayr et al. (2019b), the close phylogenetic relationship of *Xylobotryum* and *Cirrosporium* was unexpected and remarkable. The morphological comparison of these two genera is challenging, as no asexual form of *Xylobotryum* or sexual form of *Cirrosporium* has been identified. Therefore, due to the differences of their morphological traits, it seems unlikely that *Cirrosporium* and *Xylobotryum* differ only at the generic level. These differences support their classification in two separate families within the *Xylobotryales*.

***Xylonomycetes* Gazis & P. Chaverri, in Gazis, Miądlikowska, Lutzoni, Arnold & Chaverri, Molecular Phylogenetics and Evolution 65(1): 301 (2012)**
***Symbiotaphrinales* Baral & E. Weber, Mycological Progress 17 (1–2): 221 (2017)**

Subphylum : *Pezizomycotina*
Class : *Xylonomycetes*

Introduction

Symbiotaphrinales was established by Baral et al. (2018b) for its type family *Symbiotaphrinaceae* which accommodates a single genus *Symbiotaphrina* with *S. buchneri* as the type. The taxa are reported in both sexual and asexual morphs. The name "*Symbiotaphrina*" reflects the symbiotic lifestyle of the fungus and its morphological resemblance to the yeast-like asexual morph of *Taphrina* (Baral et al. 2018b).

History

The generic type *Symbiotaphrina* was invalidly described by Kühlwein & Jurzitza (1961) and was later validated by Gams & von Arx (1980). *Symbiotaphrina* was typified by *Symbiotaphrina buchneri* which was reported from a drugstore beetle (Kühlwein & Jurzitza 1961). Jurzitza (1964) added the second species, *S. kochii* that was reported from tobacco beetle. The sexually typified genus *Tromeropsis* was established by Hawksworth & Sherwood (1981). Baral et al. (2018b) proposed to keep the name *Symbiotaphrina* over *Tromeropsis* based on the economic importance of *Symbiotaphrina* as they were found as symbionts on pests. *Symbiotaphrina* was placed in *Taphrinaceae* due to yeast-like budding growth and the family was formally included in *Saccharomycetales* but differs from *Taphrina* by its symbiotic mode of life. The phylogenetic analysis based on the SSU gene region revealed the close association between *Symbiotaphrina* and the filamentous ascomycetes (Jones & Blackwell 1996, Noda & Kodama 1996). Further, S. *kochii* also formed a basal clade to *Pezizomycetes*/*Orbiliomycetes* in the SSU based phylogenetic analysis (Berbee 2001).

In the multi-gene phylogenetic analysis conducted by Bhattacharya et al. (2005), the genus formed a clade outside of any class of *Ascomycota*. Later, *Symbiotaphrina* formed a close clade to *Arthoniomycetes* and *Dothideomycetes* with low statistical support in the multi-gene phylogenetic analysis conducted by Schoch et al. (2009a). The genus formed a close clade to *Hyphozyma lignicola* in the two-locus phylogenetic analysis (Gazis et al. 2016) and the authors proposed *Symbiotaphrinales* nom. nud. for this clade. *Hyphozyma lignicola* was isolated from black galls on trunks of *Populus tremuloides* in Canada (Hutchison et al. 1993). *Hyphozyma* shares a similar morphology to *Symbiotaphrina* in having a yeast-like phase showing budding of its conidia by holoblastic conidiogenesis but differs from *S. buchneri* and *S. kochii* in producing more or less extensive mycelia in pure culture. Based on a single gene (SSU or LSU) and multi-gene phylogenetic analysis (SSU, ITS, LSU), Baral et al. (2018b) established *Symbiotaphrinales* in *Xylonomycetes*.

General description

Sexual morph is mostly uniform among species and are characterized by apothecioid ascomata that are sessile, discoid, black with a smooth margin and saccate, fissitunicate, inamyloid, multi-spored asci with broadly ellipsoid to cylindrical, hyaline ascospores. The asexual morph forms yeast-

like cells formed in colonies. *S. desertorum*, *S. lignicola*, *S. microtheca* and *S. sanguinea* show mycelial phase in pure culture (Figs. 279, 280).

Sexual morph: (See Baral et al. 2018b). Asexual morph: Yeast-like budding from ascospores or conidia or hyphae (See Baral et al. 2018b).

Families included in *Symbiotaphrinales*

Symbiotaphrinaceae Baral & E. Weber

Evolution

Symbiotaphrina buchneri and *S. kochi* formed a monophyletic group which distinct from other major lineages in the SSU-based phylogenetic analyses and they appear to have parted from other filamentous fungi during the early radiation of the euascomycetes and later became obligatory partners of the beetles (Noda & Kodama 1996).

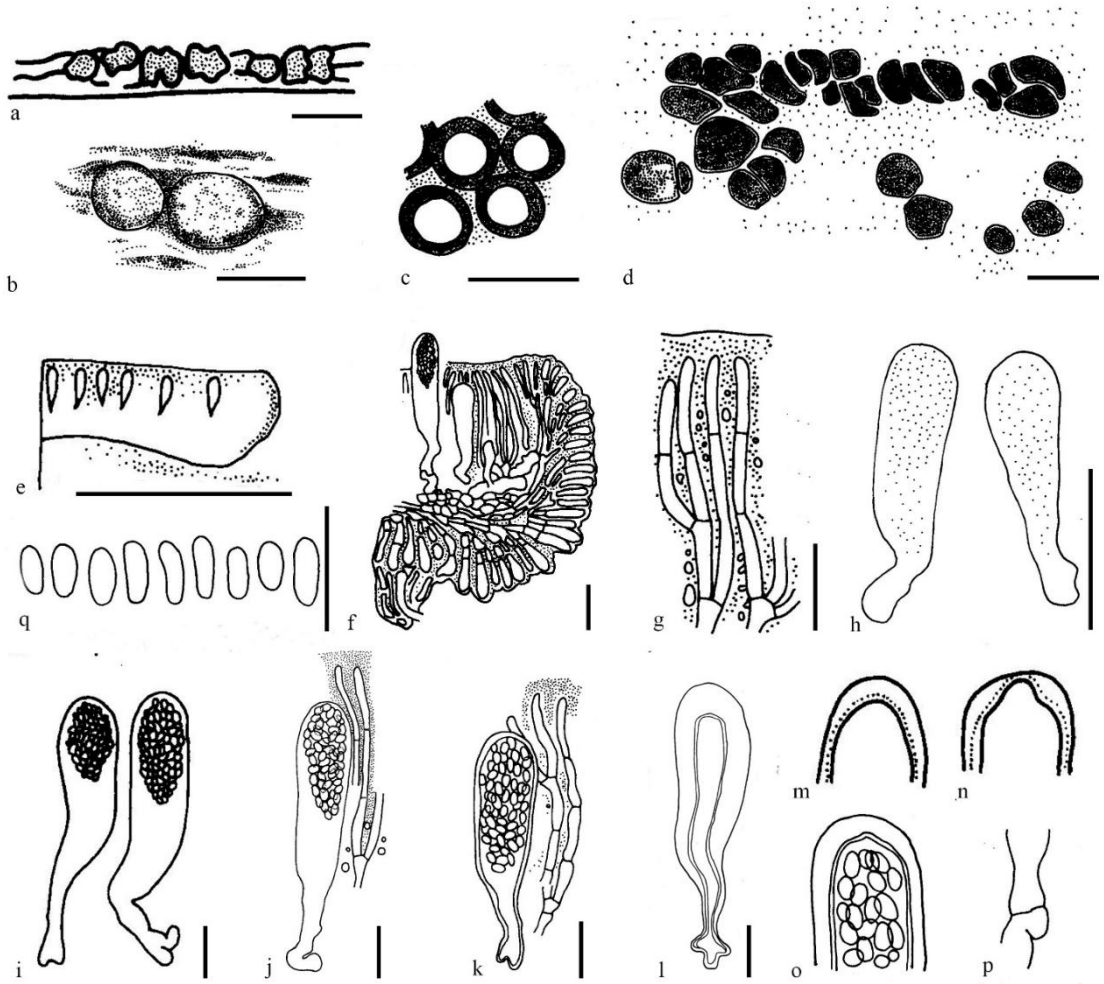


Figure 279 – Sexual morph of *Symbiotaphrinales*. a, b Apothecia (rehydrated) on the substrate (a, d *Symbiotaphrina microtheca*, b *S. larreae*). c Ectal excipulum in external view (optical cross-section) (*S. larreae*). e Apothecia in the median section (*S. microtheca*). f Marginal ectal excipulum in median section, with elongated ascus shortly before spore discharge (*S. microtheca*). g Paraphyses (*S. microtheca*). h–l Ascus (*S. microtheca*). m–o Apices of immature asci (*S. microtheca*). p Ascus base with crozier (*S. microtheca*). q Ascospores (*S. microtheca*) (redrawn and redrawn from Baral et al. 2018b). Scale bars: a, d = 500 µm, b = 250 µm, c = 10 µm, e = 100 µm, f, h = 20 µm, g, i–l, q = 10 µm.

Significance

Ecological and economic roles

Symbiotaphrina kochii was recorded as an endophyte from *Dracaena cambodiana* (Baral et al. 2018b) and the species was also reported as a symbiont with Cigarette beetle that can detoxify compounds such as plant allelochemicals, meal toxins, mycotoxins, insecticides, and herbicides (Shen & Dowd 1991). All *Symbiotaphrina* are assumed to have a symbiotic asexual morph, saprobic sexual morph, and mycelial asexual morph on the surface of dead xeric wood of gymnosperms and angiosperms. *Symbiotaphrina buchneri* was isolated from *Stegobium paniceum* (≡ *Sitodrepa panicea*, drugstore beetle) that fed on pulverized fruits of *Capsicum*. The members are reported in temperate to tropical, and humid to arid regions (Baral et al. 2018b).

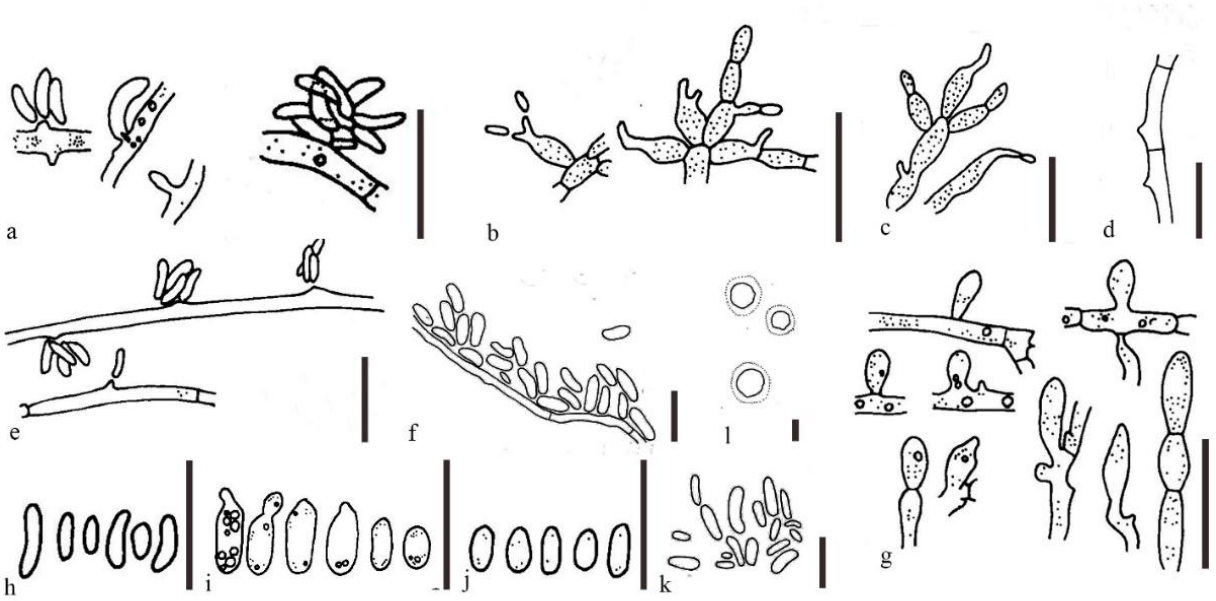


Figure 280 – Asexual morph of *Symbiotaphrinales* (*Symbiotaphrina microtheca*). a, e Hyphae with integrated peg-like conidiogenous cells. b, c Producing conidia, d, f Integrated conidiogenous cells. g Chlamydospore-like immature conidiogenous cells in old cultures, often with warted surface, in optical section showing small LBs in the cytoplasm. h Primary conidia. i Swollen primary conidia, partly forming secondary conidia. j Secondary conidia. g Chlamydospore-like immature conidiogenous cells in old cultures, often with warted surface, in optical section showing small LBs in the cytoplasm. k Conidia from pure culture (primary conidia, mostly swollen; partly also secondary conidia). l spore heap (redrawn and redrawn from Baral et al. 2018b). Scale bars: a–k = 10 µm, l = 20 µm.

Xylonales **Gazis & P. Chaverri, in Gazis, Miądlikowska, Lutzoni, Arnold & Chaverri, Molecular Phylogenetics and Evolution 65(1): 301 (2012)**

Subphylum : *Pezizomycotina*
Class : *Xylonomycetes*

Introduction

Gazis et al. (2012) established *Xylonales* to accommodate *Xylona heveae* that was isolated from *Hevea brasiliensis* in Peru. The order comprises two genera including the generic type *Xylona* and *Trinosporium*. *Trinosporium guianens*e, was described by Crous et al. (2012c), shared similarities with *Xylona heveae*, while is characterized by ostiolate pycnidia, conidiogenous cells with apical periclinal thickening and percurrent proliferation, and tetrahedral conidia. Gazis et al. (2016) placed *Trinosporium* within the *Xylonales* based on the phylogenetic analysis of ITS and LSU ribosomal regions. This species was originally described as a member of *Dothideomycetes incertae sedis* by

Crous et al. (2012c) and isolated as a contaminant in the rainforest, in France. *Xylonales* consist of a single-family *Xylonaceae* recognized as an ecologically and morphologically diverse group (Gazis et al. 2016, Wijayawardene et al. 2020, Hashimoto et al. 2021). Hashimoto et al. (2021) revised resin-dwelling fungi, focusing on *Sarea difformis* and *S. resinae* and reclassified these species under *Xylonales*. They reinstated *Tromera* as a distinct genus to accommodate *Tromera resinae* (= *Sarea resinae*) and accepted four genera (*Sarea*, *Trinosporium*, *Tromera*, and *Xylona*), within *Xylonales*. During the taxonomic investigations of *Symbiotaphrinales*, Gazis et al. (2016), considered it as a member of *Xylonomycetes* but this classification was not confirmed based on phylogenetic, morphological, and ecological observations. This order was subsequently reclassified as *Pezizomycotina*, *incertae sedis* (Hashimoto et al. 2021). Based on phylogenetic analysis *Sarea difformis* and *Zythia* Fr (= *Tromera*) were placed in *Sareomycetes* (Mitchell et al. 2021). Díaz-Escandón et al. (2022), accepted only two orders *Xylonales* and *Symbiotaphrinales,* within *Xylonomycetes.*

History

Initial studies on *Xylonales*, focused on endophytic strains discovered in the sapwood of *Hevea* spp. from Peru (Gazis et al. 2012). Their phylogenetic analyses of LSU, SSU, 5.8S, mtSSU, RPB1, and RPB2 gene sequences suggested establishing a new genus *Xylona*, order *Xylonales* and class *Xylonomycetes*. This species was reported in its asexual morph characterized by non-oscillate pycnidial conidiomata, and hyaline aseptate, heart-shaped melanized conidia (Gazis et al. 2012). The range of genera in the *Xylonomycetes* enlarged over time. Gazis et al. (2016) included two genera *Symbiotaphrina* and *Trinosporium* based on phylogenetic evidence and morphological resemblance. *Trinosporium*, unlike *Xylona*, does not have a sexual morph, but unlike *Xylona* is characterized by pycnidial conidiomata with ostioles and produces trigonous brown conidia (Crous et al. 2012c). Based on phylogenetic analysis conducted by Gazis et al. (2016), which utilized two gene regions (ITS and LSU), identified two distinct clades: 1) *Xylona* and *Trinosporium* were grouped as *Xylonales* and 2) *Symbiotaphrina* and *Hyphozyma lignicola* formed another clade tentatively designated as *Symbiotaphrinales*. Baral et al. (2018b) validated the order *Symbiotaphrinales* within *Xylonomycetes*, alongside the family *Symbiotaphrinaceae*. Beimforde et al. (2020) proposed the establishment of a new class, *Sareomycetes* to classify *Sarea*, supported by a phylogenetic analysis incorporating ITS, SSU, and mtSSU, LSU sequence data.

Hashimoto et al. (2021) disagreed with Beimforde et al. (2020) for creating a new class, order, and family, preferring to classify these fungi within *Xylonaceae*. *Xylonomycetes* and *Sareomycetes* were recovered as monophyletic in the six-gene phylogenetic analysis conducted by Hashimoto et al. (2021). Further, they mentioned that *Sarea sensu lato* closely resembled *Agyrium*, but mentioned *Trinosporium guianens*e, closely related to *Xylonaceae* in BLAST comparisons. Morphological observations also supported their argument for retaining these fungi within *Xylonaceae* rather than adopting new taxonomic ranks proposed by Beimforde et al. (2020). Recent taxonomic revisions by Hashimoto et al. (2021) have integrated *Sareomycetes* into *Xylonomycetes*, based on phylogenetic analyses along with ecological and morphological data. *Saera* is a resinicolous taxon that was established by Fries (1825) and is characterized by its sexual and asexual morphs such as orange or black, rounded ascomata, clavate, polysporous asci with a Lecanora-type ascus apex and round aseptate ascospores and pycnidial conidiomata (Hawksworth & Sherwood 1981). However, the taxonomic position of *Sarea* was debated for long time. Poelt (1974a) placed it in *Acarosporaceae* (*Lecanorales*, *Lecanoromycetes*) based on the polysporous asci with a thickened ascus apex (*Lecanora*-type). Hawksworth & Sherwood (1981) placed it within *Agyriaceae* (*Lecanorales*) due to the similarity to *Agyrium* in terms of its polysporous asci, peridium structure and saprobic habitats. Bellemére (1994b) accepted the genus within *Lecanorales* based on ultrastructural observation of the ascus apex. Eriksson et al. (2004) placed it in *Agyriales* without providing any reasons. Reeb et al. (2004) treated it in *Pezizomycotina incertae sedis* based on multi-gene phylogenetic analysis. Hodkinson & Lendemer (2011) stated that the sequences used for *Sarea* in the study of Reeb et al. (2004) could potentially have been contaminated and placed it in *Trapeliaceae* based on

morphological similarities. The genus formed a clade outside of *Lecanoromycetes* in the study of Miadlikowska et al. (2014). Beimforde et al. (2020) established a new class (*Sareomycetes*) to accommodate *Sarea* based on morphology and phylogenetic analyses. However, the relationship between *Sareomycetes* and *Xylonomycetes* was not discussed in the study of Beimforde et al. (2020). However, based on ITS sequence similarity and morphological traits such as pycnidial conidiomata and unique conidiogenous cells similar to *Trinosporium* and *Xylona*, *Sarea* was proposed as a closely related group *Xylonomycetes*. *Sareomycetes* is distinctive due to resinicolous habitats and polysporous asci, features that are not commonly found in other *Ascomycota* classes like *Dothideomycetes*, *Eurotiomycetes*, *Leotiomycetes*, and *Sordariomycetes*. *Sarea difformis* and *S. resinae* exhibit both sexual and asexual morphs on gymnosperms and monocotyledons. Previously, Hawksworth & Sherwood (1981) merged *Tromera* with *Sarea* based on shared ecological and morphological characteristics. However, Hashimoto et al. (2021) refuted this association, highlighting significant morphological distinctions between *Tromera* and *Sarea*. Mitchell et al. (2021) treated *Sarea difformis* and *Zythia* Fr (=*Tromera*) to *Sareomycetes*. Díaz-Escandón et al. (2022) conducted phylogenomic analyses revealing that *Xylonomycetes* comprises two orders: *Xylonales* and *Symbiotaphrinales*. *Xylonales*, was accepted with a single-family *Xylonaceae* including two genera, *Trinosporium* and *Xylona* (Wijayawardene et al. 2020, Hashimoto et al. 2021, Díaz-Escandón et al. 2022).

Different studies utilizing various gene sequences for concatenated datasets (SSU, ITS, LSU, mtSSU, RPB1, and RPB2 sequences) have confirmed that *Xylona* and *Trinosporium* form a distinct clade alongside the genus *Sarea* (Beimforde et al. 2020, Hashimoto et al. 2021, Mitchell et al. 2021, Díaz-Escandón et al. 2022). In terms of morphology, the genus *Sarea* has both sexual and asexual structures, but only asexual structures have been observed for both *Trinosporium* and *Xylona* (Beimforde et al. 2020, Hashimoto et al. 2021, Mitchell et al. 2021). The phylogenetic analysis based on the SSU-LSU-RPB1-RPB2-mtSSU sequences indicated that four genera (*Sarea*, *Trinosporium*, *Tromera*, and *Xylona*) were introduced in the class *Xylonomycetes*, with *Sareomycetes* considered a synonym for *Xylonomycetes*. Thus, only one class, *Xylonomycetes*, is accepted in this study by Hashimoto et al. (2021). Furthermore, Mitchell et al. (2021) conducted a phylogenetic analysis using ITS, LSU, and mtSSU, confirming that *Sareomycetes* includes three genera: *Atrozythia*, *Sarea*, and *Zythia*. This study did not mention any investigation into *Xylonomycetes*. Some reclassifications were made by Hashimoto et al. (2021), but the reclassifications by Mitchell et al. (2021) completely superseded those of Hashimoto et al. (2021), leading to the introduction of *Atrozythia* and *Zythia* within *Sareomycetes*. Additionally, phylogenomic topologies from analyses using concatenated alignments and gene tree coalescence by Díaz-Escandón et al. (2022) showed that *Xylona* and *Sarea* clustered in one clade, forming a monophyletic clade. However, this does not imply that this clade represents a single class; to achieve better results, all genera of the class must be included in the phylogenetic analysis. Earlier researchers have described the asci of *Sareomycetes* as “lecanoralean” (or “rostrate”) and noted that they are “not functionally bitunicate” or fall under the broadly interpreted "archaeascé" category (Mitchell et al. 2021). The findings show that the three genera, particularly *Atrozythia*, exhibit ascus dehiscence characterized by the outer layer rupturing at the tip of the ascus, allowing the inner wall to protrude. The inner wall extends a certain distance past the outer wall, with variations observed among different species (Mitchell et al. 2021). This observation aligns with the electron microscopy studies conducted on a *Sarea* species by Bellemére (1994a, b). It remains uncertain in the findings of Mitchell et al. (2021) whether there exists a fully separated zone between the inner and outer layers; therefore, the results support the notion that this represents the "rostrate" type of ascus dehiscence (Mitchell et al. 2021). The differences observed in both morphological and phylogenetic analyses emphasized that two classes can be present, namely *Sareomycetes* (*Atrozythia*, *Sarea*, and *Zythia*) and *Xylonomycetes* (*Trinosporium* and *Xylona*) (Beimforde et al. 2020, Hashimoto et al. 2021, Mitchell et al. 2021, Díaz-Escandón et al. 2022). Hashimoto et al. (2021) indicated that these two classes should be combined based on morphological and molecular indicators. However, these two classes exhibit numerous differences in terms of morphology (both sexual and asexual stages), molecular (distinct branches), and ecological (life cycle

and substrates) aspects (Gazis et al. 2012, Beimforde et al. 2020, Mitchell et al. 2021, Díaz-Escandón et al. 2022). Thus, *Sarea* is categorized within *Sareomycetes*, *Sareales*, and *Sareaceae*, determined by its morphological characteristics, phylogenetic relationships, and ecological contexts. This distinction not only highlights unique evolutionary lineage of *Sarea* but also paves the way for further research into its ecological functions and robust phylogenetic analysis.

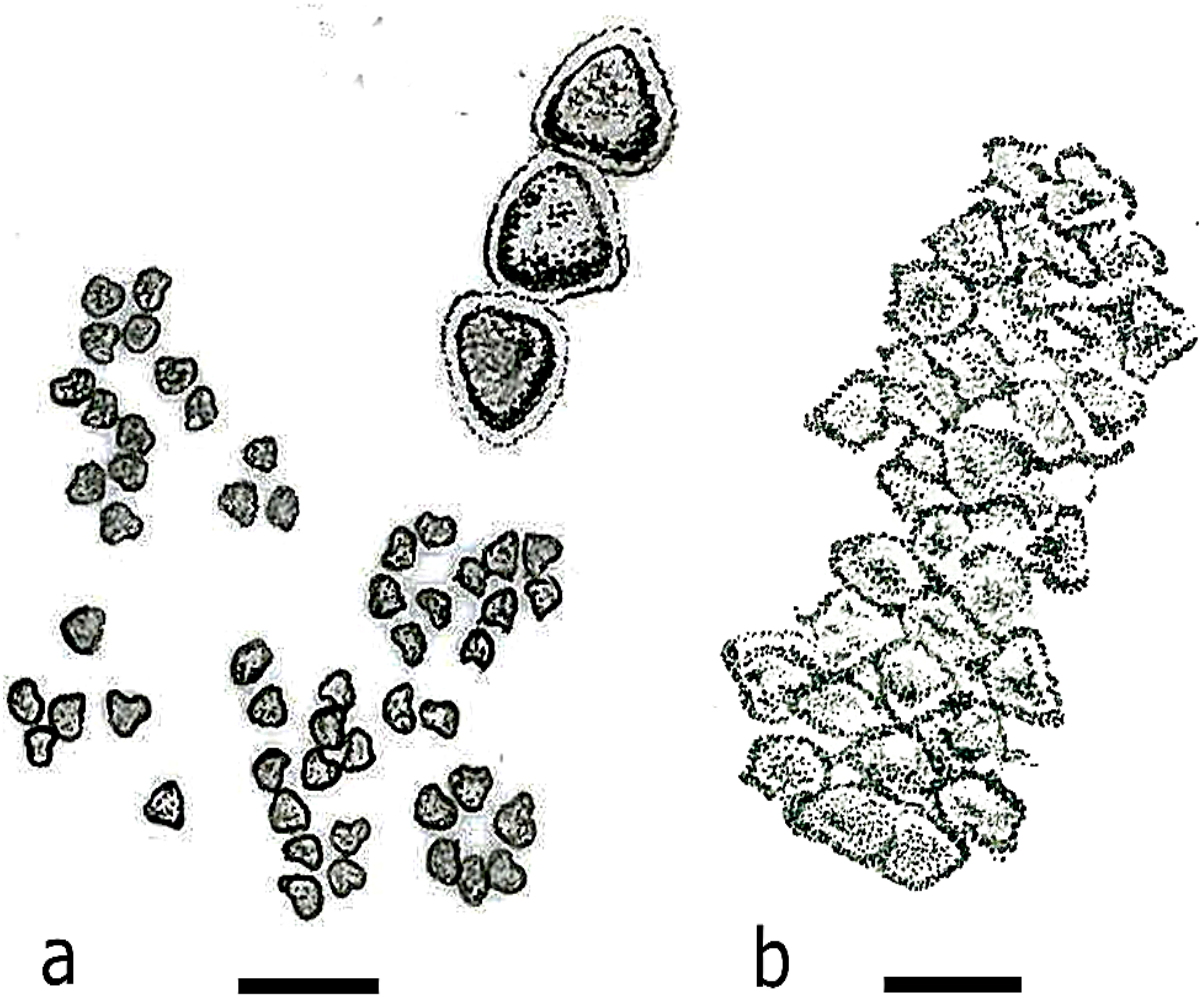


Figure 281 – Conidia morphology of *Xylonales*. a *Xylona*. b *Trinosporium*. (redrawn from Gazis et al. 2012, Crous et al. 2012c). Scale bars: a = 20 μm, b = 10 μm.

General description

Sexual morph has not been observed among the members of *Xylonales*. The mycelium is septate, branched, hyaline, and smooth. Conidiomata are pycnidial, astromatic, initially immersed and young, becoming fuscous black and subspherical and the ostiole is absent. Chlamydospores are rarely formed (Crous et al. 2012c, Gazis et al. 2016). In *Xylona*, conidiophores are absent, and conidiogenous cells are enteroblastic, phialidic, discrete, and hyaline, with a single collarette. In *Trinosporium*, conidiogenous cells are hyaline to pale brown, smooth, thin-walled, ampulliform to subcylindrical, with a periclinal thickening at the apex and occasionally percurrent proliferations. Conidia are brown, smooth, widest at the apex with three lateral rounded lobes, tapering towards a truncate base. In *Xylona*, conidia are abundantly produced singly, with an apically rounded shape and two lateral obtuse projections resembling a heart shape, narrowing and truncated at the base. They are hyaline when young, turning dark brick and brown as they mature, aseptate, thick-walled, and smooth (Gazis et al. 2012). The close association of *Trinosporium* and *Xylona* is supported by shared morphological characteristics such as pycnidial conidiomata and brown conidia, enteroblastic conidiogenous cells and the absence of a sexual morph (Crous et al. 2012c, Gazis et al. 2016, Mitchell

2021). *Xylona heveae* is characterized by its unique heart-shaped melanized conidia and adaptation to an endophytic lifestyle (Gazis et al. 2012). The asexual morph of *Xylona* and *Trinosporium* are illustrated in Figs. 281, 282.

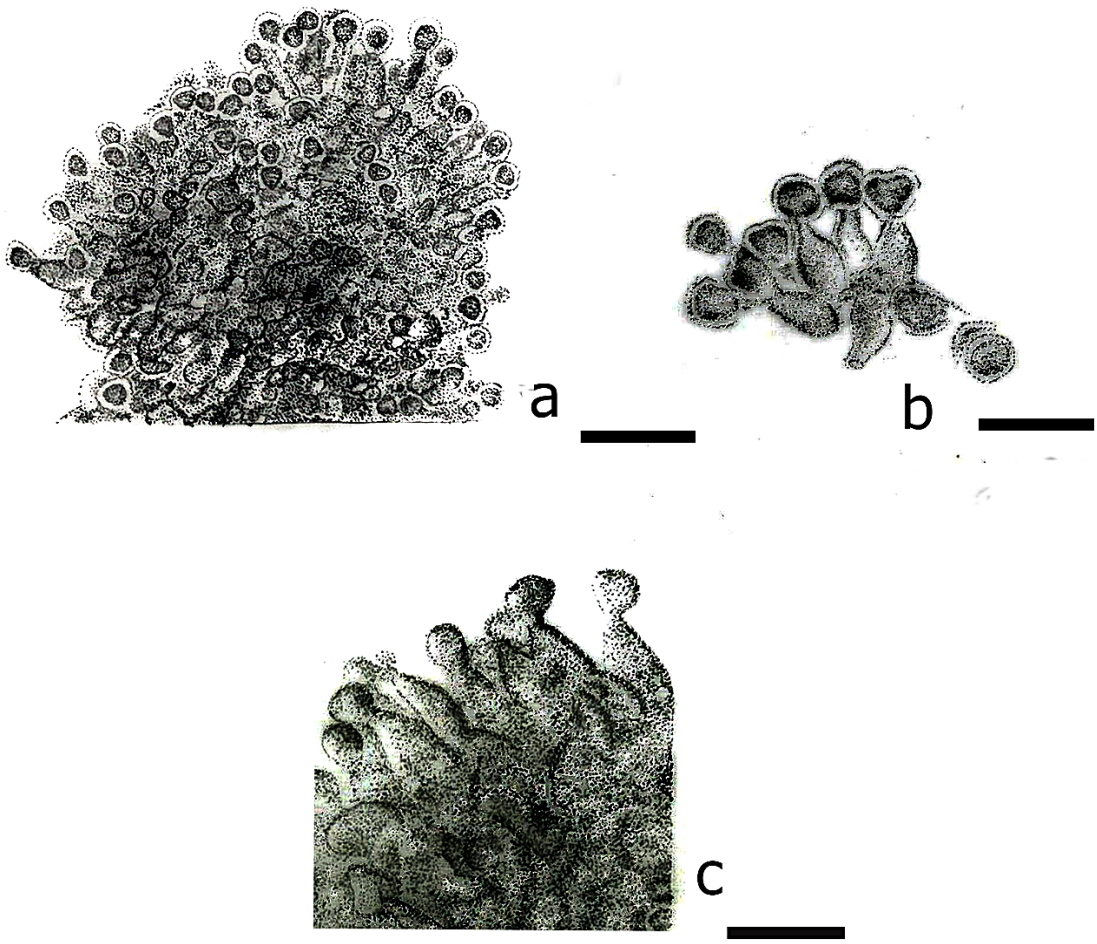


Figure 282 – Conidiogenous cells morphology of *Xylonales*. a, b *Xylona*. c *Trinosporium* (redrawn from Gazis et al. 2012, Crous et al. 2012c). Scale bars: a, b = 20 µm, c = 10 µm.

Families included in *Xylonales*

Xylonaceae Gazis & P. Chaverri

Evolution

Based on Gazis et al. (2012), *Xylonomycetes* evolved within the broader context of the *'Leotiomyceta*' radiation and is revealed by multi-locus phylogenetic analyses. It has been postulated that endophytic lineages, such as *Xylonomycetes*, may have arisen multiple times from plant pathogenic ancestors. Conversely, there is speculation that plant pathogenic species could have originated from endophytic lineages (Delaye et al. 2013, Xu et al. 2014) and were initially classified as a novel class *Xylonomycetes* within *Pezizomycotina*.

Justification of order and problems

The close association of *Trinosporium* and *Xylona* was supported by shared morphological characteristics in having ostiolate pycnidial conidiomata and trigonous brown conidia (Crous et al. 2012c). However, Crous et al. (2012c) suggested that based on ITS sequences, *Trinosporium guianense*, is related to *Sarea difformis* and *S. resinae*. The sexual form has not been reported in *Trinosporium* and *Xylona*. Thus, broad taxon sampling can help with detailed reviews of these genera.

Significance

Ecological and economic roles

Based on genome content, *Xylonales* order displays unique ecological traits (Gazis et al. 2016) from saprobes like *Trinosporium* (Crous et al. 2012c) to endophytes such as *Xylona*, found in the sapwood of *Hevea brasiliensis* (Gazis et al. 2016). *Xylona,* as an endophyte, does not reduce its fitness of its host and cannot adapt to a different lifestyle (Arnold et al. 2003, Rodriguez et al. 2009). *Xylona heveae* has a low amount of CAZymes in contrast with the other endophytes, and this enzyme causes host colonization and plant cell wall degradation. Therefore, it cannot become pathogenic, and the transition to a saprotrophic lifestyle after host senescence appears improbable (Misas-Villamil & van der Hoorn 2008, Gazis et al. 2016). Due to a lack of enzymes like cutinases and pectinases, *Xylona* strains cannot invade their hosts through direct penetration. Therefore, they penetrate their host through the pores of the host, such as stomata or lenticels lenses, stomata, or through the vascular system of root. *Xylona heveae* uptakes sucrose directly by feeding from the apoplastic washing fluid (AWF), which contains monosaccharides, such as glucose, fructose, and sucrose and this strategy can prevent plant defense mechanisms. *Xylona* strains are known as a horizontally transmitted endophyte (HTE), so they can be used as new antibiotics, enzymes with applications in the bio-fuel industry, and drugs (Strobel & Daisy 2003, Arnold & Lutzoni 2007, Rodriguez et al. 2009, Suryanarayanan et al. 2009). *Trinosporium* is saprobic and reported in wood, and plays a role in the decomposition of plant material in its natural habitats. *Trinosporium guianense* identified as a saprobe, was detected in sporocarp tissue of *Amauroderma* (*Ganodermataceae*) from French Guiana as a contaminant (Baral et al. 2018b). *Xylona heveae* has a limited capacity to thrive as a saprotroph in soil. It also shares a close phylogenetic relationship with beetle endosymbionts such as *Symbiotaphrina kochii* and *Symbiotaphrina buchneri*. As a result, there is speculation that *X. heveae* may utilize an insect-associated transmission strategy. This hypothesis proposes that the pathogen could exploit insects as vectors for dissemination between plants, diverging from conventional mechanisms of direct host invasion seen in many plant pathogens (Gazis et al. 2016).

Pezizomycotina orders *Incertae sedis*

Thelocarpales Lücking & Lumbsch, Syllabus of Plant Families Ed 13 (Berlin): 281 (2016)

Subphylum : *Pezizomycotina*
Class : *Incertae sedis*

Introduction

Thelocarpales comprises pioneer lichens. The position of *Thelocarpales* in *Pezizomycotina* (*Ascomycota*) is controversial. Fungi in this order include non-lichenized, lichen-forming and lichenicolous species, all of which have highly variable morphology. There is variation in the nutritional mode in this small group of fungi. Among *Thelocarpales*, there is only one family *Thelocarpaceae*, containing four genera: *Carneothele*, *Melanophloea*, *Sarcosagium* and *Thelocarpon*. They are characterized by perithecioid to apothecioid ascomata that are mostly round to globose. The genus *Carneothele*, with red-brown ascomata, was described by Spribille et al. (2020), which comprises only one species (*C. sphagnicola*). The genus *Melanophloea* is known for its polysporous ascus. Three species have been classified into the genus *Trimmatothelopsis* in the family *Acarosporaceae* (Knudsen & Lendemer 2016). Differences in the morphology of both genera were reported by Gueidan et al. (2014b). *Sarcosagium* is an ephemeral genus with crustacean thallus as its apothecial species. There are only two species reported in this genus: *Sarcosagium biatorellum* and *S. campestre*. *Thelocarpon* is the largest genus in *Thelocarpales*. It is characterized by thin, filmy thallus with lichenized pin-shaped or wide-open warts that have a single ascocarp. Twenty-five species have been described in this genus (Nimis 2016). Despite their widespread distribution, even in polluted environments, the species are rarely noticed due to their small size and short life span.

History

Nylander (1853) was the first to introduce the genus *Thelocarpon*, in *Thelocarpales*. It was moved to the family *Hypocreaceae* (Rehm 1891), then reclassified with discolichens in the family *Acarosporaceae* (Zahlbruckner 1907, 1926, Magnusson 1936). Three monographs have been published on the genus *Thelocarpon* (Magnusson 1935, Salisbury 1953, 1966). A monograph published by Salisbury (1966) reviewed different herbaria and described 13 species. Poelt & Hafellner (1975) and Kocourková-Horáková (1998) accommodated 18 valid species. *Thelocarpaceae* was first described by Zukal (1893) as *Thelocarpeae*, and was originally placed between *Hypocreaceae* and *Sordariaceae*.

Sarcosagium was collected from soil by Massalongo (1856a) and described as a new genus. Zahlbruckner (1907) and Magnusson (1936) classified it in *Acarosporaceae*. The genus *Melanophloea* was described for the first time by James & Vezda (1971) and was initially assigned to the family *Acarosporaceae* (Eriksson & Hawksworth 1991b). Based on similarities with the genus *Thelocarpon*, this genus was assigned to the family *Thelocarpaceae*. *Melanophloea pacifica* is the type species of this genus. The second species was introduced into the genus in 2008, *M. montana* (McCarthy 2008), from Queensland rainforests. The third species, *M americana*, was introduced in 2011 (Knudsen et al. 2011). The three *Melanophloea* species were merged in 2016 into the genus *Trimmatothelopsis*, family *Acarosporaceae* (Knudsen & Lendemer 2016). However, *Melanophloea coreana* (Kondratyuk et al. 2015) was reported a year before this merger. According to Spribille et al. (2020), *Carneothele,* which only consists of one species, *C. sphagnicola* belongs to the family *Thelocarpaceae* because it is similar to *Thelocarpon*. The order *Thelocarpales* was introduced by Lücking & Lumbsch (Jaklitsch et al. 2016a) and accepted in *Pezizomycotina* order *incertae sedis* (Wijayawardene et al. 2022a).

General description

Thelocarpales commonly have sessile, globose perithecial ascomata, but several species have apothecial ascomata. The algal sheet surrounding the ascomata is present or absent. Salisbury (1966) classified *Thelocarpon* into two groups based on the presence or absence of corticated algal sheets. Ascomata are partly or fully immersed in the wart. Ascocarp diameters range from 0.2 to 0.5 millimeters. Additionally, *Thelocarpon* paraphyses are essential for species identification. It is not present in some cases, or if it is present, it may be simple or branched (Salisbury 1966). Perithecioid ascoma are found in several species of *Thelocarpon,* such as *T. epibolum* (Harada 2015), *T. imperceptum* (Salisbury 1966), *T. palniens* (Awasthi & Singh 1975), *T. pallidum* (van der Kolk 2015) and *T. robustum* (Vondrák et al. 2010). These perithecioid ascomata are characterized by dark brown to black, disk-shaped, simple or absence of paraphyses, simple to branched periphyses, algal sheet present or absent and a size ranging from a few millimeters to a few centimeters. Apothecioid ascoma forming species include *T. impresellum* (Salisbury 1966), *T. intermediellum* (Kocourková-Horáková 1998), *T. lichenicola* (Ihlen 1998), *T. olivaceum* (Szcepańska & Staniaszek-Kik 2012) and *T. superellum* (Kocourková-Horáková 1998). Apothecioid ascomata were characterized by small, round to irregular-shaped apothecia, scattered or clustered, flattened, aconvex, slightly convex or concave and dark olive green to brownish-black. Pycnidia reproduce asexually in all *Thelocarpales* species, but pycnidiospore formation is rare (Kocourková-Horáková, 1998). In contrast, Salisbury (1966), Magnusson (1936) and Purvis et al. (1992) observed pycnidia in the thallus of *Thelocarpon albidum*, *T. olivaceum*, *T. epibolum*, *T. lichenicola*, *T. intermediellum* and *T. robustum*.

Sexual morph: *Thallus* simple, smooth to slightly rough, thin, crustose, circular to irregular. *Prothallus* present or absent. *Ascomata* round to irregular, disk-shaped, scattered or clustered, convex or concave, sometimes flattened, proper margin present or absent. *Mazaedium* present or absent. *Pruinose* present or absent. *Hypothecium* hyaline to pigmented. *Excipulum* well or poorly developed. *Hymenium* hyaline to brown, comprising branched or unbranched paraphyses and asci. *Paraphyses* simple to branched, sometime enlarged at apex. *Epihymenium* present or absent. *Asci* persistent, clavate, cylindrical, bitunicate, amyloid or non-amyloid, enveloped in viscous hymenial gel, multi-spored, tapering at apex. *Ascospores* simple, spherical or cylindrical, one celled or septate, mostly

hyaline, uniseriate to biseriate, sometimes slightly constricted at the septum. Asexual morph: *Pycnidia* irregular, flask-shaped, hyaline, sessile, globose, base slightly immersed. *Conidiophores* erect, simple, thick at base, tapering towards the apex, rarely branched. *Conidia* apically produced, simple, hyaline, septate or aseptate, guttulate or aguttulate (Figs. 283, 284, 285).



Figure 283 – Thallus morphology of *Thelocarpales.* a *Carneothele* sp. b *Melanophloea americana* sp. c *Melanophloea coreana*. d *Sarcosagium campestre*. e *Thelocarpon andicola*. f *T. leureri*. g *T. pallidum*. h *T. epibolum*. Scale bars: f = 0.2 mm, a–b, e = 0.5 mm, c, d = 1 mm.

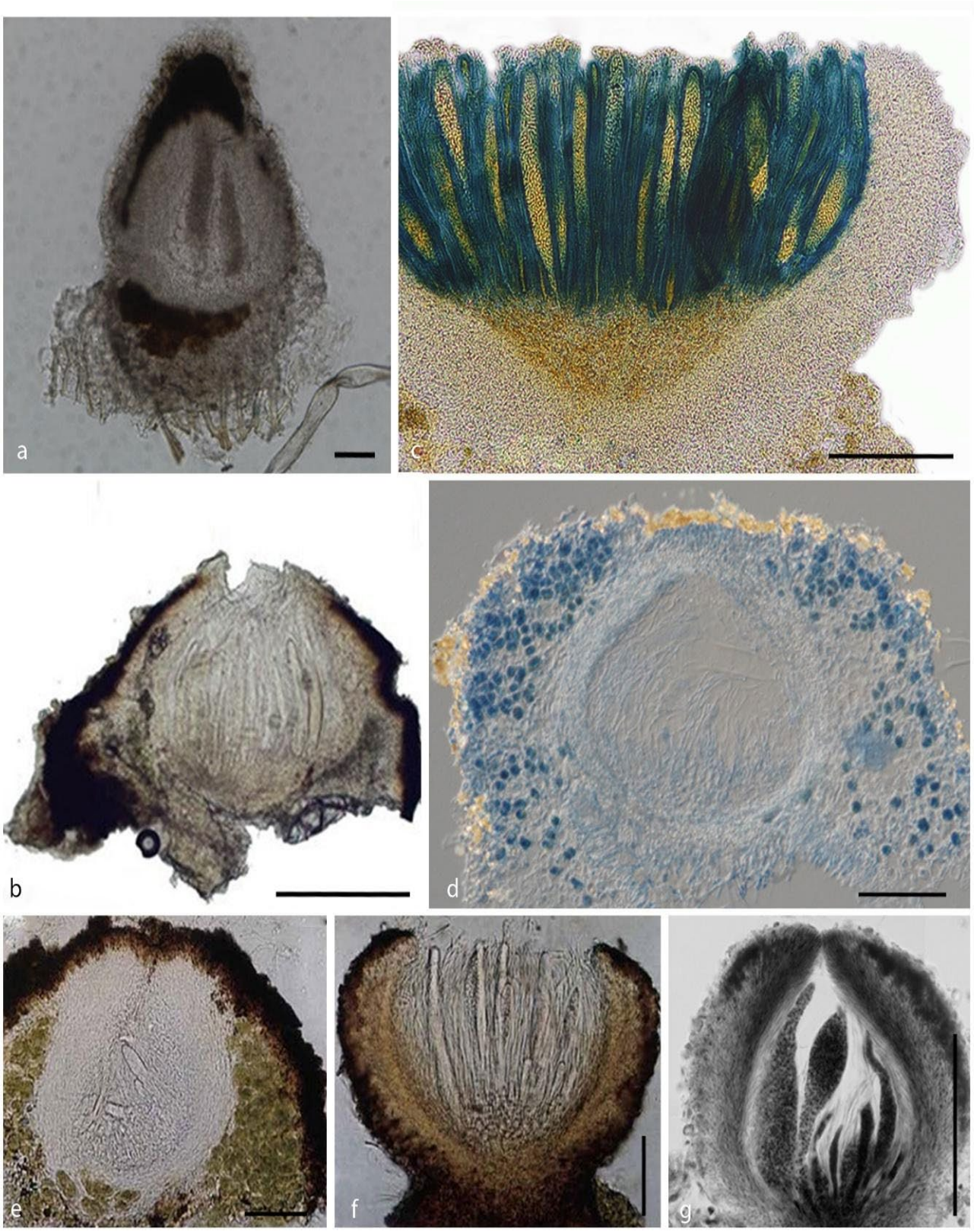


Figure 284 – Ascomata morphology of *Thelocarpales.* a *Carneothele* sp. b *Melanphloea* sp. c *Sarcosagium* sp. d *Thelocarpon andicola*. e *T. leureri*. f, g *T. epibolum*. Scale bars: a, d, e, f = 50 µm, c, g = 100 µm, b = 200 µm.

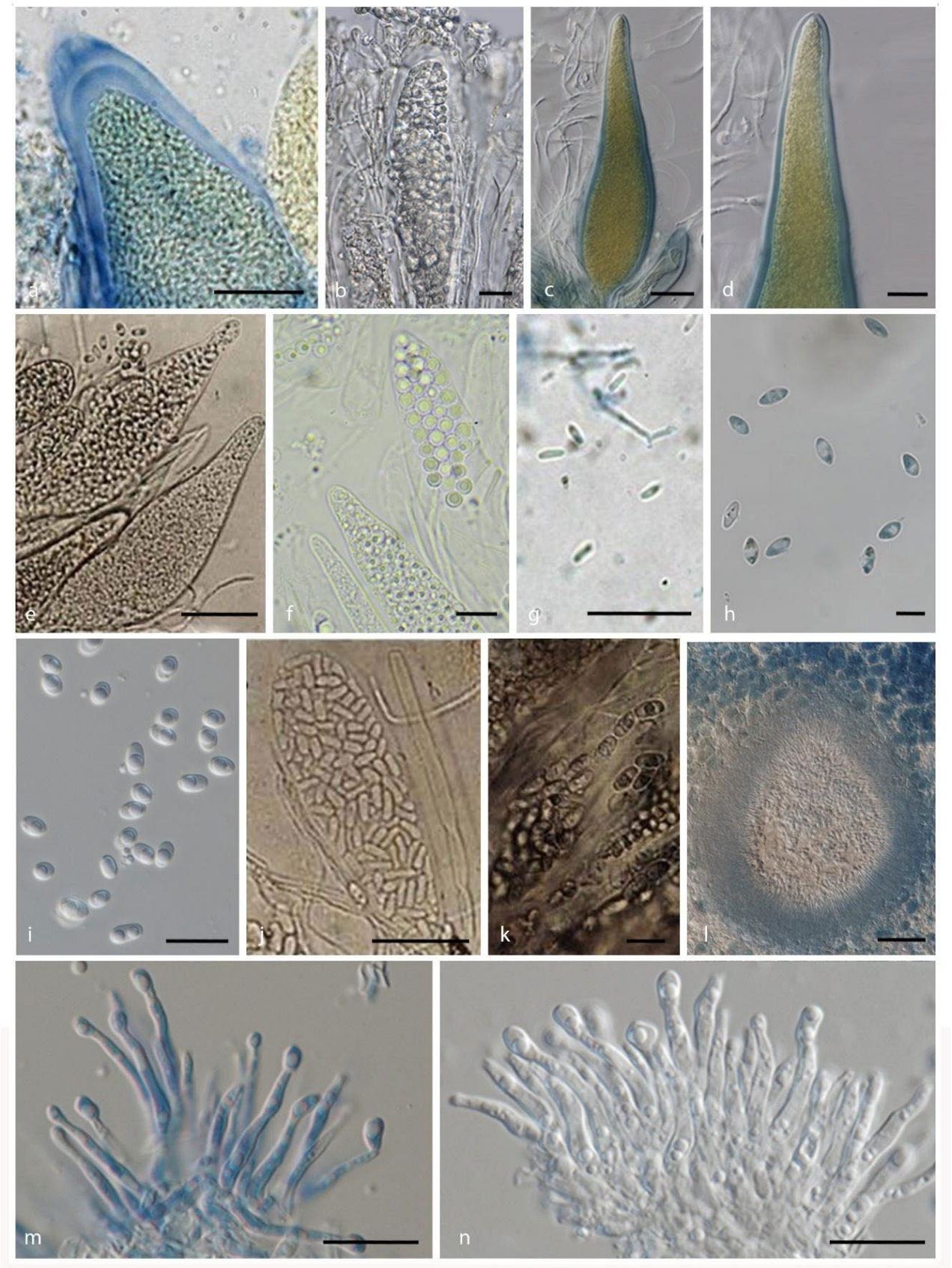


Figure 285 – Asci and ascospores morphology of *Thelocarpales*. a *Melanophloea americana*. b *Sarcosgium* sp. c–d *Thelocarpon andicola*. e *T. leureri*. f *Thelocarpon coccosporum*. g *Melanophloea americana*. h *Carneothele sphagnicola*. i *Thelocarpon andicola*. j *T. leureri*. k *T. superellum*. Conidiomata and conidiophores morphology of *Thelocarpales.* l–m *Thelocarpon andicola*. Scale bars: b, d, f, h, I, k, m, n = 10 µm, a, c, e, g, j = 20 µm, l = 25 µm.

Families included in *Thelocarpales*

Thelocarpaceae Zukal

Evolution

Thelocarpales exhibits diversity in morphological, sexual, and other taxonomically important characters, indicating that it is an evolutionary active group of fungi. For example, the species' adaptation to different habitats, varied modes of nutrition and delichenization ability, which has also been observed in other lichen-forming species (Lutzoni et al. 2001). It has been assumed that delichenization has occurred in some advanced species (Flakus & Kukwa 2014). It is known that some *Thelocarpales* species are lichenicolous, which indicates that they feed parasitically. Additionally, high plasticity among ascomata (perithecioid to apothecioid) confirms highly modifying characteristics of lichen fungi, which is supported by a molecular study demonstrating monophyly of the group (Lumbsch et al. 2009b). *Thelocarpales* undergo highly variable mitotic divisions after reduction divisions during ascospore formation. *Thelocarpaceae*, *Lacanoraceae*, and *Acarosporaceae* share the characteristic of polyspory. It is suggested that true polyspory may have developed in their common ancestor (Hafellner 1995). Although most species classified in *Thelocarpales* are polysporous, there are a few anomalous species within the family *Thelocarpaceae* characterized by eight ascospores (da Silva Cáceres & Aptroot 2016). One, two, or even three septa can appear in ascospores, although most species produce single-celled and simple ascospores. In lichenized fungi (including different species of the order *Thelocarpales*), genome size has been greatly reduced during lichenization (Díaz-Escandón et al. 2022). During evolution, carbohydrate degradation and secondary metabolite gene clusters were specifically shortened due to the availability of prepared nutritional sources.

Justification of order and problems

Thelocarpon is known for its small fruiting bodies. *Thelocarpon* was previously considered a member of the *Acarosporales* (resp. *Lecanorales* - *Acarosporineae*), but in the 20th century phylogenetic reconstructions of multiple polyspored ascomycetes demonstrated that *Thelocarpon* is not a member of the *Lecanoromycetes* (Poelt 1974a, Reeb et al. 2004, Lumbsch et al. 2009b). Its precise position in the *Pezizomycotina* system is unknown (Miadlikowska et al. 2014). Several species of *Thelocarpon* are ephemeral, that is, the ascomata and thalline warts appear after disturbance or fire, but disappear in a short period. In *Thelocarpon*, the ascomata are mostly photobiont, pale, fragile, multi-spored, and minute. Although the diverse morphology of ascomata, asci and ascospores would suggest polyphyly, a study of molecular features conducted by Lumbsch et al. (2009b) revealed it to be monophyletic. Species of this order may be expected to be diverse based on their morphological differences. In order to justify and differentiate the species in *Thelocarpales* from other lichenized fungi, some unusual traits must be examined in detail (Díaz-Escandón et al. 2022).

The majority of lichen-forming *Ascomycetes* are found in the family *Acarosporaceae*, growing on rocks and forming crustose thalli. The main characteristics of genera in this family are irregular discs and polyspored asci (Zahlbruckner 1907). Polyspory is a distinctive feature of species classified in different genera of *Thelocarpales*. An apothecium is common in many species of *Thelocarpon*. The number of spores produced per ascus differs between members of the family *Acarosporaceae* and *Thelocarpaceae*. Due to several mitotic divisions after meiosis, each ascus produces over 100 single celled, simple spores. Differentiation within the *Acarosporaceae* has been reported based on thallus development, apothecium structure, and ascus ontogeny (Elenkin 1911a, Dodge 1973, Vezda 1978, Hafellner 1995). *Thelocarpaceae* members have also been identified similarly. Further studies are needed to reveal the origin of polyspory and other similar characters during the evolution of *Acarosporaceae* and *Thelocarpaceae*. According to previous evidence (Hafellner 1995, Ozenda & Clauzade 1970), true polyspory originated in the order *Lecanorales* (*Lecanoromycetes*, *Ascomycota*), where the *Acarosporaceae* and *Thelocarpaceae* reside. *Acarosporaceae* genera such as *Biatoridium* and *Timdalia* have been classified as *Lecanorales* genera *incertae sedis*, whereas *Thelocarpon* and

Sarcosagium (*Thelocarpaceae*) have sometimes been included. Although these two families share various ancestral traits such as crustose saxicolous thallus, a cryptolecanorine apothecium, and an inamyloid thallus, this suggests a more basal position than previously assumed (*Lecanorales*). In multi-gene phylogenies, the *Acarosporaceae* have been found to form a separate lineage outside *Lecanorales* (Kauff & Lutzoni 2002, Miadlikowska & Lutzoni 2004). According to available data, the order *Thelocarpales* may belong to the class *Lecanoromycetes* with *Acarosporales*. Lücking et al. (2017), treated *Thelocarpales* as a separate order within *Pezizomycotina*. Wijayawardene et al. (2022a) also categorized this order as *Pezizomycotina incertae sedis*. A study of freshly collected *Sarcosagium* and *Thelocarpon* assigned these taxa to the new clade *Lichinomycetes* (Díaz-Escandón et al. 2022). More sampling is needed, especially from previously overlooked regions and previously described taxa require further study of their chemical and molecular properties.

Significance

Ecological and economic roles

A wide range of pioneer lichen fungi species are found in the order *Thelocarpales*. Despite their simple structure, they play an important ecological role in a variety of habitats. Barren substrates are the most common place for these species to colonize. *Thelocarpon* species are commonly found in rocky areas. *Thelocarpon epibolum* is highly effective at colonizing and stabilizing barren or disturbed habitats as well as assisting in the breakdown of organic materials. It also provides habitat and shelter for many small invertebrates and microorganisms (Kocourková-Horáková 1998). Through a commensal and parasitic relationship with its host lichen, *Thelocarpon lichenicola* obtains nutrients from the host and produces a variety of effects on its host. In addition to contributing to soil formation, *Thelocarpon robustum* stabilizes rocky substrates for the survival of other organisms. The species of *Sarcosagium* are effective indicators of Zn and Pb presence and are limited to habitats with these elements (Cuny et al. 2004). They contribute to soil formation in the environment, as well as acting as a bioindicator of environmental quality (Reeb et al. 2004). *Melanophloea* are rare species of lichens that live on deep shaded, moist, siliceous rocks in rainforests throughout Asia, Europe, and North America. The morphology of *Melanophloea montana* makes it an important component of montane ecosystems. There are a variety of bioactive compounds produced by *M. montana*. Insects, birds, and small mammals also use it as a source of food (McCarthy 2008).

Chemical diversity

The majority of species have a thin thallus, which results in low biomass. Therefore, it is difficult to determine the species biochemical profile. However, most *Thelocarpon* species are yellow to yellow-green, indicating the presence of lichen substances in this species. In *Thelocapon* species (including *T. epibolum* and *T. laureri*), pulviniv acid, dilactaone, vulpic acid, and their derivatives have been reported (Santesson 1967). A lichenicolous fungus (*T. lichenicola*) was reported as the first to contain pulvic acid by Santesson (1967). These pigments give yellow coloration to the thallus and fruiting body of fungal species. Pigments are more concentrated in sunlight-rich regions (Nguyen et al. 2013). Thus, they provide protection against UV radiation damage. Both *Melanophloea americana* and *M. montana* have melanized outer walls, but inner walls are hyaline. According to Knudsen & Kocourková (2013), melanization protects photobionts. The *Sarcosagium* thallus is ephemeral and has low biomass. Despite the black, brown gelatinous crust of the thallus, the pigmentation of the apothecia varies from pink to orange to white (Gilbert 2004). There are pigments on the wall of perithecia of *Carneothele sphagnicola* that form magenta crystals in potassium hydroxide, but no specific compound has been detected by thin-layer chromatography (Spribille et al. 2020).

Future recommendations

Despite their ecological importance and global distribution, *Thelocarpales* is one of the most neglected groups of lichen fungi. Some species of this group can grow on polluted substrates (Bielczyk et al. 2009, Medeiros et al. 2014), but further research is required to understand their role in heavy metal uptake. There is wide variation between species in their sexual reproduction,

especially in the shape of the ascoma and the characteristics of the ascospores. It is also necessary to reconstruct the *Thelocarpales* taxa. Examination of evolutionary trends within the genus *Thelocarpon* could test previous hypotheses about the loss of lichenization (Lutzoni et al. 2001, Flakus & Kukwa 2014). Previously less-studied characters, such as cell wall composition and asexual characteristics, need to be investigated in detail (Díaz-Escandón et al. 2022).

***Vezdaeales* Lumbsch & Lücking, Syllabus of Plant Families Ed 13 (Berlin): 281 (2016)**

Subphylum : *Pezizomycotina*
Class : *Incertae sedis*

Introduction

Vezdaeales is a poorly studied order which belongs to *Pezizomycotina* order *incertae sedis* (Wijayawardene et al. 2022a). Lücking et al. (2017), suggested that the order can be a part of an expanded *Lecanoromycetes*. Currently, there are four species supported by the molecular, however, Lücking et al. (2017) suggested that it needs a broad data set to resolve its uncertain phylogeny or using high-throughput sequencing of a broad selection of markers might be a new initiative to resolve the phylogenetic ambiguity. It comprises one family, *Vezdaeaceae*. *Vezdaeaceae* is a monotypic family comprised of *Vezdaea* which comprises 14 species (Németh & Eckstein 2018, Species Fungorum 2025).

History

The genus *Vezdaea* was introduced to accommodate *Pachyascus byssaceus*, introduced by Vězda (1963, 1970). The genus is typified by *Vezdaea aestivalis*, and contains lichenized fungi, with most of the species delimited only based on morphology. *Vezdaea aestivalis* is the largest among the *Vezdaea* species, and its apothecia are mostly visible compared to others (Németh & Eckstein 2018). Coppins (1987) provided a key to the European species of *Vezdaea*. Recently, Chambers et al. (2021) provided a key to the *Vezdaea* species, including *V. acicularis*, *V. cobria*, *V. aestivalis*, *V. leprosa*, *V. stipitata*, *V. rheocarpa*, and *V. retigera*.

General description

Both sexual and asexual morphs have been reported from *Vezdaea*. But studying the morphology is critical because the asci and vegetative hyphae can be collapsed beyond the critical point of drying. Low Temperature Scanning Electron Microscopy is an alternative method for studying them (Scheidegger 1995).

Sexual morph: *Ascomata* apothecial, hemispherical or turbinate, sometimes appearing irregular, minute, and when dry; it is hardly visible. *True exciple* and *hypothecium* are absent. *Hamathecium* has branched paraphyses, variably developed and sometimes clasping and entwining the asci when well-developed. *Hymenium* does not have a gelatinous matrix. *Asci* 8-spored, cylindrical, thick-walled, thickened apex and K/I+ blue except for an apical pore. *Ascospores* are aseptate to multi-septate, colorless, with smooth or verrucose walls. Asexual morph: *Conidiomata* have not been reported; conidiogenous cells produce colorless aseptate, simple conidia. *Conidiogenesis* occurs from thallus hyphae or germinating ascospores in *V. aestivalus* and *V. foliicola* (Chambers et al. 2021, Coppins 1987), and conidiophores were observed in *V. aestivalis* and *V. stipitata* (Scheidegger 1995) (Fig. 286).

Families included in *Vezdaeales*

Vezdaeaceae Poelt & Vězda

Justification of order and problems

As suggested by Coppins (1987), in some *Vezdaea* species, such as *V. retigera* and *V. rheocarpa*, germ tubes can be seen as colorless elongated cellular appendages developing from one or both ends of the ascospores. However, in contrast, Chambers et al. (2021) have mentioned that these developments can be seen even in immature ascospores and within the ascus.

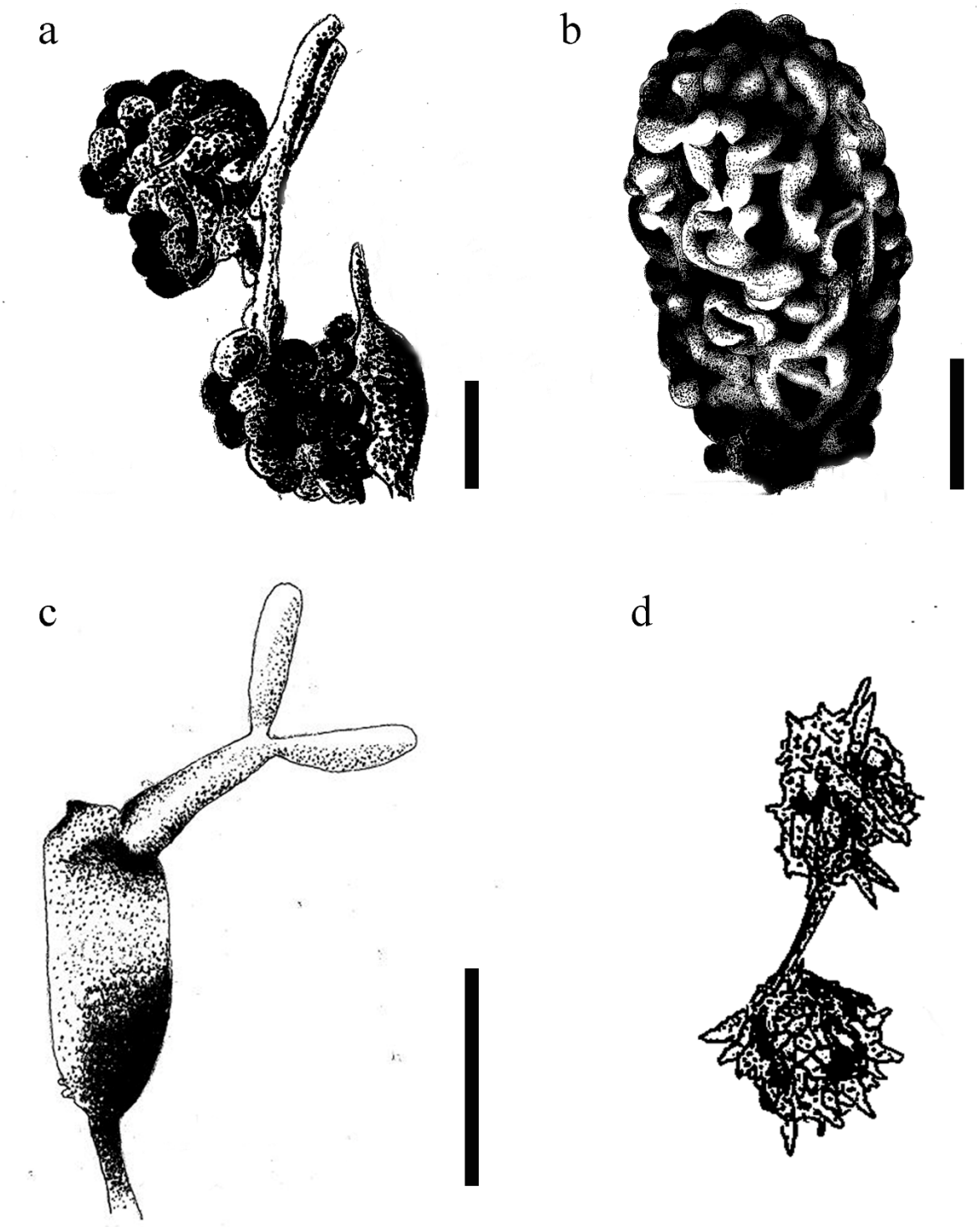


Figure 286 – Asci and ascospores morphology of *Vezdaeales.* a Sessile ascoma ensheathed by ramified and anastomosing paraphysoids. b Mature ascus. c Germinating one-septate ascospore with germ tube from both ends and apically hyphomycete is developing with two conidia (a, b, c *V. aestivalis*). d Connecting the two goniocysts latter can initiate somatogamy (*V. rheocarpa*). Scale bars: a–c= 10 µm (redrawn from Scheidegger 1995).

Some *Bacidina* (*Ramalinaceae*, *Lecanoromycetes*, Hyde et al. 2024b), *Fellhanera (Pilocarpaceae*, *Lecanoromycetes*, Hyde et al. 2024b) and *Vezdaea* species are similar in having hyaline and almost colorless apothecia. However, *Vezdaea* can be differentiated because the excipulum is not developed and has simple and larger ascospores. Ascospores in *Bacidina* species

are acicular, multi-septate and in *Fellhanera* they are fusiform and transversely septate. Despite those differences, three genera have similar characteristics, such as occurrence on bryophytes, and all produce external, well-developed thalli. *Biatora veteranorum* produces pale cream and whitish-pruinose apothecia and simple, small ascospores, but it can be differentiated from *Vezdaea* because it is exclusively lignicolous, and its thallus is not superficial, reaching in stipitate, pruinose pycnidia (Czarnota & Hernik 2014). The type species *Vezdaea aestivalis* has similarities with *Bilimbia sabuletorum* (*Ramalinaceae*, *Lecanoromycetes*, Hyde et al. 2024b). However, it can be differentiated by the paraphyses, asci and ascospores characteristics by having large (visible without a microscope) apothecia, 2-septate ascospores, highly branched, anastomosed paraphyses, entwining individual asci and well-developed, non-granular, external thallus (Chambers et al. 2021).

Most *Vezdaea* species produce relatively smaller diaspores (Scheidegger 1995). Coppins (1987) mentioned that the morphological characteristics within the same species can be varied based on the substrate or habitats. For example, *V. retigera* is generally reported to have smooth ascospores and numerous long paraphyses that become entwined around individual asci. However, this species reported from Britain has goniocysts with relatively shorter spines than the type species (Coppins 1987, Chambers et al. 2021). Thus, species delimitation based on the morphological characteristics is a constraint related to this genus. Thus, this order needs to be revised based on comprehensive phylogenetic analyses (Lücking et al. 2017).

Significance

Ecological and economic roles

Vezdaea occurs in different types of substrates that have been recorded from various locations in the world. Many *Vezdaea* species have been discovered in the European (England, Poland) and American regions (Coppins 1987, Németh & Eckstein 2018, Chambers et al. 2021), and some have been recorded from Africa (Sérusiaux 1979). However, only a few studies focus on the Asian region and Aptroot & Sparrius (2003) reported *Vezdaea* species from a region in China. *Vezdaea* are distributed in many substrates such as moribund bryophytes and algal films in sheltered, moist situations, on mine sites, sea cliffs, below wire fences and in pinewoods, bark of trees, mostly on metal-contaminated ground, soils, and various rocky substrates (Czarnota & Hernik 2014). Species such as *Vezdaea retigera* occur in metal-enriched habitats in post-mining areas or on waste heaps and are considered as toxitolerant species (Scheidegger 1995).

Vezdaea species are comparatively inconspicuous lichens forming thalli composed of corticate granules (goniocysts), and apothecia and asci are only formed in prolonged wet periods. Due to having inconspicuous thalli and ephemeral presence of apothecia, they are overlooked and difficult to collect. Because of this short life span of apothecia, the winter and spring seasons are most suitable for specimen collection. Specimens collected during the summer possess overly mature stages, and apothecia can be prone to dark-colored hyphae and algae invasions. Another constraint is that some *Micarea* (*Pilocarpaceae*, *Lecanoromycetes*, Hyde et al. 2024b) species have a similar appearance, possibly misidentified as *Vezdaea* in the field. However, *Micarea* has hymenial gel, a true exciple, distinct conidiomata, lichen products and a relatively different ascus structure than *Vezdaea*. Non-lichenized *Mniaecia* (*Mniaeciaceae*, *Leotiomycetes*) species have K/I asci, which can be differentiated by *Vezdaea* that have K/I+ blue asci and lichen products not detected by TLC (Scheidegger 1995, Chambers et al. 2021).

Vezdaea produces minute vegetative and generative hyphae. All the *Vezdaea* species produce non-lichenized propagules or hyphae. In the lichen formation process, goniocysts need to be developed and use a free-living photobiont available in the substrate (Scheidegger 1995). In the development of goniocysts, photobionts are completely ensheathed by the fungus. No free algae are present on the surface of the goniocysts, and hyphae are extended, and once in contact with another photobiont cell, the next goniocyst is produced (Scheidegger 1995).

Chemical diversity

Generally, lichens may have defensive chemicals; however, no defensive chemicals have yet been discovered from this genus. As many of the *Vezdaea* species are toxitolerant, they may have the potential to produce bioactive compounds, which will be useful in biotechnology (Scheidegger 1995, Chambers et al. 2021).

Other relevant data and future recommendations

Vezdaea is known as a stress-tolerant genus, and some species have survival strategies such as a low growth rate and produce diaspores and lichen formation. Thus, even though *Vezdaea* is rare in the field, it is not an endangered species due to its survival mechanisms. Most of the previous studies are concentrated in European and American regions, and only a few studies have been conducted in Asian and African regions. Hence, the geographical distribution of this order is yet to be studied. Many of them focus only on the morphological and ecological characteristics of this genus. Many publications on *Vezdaea* were carried out a few decades ago; thus, those are based on morphology, and studies based on phylogeny are rare. Hence, it is necessary to focus on the phylogeny and evaluation study of *Vezdaeales*, which will provide a broad understanding and identify the exact taxonomic placement of this order. NGS will be an option to infer its taxonomy and the bioassay of the *Vezdaeales* species. However, less attention has been paid to the ecological role of *Vezdaeales*. As these species are involved in lichen formation and potentially occur in both natural and metal-enriched disturbed habitats, they can be expected to have a high impact on the ecosystem regarding regulating and adapting. Thus, further studying of the taxonomy, ecology and diversity of *Vezdaeales* is essential.

Taphrinomycotina **O.E. Erikss. & Winka, Myconet 1: 11 (1997)**
Archaeorhizomycetes **Rosling & T.Y. James, Science N.Y. 333: 879 (2011)**
Archaeorhizomycetales **Rosling & T.Y. James, Science, N.Y. 333(no. 876): 879 (2011)**

Subphylum : *Pezizomycotina*
Class : *Archaeorhizomycetes*

Introduction

Archaeorhizomycetales belongs to the class *Archaeorhizomycetes*. *Archaeorhizomycetes* is phylogenetically placed in the subphylum *Taphrinomycotina*. It was introduced to accommodate a single soil fungal species *Archaeorhizomyces finlayi* (Rosling et al. 2011). The name *Archaeorhizomycetes* is derived from Greek word; arkhaio, implying the basal position within the *Ascomycota*; and from Greek word rhiza, which means the root (Rosling et al. 2011). Despite having only six genera and 150 fungal species, *Taphrinomycotina* contains five distinct classes, which have extreme phylogenetic and ecological diversity. They include the model fission yeast *Schizosaccharomyces*, the mammalian pathogen *Pneumocystis* (associated with HIV patients), and the mysterious genus *Neolecta*, which grows on conifer rootlets, is the only *Taphrinomycotina* known to produce fruiting bodies, and has yet to be cultured (Schoch et al. 2009a). *Archaeorhizomycetales* includes hundreds of filamentous fungal species which reproduce cryptically and do not develop apparent mycorrhizal structures with saprotrophic potential. Nevertheless, they are ubiquitous in rhizosphere soil and in roots and exhibit ecosystem and host root habitat specificity (Rosling et al. 2011). *Archaeorhizomycetales* only contains one family; *Archaeorhizomycetaceae*, which consists of a single genus; *Archaeorhizomyces* (Rosling et al. 2011) with four species. Environmental sequence studies demonstrate that the class is diverse and abundant in a variety of terrestrial ecosystems (Khan et al. 2020). There is little other knowledge regarding its lifestyle and ecology.

History

Prior to Rosling & colleagues (2011), *Archaeorhizomycetes* was known as Soil Clone Group 1 or SCGI - because Schadt et al. (2003) discovered it in tundra soils. The accessibility of cultures enabled a reliable and robust multi-locus phylogenetic analysis with clear linkage relationships

between rRNA genes and protein-coding genes, which was not feasible with environmental DNA (Rosling et al. 2011). *Archaeorhizomycetales* sequences are found in environmental DNA collected from roots and soil. They have been identified in over 100 environmental studies (Hibbett 2016, Menkis et al. 2014). In accordance with the clustering of published environmental amplicon sequences, the class is likely to include at least 500 species with a wide geographical distribution that occur in terrestrial environments worldwide (Menkis et al. 2014).

General description

Archaeorhizomycetes is a particularly enigmatic lineage which is rich in "dark taxa" (Rosling et al. 2011). The genus *Archaeorhizomyces* was established to describe a slow-growing and cryptically reproducing, soil fungal species; *A. finlayi* which is commonly associated with plant roots (Menkis et al. 2014) which is also the type species for the class *Archaeorhizomycetes* (Pinto-Figueroa et al. 2019). It is a putatively saprotrophic, non-pathogenic, plant root and rhizosphere associated fungus (Rosling et al. 2011) and was isolated from cultures obtained from surface-sterilized coniferous ectomycorrhizal root tips (Rosling et al. 2011). After initial species identification based on the rapidly evolving ITS rRNA locus, direct sequencing proved insufficient for phylogenetic placement of the isolates (Rosling et al. 2011). The name *A. finlayi* was given to honour Prof. Roger D. Finlay of SLU in Uppsala, Sweden, for his numerous contributions to rhizosphere ecology (Rosling et al. 2011).

Archaeorhizomyces finlayi is a mycelial fungus that grows slowly and has simple septa without pores. The hyphal cell wall is thick and double-layered. In culture, the hyphae are extensively covered in extracellular material and entangled to form structures that resemble undifferentiated cords. The nuclei of a cell can be single or multiple. The swellings frequently have thick walls and numerous nuclei, which suggests that they may have chlamydosporogenic properties. Rosling et al. (2011) employed a 97% sequence similarity threshold within the ITS region to differentiate over 100 operational taxonomic units (OTUs) of *Archaeorhizomycetes*. Their meta-analysis of publicly available ITS and LSU sequences indicated a projected total diversity surpassing 250 OTUs for this group. By combining ecological and phylogenetic evidence, three more species have been introduced into *Archaeorhizomyces* including *Archaeorhizomyces borealis* and *A. secundus* and *A. victor* (Index Fungorum 2023). According to Rosling et al. (2011), no sexual morphs of *Archaeorhizomycetales* species have been found (Fig. 287).

Families included in *Archaeorhizomycetales*

Archaeorhizomycetaceae Rosling & T.Y. James

Evolution

In the combined gene analysis of ITS, LSU, SSU, EF1, RPB1, RPB2 sequences, *Archaeorhizomycetes* is assigned to *Taphrinomycotina*. The lack of strong support in the merged gene phylogeny is likely attributable to incongruence between rRNA and protein-coding genes, along with the significant ancient divergence time of *Taphrinomycotina*. In each individual locus phylogeny, *Archaeorhizomycetes* forms a monophyletic or paraphyletic group within *Taphrinomycotina*, with previous studies having statistically confirmed the monophyly of *Taphrinomycotina* (James et al. 2006, Schoch et al. 2009a, Rosling et al. 2011). Despite the fact that the only described order in the class *Archaeorhizomycetes* is *Archaeorhizomycetales* with a single family, *Archaeorhizomycetaceae*, and a genus, the classification might remain subject to change, given that this lineage remains predominantly uncharacterized (Rosling et al. 2011).

Justification of order and problems

Even in locations with established high richness and abundance as determined by amplicon sequencing, the process of obtaining pure cultures of *Archaeorhizomyces* species has proven to be exceptionally difficult. As a result, novel species have been introduced using alternative evidence inferred from environmental sequence data. This approach precludes the utilization of conventional

sources, such as morphological characterization, for species descriptions (Khan et al. 2020). Thus, neither fruiting bodies nor spores have been recorded for the species (Rosling et al. 2011).

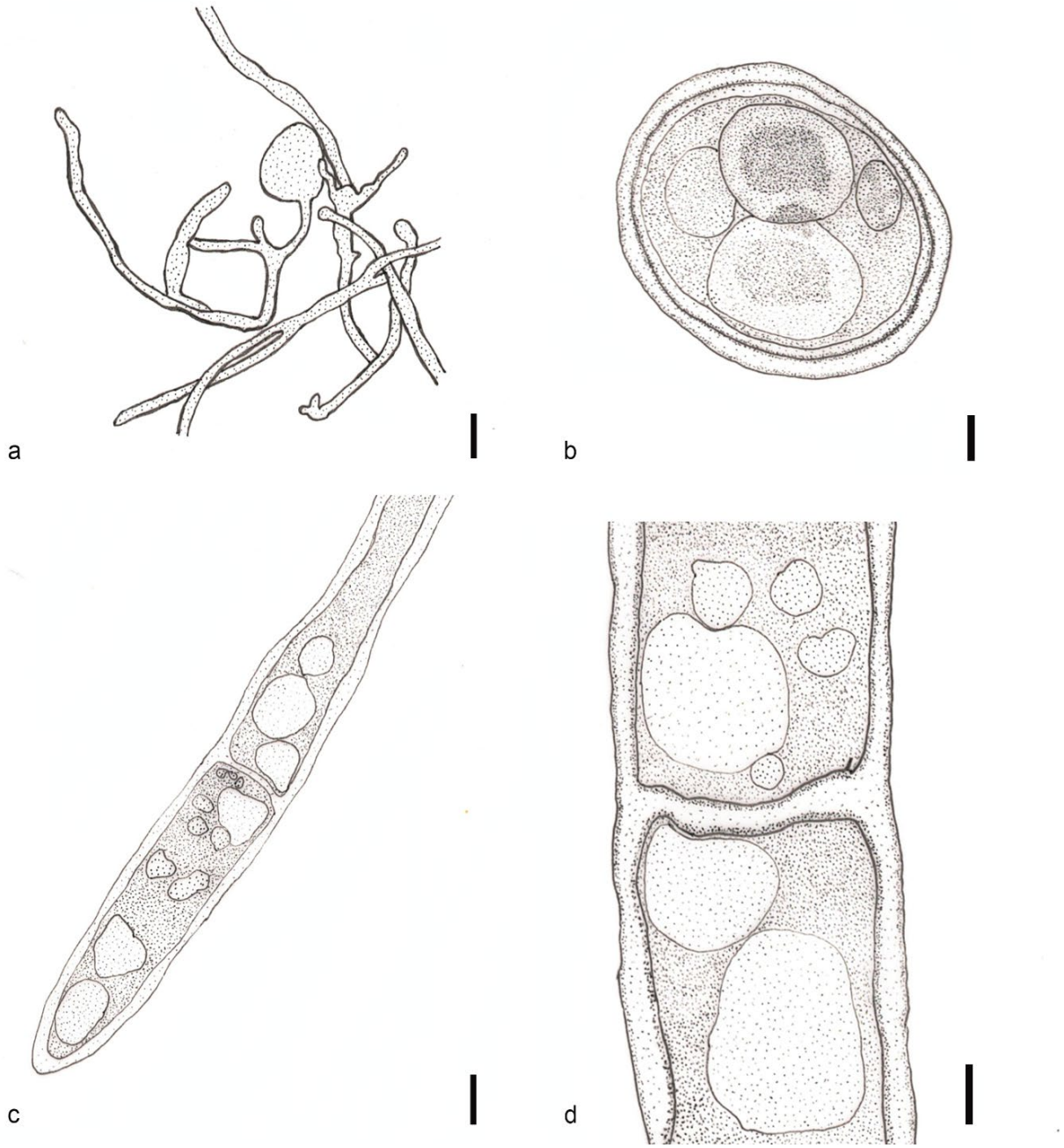


Figure 287 – Mycelia and Hyphae of *Archaeorhizomyces finlayi.* a Scanning electron micrograph image of fixed mycelia from 3-month-old mycelia with both terminal and intercalary swellings. b Transmission electron micrograph (TEM) cross section of hyphae in 3-month-old mycelia. c, d TEM image of cross section of hyphae with septa. Scale bars: a = 1 µm, b = 200 nm, c = 300 nm, d = 100 nm.

Significance

Although their exact function is unclear, the discovery of these fungi will be crucial for research into how fungi function in ecosystems and for the understanding of how they evolved (Rosling et al. 2011).

Ecological and economic roles

Archaeorhizomycetales appeared to be seasonal, thriving in the summer in tundra soil fungal communities while being dormant the rest of the year. This implies that these species are dependent on carbon compounds obtained from the roots. *Archaeorhizomyces finlayi*, however, grows slowly in culture when given only glucose or cellulose as a source of carbon, suggesting that it might be a decomposer and not need to directly receive carbon from the plant through symbiosis (Rosling et al. 2011). The widespread occurrence of the diverse fungal class *Archaeorhizomycetes* in various terrestrial ecosystems has led to an underestimation of its abundance due to amplification biases. Although the exact environmental functions and life cycles of these organisms are unknown, isolating and characterizing their cultures will enable *in vitro* characterization and genome sequencing to determine their roles in terrestrial ecosystems (Rosling et al. 2011).

The class includes widely dispersed species that are found in soil and plant roots (Rosling et al. 2011). This fungal group, which is ubiquitous in many soil environments, incorporates cryptic filamentous species that form associations with plants' roots but whose function in terrestrial ecosystems is unknown (Pinto-Figueroa et al. 2019). Hemlock, spruce, pine, and heather are specific host trees for different *Archaeorhizomyces* species, as well as other species which generally colonize hardwoods (Rosling et al. 2011). According to Rosling et al. (2011), the mycelium of *A. finlayi* associates with roots when inoculated onto sterile pine seedlings, but it does not exhibit favored growth toward the main, primary, or secondary roots, and it does not change the morphology of the root tip. The inoculated seedlings continued to be healthy for months without exhibiting any indications of fungal pathogenicity, despite the absence of typical mycorrhizal or endophytic structures. Several OTUs demonstrate apparent specificity to certain hosts and habitats associated with plants. However, this specificity may not solely arise from a preference for the host; instead, it could signify an affiliation with other fungi inhabiting plant roots (Rosling et al. 2011).

Chemical diversity

Archaeorhizomycetales are thought to proliferate at soils with higher carbon contents and may therefore be dependent on nearby sources of organic carbon, as was initially proposed (Rosling et al. 2011). This is indicated by a positive correlation with total organic carbon. Several other studies had verified that they dominated the rhizosphere with deeper soil and possibly greater nutrient turnovers (Clemmensen et al. 2015, Fernández-Martínez et al. 2017), as well as in soils with lower pH and more available phosphorus (Carrino-Kyker et al. 2016). *Archaeorhizomycetales* may be associated with biological weathering, in accordance with other noteworthy associations with edaphic elements, such as hydrogen, aluminum oxide, and particularly phyllosilicates (Pinto-Figueroa et al. 2019).

Other relevant data and future recommendations

From network analysis, Pinto-Figueroa et al. (2019) deduced substantial positive as well as negative correlations between the abundance of *Archaeorhizomycetales* and various other fungi. Psychrophilic soil fungi, *Typhula*, one of the positively associated fungi, are active on dormant plant hosts during the winter as saprobes and pathogens (Chang et al. 2006). Other co-occurring fungi include species that have been identified as potentially pathogenic and active (Barnes et al. 2016). However, there are also saprotrophic species among negatively correlated fungi, such as those in the *Tubeufia* and *Omphalotus* (Fukasawa et al. 2010, Chaiwan et al. 2017). Additionally, *Suillus* species, which were identified as ectomycorrhizal (Jarvis et al. 2015) and associated with weathering processes, were negatively correlated with *Archaeorhizomycetales*. While several studies have revealed potential abiotic and biotic preferences of *Archaeorhizomycetales*, more experimental approaches are required to validate these findings.

***Neolectomycetes* O.E. Erikss. & Winka, Myconet 1: 8 (1997)**
***Neolectales* Landvik, O.E. Erikss., Gargas & P. Gust., Systema Ascomycetum 11 (1993)**

Subphylum : *Taphrinomycotina*
Class : *Neolectomycetes*

Introduction

Neolectales was introduced by Landvik et al. (1993) to accommodate the monotypic family, *Neolectaceae* (type: *Neolecta*). Eriksson & Winka (1997) upgraded *Neolectales* to the class *Neolectomycetes*. Currently, only one order is placed in *Neolectomycetes*, in the subphylum *Taphrinomycotina*.

History

The genus *Neolecta* was introduced by Spegazzini (1881a) but only four species have been described (Species Fungorum 2023). Since it was introduced, *Neolecta* was placed in *Geoglossaceae* but based on unique morphological characteristics, Redhead (1977) introduced *Neolectaceae* but placed it in *Lecanorales*. Eriksson (1981, 1982) tentatively assigned *Neolecta* to *Pezizales*. Based on 18S sequence data, Landvik et al. (1993) showed that *Neolecta* is phylogenetically distinct from *Pezizales* and thus introduced *Neolectales*. Wijayawardene et al. (2020, 2022a) confirmed the placement of *Neolectales* in *Ascomycota*.

General description

Sexual morph: *Ascomata* long, irregularly clavate, lanceolate or spathulate, usually attenuated above, fleshy, stuffed or hollow. *Clavula* smooth, rugose or subplicate, luteous to pale luteous, confluent with the stipe along an uneven border. subglabrous, pubescent or tomentose, white to straw or pale luteous, tapering below and rooting, frequently rotted off. *Asci* cylindrical to cylindric-clavate, eight-spored. *Ascospores* uniseriate, occasionally biseriate, reniform, ellipsoid or ovoid, hyaline, smooth, thin-walled, aseptate, inamyloid. Asexual morph: produced only in some species; *Conidia* globose to subglobose, smooth, thin-walled, hyaline (adapted from Redhead 1977) (Fig. 288).

Families included in *Neolectales*

Neolectaceae Redhead

Significance

Ecological and economic roles

The *Neolecta* species are reported as saprobic or weakly parasitic on plant roots, leaves and soil from Italy, Luxembourg, New York and São Paulo. However, the ecology of the members are largely unknown (Landvik et al. 1993, 2003).

Novakomycetes Dlauchy, Péter & Čadež, Microorganisms 9 (2, no. 301): 14 (2021)

Novakomycetales Dlauchy, G. Péter & Čadež, in Čadež, Dlauchy, Tome & Péter, Microorganisms 9(2, no. 301): 14 (2021)

Subpylum : *Taphrinomycotina*
Class : *Novakomycetes*

Introduction and History

Novakomycetales was introduced by Čadež et al. (2021) to accommodate a newly established family *Novakomycetaceae*, a new genus *Novakomyces* and a single species *N. olei*. The order placed in the subphylum *Taphrinomycotina* based on unique morphological characters along with the evidence from phylogeny. This is the first representative of *Taphrinomycotina* that was reported from olive oil as a yeast strain and the taxon formed a close phylogenetic relationship to *Schizosaccharomyces*.

General description

The taxon shows both sexual and asexual morph. Asexual reproduction proceeds by multilateral budding and in sexual morph, asci unconjugated or formed following conjugation of mother cell and its bud.

Sexual morph: *Asci* contains one or two subspheroid or ellipsoid ascospores. *Ascospores* deliquescent. Asexual morph: *Yeast cells* subspheroid or ellipsoid and asexual reproduction proceeds

by multilateral budding. *Cell wall* consists of two layers and budding is enteroblastic. *Pseudohyphae* and true hyphae are absent (Adapted from Čadež et al. 2021) (Fig. 289).

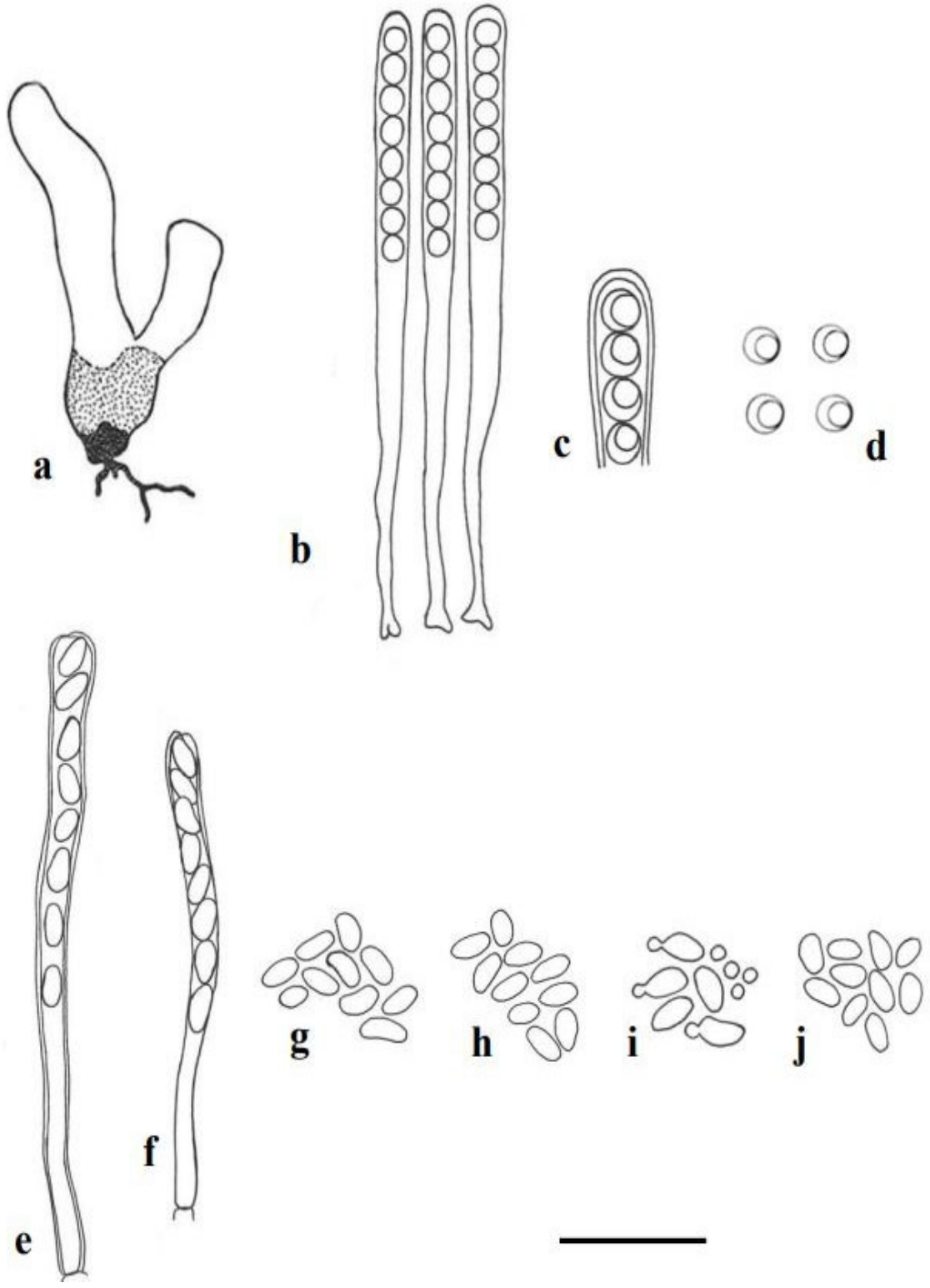


Figure 288 – Morphological characters of *Neolecta* species. a *N. vitellina* (UME 3113) Ascomata attached to a rootlet of Norway spruce (*Picea abies*). b, c, d redrawn of *Neolecta flavovirescens* (LPS 4099-holotype) illustration on the envelop containing the type material, dated 1881 as in Landvik et al. 2003. e, g, h. *Neolecta irregularis*. f, i, j *N. vitellina*. Figs. e (TRTC 9645) and f (TRTC 10076) Asci with apical nasse. Figs. g (TRTC 23530), h (TRTC 44558), and i (S.A.R. 1430) Ascospores. Fig – j (S.A.R. 1794) Ascospores producing conidia (arrow). (a-d redrawn from Landvik et al. 2003, e-i redrawn from Redhead 1977).

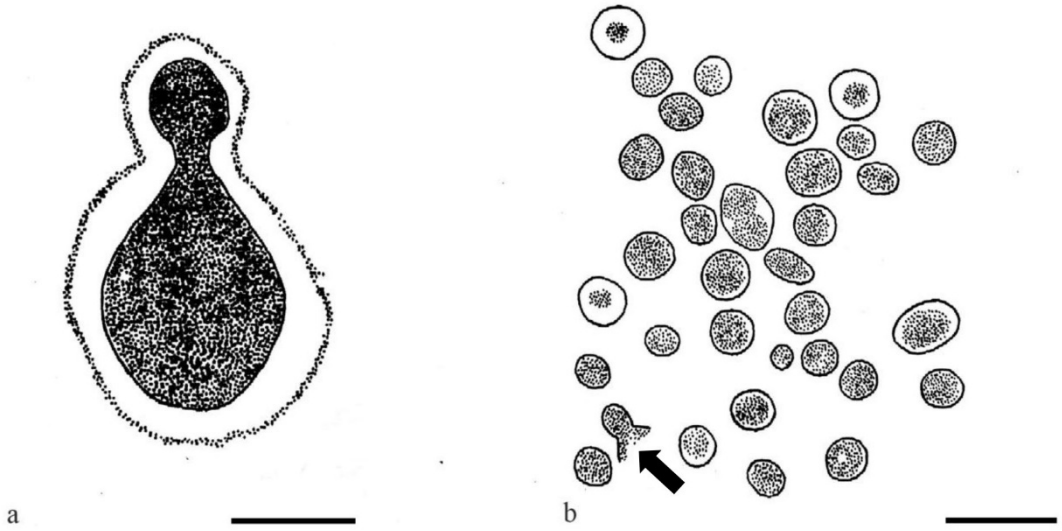


Figure 289 – Morphology of *Novakomycetes* (*Novakomyces olei*). a TEM micrograph of a section of a budding cell. b Remnant of an ascus formed by the conjugation of the mother cell and its bud is indicated by an arrow (drawn from Čadež et al. 2021). Scale bars: a = 1000 nm, b = 10 µm.

Families included in *Novakomycetales*

Novakomycetaceae Dlauchy, Péter & Čadež

Significance

Ecological and economic roles

The only known species in the order was isolated from extra virgin olive oil as a yeast strain from Spain. The strain was identified as uncommon as no similar strains were found in other samples which implies the need for further study of this group (Čadež et al. 2021).

Chemical diversity

Several carbon compounds, hexadecane, Ethylamine hydrochloride, L-lysine, and creatine are assimilated in *Novakomyces olei*. Urease and starch-like compounds are also produced (Čadež et al. 2021).

***Pneumocystidomycetes* O. E. Erikss. & Winka, Myconet 1: 9 (1997)**
***Pneumocystidales* O. E. Erikss., Systema Ascomycetum 13: 170 (1994)**

Subphylum : *Taphrinomycotina*
Class : *Pneumocystomycetes*
Subclass : *Pneumocystomycetidae*

Introduction

Pneumocystidales comprises the monotypic family *Pneumocystidaceae*, which includes the *Pneumocystis* taxa (Wijayawardene et al. 2020). *Pneumocystis carinii* is the type species of *Pneumocystis*. It was originally identified by Delanoë & Delanoë (1912) in *Rattus norvegicus*. The morphological, phylogenetic, and experimental approaches have proven that *Pneumocystis* represents a highly diverse biological group (Aliouat-Denis et al. 2008, Catherinot et al. 2010). They are unable to be grown *in vitro* fungal culture media (Catherinot et al. 2010, Sokulska et al. 2015). The members of *Pneumocystis* are unicellular parasitic organisms (Chabé et al. 2011). They exhibit

specific host preferences and are exceptionally well-suited for survival within the alveoli of lungs in various mammalian species (Guillot et al. 2001, Hugot et al. 2003). They can be pathogens in the lungs of a wide range of mammals, including those dwelling in terrestrial, aerial, and aquatic environments (Laakkonen et al. 1993, Laakkonen & Sukura 1997, Mazars et al. 1997, Guillot et al. 1999, 2001, Laakkonen 1998, Durand-Joly et al. 2000, Demanche et al. 2001, Laakkonen et al. 2001, Demanche 2003). In certain cases, particularly in hosts with compromised immune systems, they can provoke severe pneumonitis (Dei-Cas 2000, Stringer 2002, Dei-Cas et al. 2006). In such circumstances, *Pneumocystis* species can progressively inhabit and fill the cavities of the pulmonary alveoli, ultimately leading to respiratory failure (Dei-Cas 2000, Dei-Cas et al. 2006). Currently, there are five accepted taxa under *Pneumocystis* namely, *P. carinii* (Delanoë & Delanoë 1912), *P. jirovecii* (Frenkel 1976), *P. murina* (Keely et al. 2004), *P. oryctolagi* (Dei-Cas et al. 2006) and *P. wakefieldiae* (Cushion et al. 2004, 2005).

History

The fungal genus, currently recognized as *Pneumocystis*, was initially discovered by Chagas (1909), within the lungs of guinea pigs that had been experimentally infected with *Trypanosoma cruzi*. Chagas (1909) mistakenly believed that he had found a new form of trypanosome. Carini (1910) observed similar organisms in the lungs of rats infected with *Trypanosoma lewisi* and also initially classified them as a new form of trypanosome. However, Delanoë & Delanoë (1912), conducted a reassessment of Carini's findings. They identified this as a distinct organism unrelated to trypanosomes, within the lungs of Parisian rats. Consequently, they named it "*Pneumocystis carinii*". The name '*Pneumocystis*' was derived from the organism's affinity for the lungs ('*Pneumo-*'), its round shape ('*-cystis*'), and the name of Dr. Antonio Carini, who contributed to the identification ('*carinii*') (Delanoë & Delanoë 1912).

The debate regarding the taxonomic classification of *Pneumocystis*, whether it should be classified as a fungus or a protozoan, began and persisted until the late 1980s. However, since 1988, a substantial body of evidence has accumulated, strongly indicating that *Pneumocystis* should be classified within the fungal kingdom.

The phylogenetic analyses of *Pneumocystis* conducted using the rRNA gene (Edman et al. 1988, Stringer et al. 1989) and mitochondrial gene sequences (Pixley et al. 1991, Sinclair et al. 1991, Wakefield et al. 1992) revealed significant similarities with DNA sequences found in fungi. The analyses of expressed sequence tags (EST) and cDNA sequences from *P. carinii*, conducted as part of the *Pneumocystis* genome project (PGP) initiative provided strong confirmation of the close genetic relationship between *Pneumocystis* and fungi (Cushion et al. 2007). The discovery that *Pneumocystis* genes encoding thymidylate synthase (TS) and dihydrofolate reductase (DHFR) located on separate chromosomes indicated that the enzymatic functions of TS and DHFR are carried out by distinct polypeptide chains, which is a distinct characteristic from all protozoa studied to date (Krungkrai et al. 1990, Anderson 2005, Sienkiewicz et al. 2008). The identification of a gene encoding protein that exhibited significant structural similarity to the elongation factor 3 (EF-3) found in *Saccharomyces cerevisiae* and *Candida albicans* was a significant finding in *Pneumocystis* (Ypma-Wong et al. 1992). While EF-1 and EF-2 are conserved across both fungi and higher eukaryotes, EF-3 is a unique feature of fungi. Therefore, additional evidence to support the classification of the *Pneumocystis* within the fungal group was no longer needed. Finally, Eriksson (1994a) established *Pneumocystidales* to accommodate *Pneumocystis*.

General description

The asexual reproduction of *Pneumocystis* species primarily takes place through binary fission of the unicellular trophic forms. These trophic forms are usually ellipsoidal but can display pleiomorphism. *Pneumocystis* species do not exhibit budding, and neither pseudohyphae nor hyphae are present in their life cycle (Cushion 2010, Chabé et al. 2011, Cushion & Keely 2011).

During sexual reproduction, a putative sexual cycle occurs following the mating of trophic forms, leading to the formation of a diploid zygote (Cushion & Keely 2011). This zygote then

develops into prototunicate asci, often referred to as "cysts." These cysts contain eight ascospores produced through a combination of meiosis and an additional mitotic division. Ascospores are typically spherical, measuring around 1 μm in diameter, but they can elongate within the ascus (Cushion & Keely 2011). The release of spores from the prototunicate asci may occur through a rupture in the wall. Throughout their life cycle, all stages of *Pneumocystis* are enclosed by two-unit membranes. *Pneumocystis* species remain unicellular in nature (Cushion 2010, Cushion & Keely 2011).

Life cycle

Pneumocystis species undergo extracellular reproduction within the alveoli of mammalian lungs. They are obligate, host-specific, non-mycelial fungi. They display three distinct developmental forms namely, trophozoite (trophic/ vegetative stage), precyst (sporocyte/ young asci) and cyst (asci stage) (Cushion 2010, Cushion & Keely 2011). Trophozoite (trophic/vegetative stage) consists of small structures, measuring between 1 to 5 μm in diameter, irregularly-shaped and consists of a single nucleus (Hawksworth et al. 1995, Cushion 2010, Cushion & Keely 2011) and have the ability to undergo binary fission. Trophozoites typically attach themselves to Type I epithelial cells lining the alveoli in the lungs of mammals. They are often found clustered together (Eriksson 1994a, Cushion 2010, Cushion & Keely 2011). Precysts (sporocyte/ young asci) form is relatively larger, ranging from 5 to 8 μm in diameter. This stage is an integral part of the sexual reproductive cycle of *Pneumocystis* (Cushion & Keely 2011). Cysts (asci stage) are approximately 8 μm in diameter, ovoid or more rounded at the mature stage and represent the asci stage of *Pneumocystis*. They are spherical structures and typically contain up to eight intra-cystic bodies (ascospores), each measuring 1 to 2 μm in diameter, initially subglobose, then becoming elongate and finally falcate (Hawksworth et al. 1995). The presence of these cysts is a characteristic feature of *Pneumocystis* species (Eriksson 1994a, Cushion 2010, Chabé et al. 2011, Cushion & Keely 2011).

Families included in *Pneumocystidales*

Pneumocystidaceae O.E. Erikss.

Evolution

One of the earliest phylogenetic trees illustrating the evolutionary relationships among ascomycetes was presented by Berbee & Taylor (1992b). In their study on morphological convergence in true fungi, *Pneumocystis* was identified as a part of the basal ascomycetes, which also encompassed the *Schizosaccharomycetales*. Then, *Pneumocystis* was categorized within *Taphrinomycotina*, which was previously known as '*Archiascomycetes*' (Eriksson & Winka 1997). There were debates regarding whether *Pneumocystis* should be grouped with *Saccharomycotina* (Sugiyama et al. 2006). However, the phylogenomic analysis confirmed that *Pneumocystis* belongs to *Taphrinomycotina*, and *Schizosaccharomyces pombe* was identified as its closest extant relative species (Liu et al. 2009).

Pneumocystis species exhibit a high degree of host species specificity, suggesting a long history of co-evolution and co-speciation with their mammalian hosts (Chabé et al. 2011). Various studies have explored the relationship between the phylogenies of *Pneumocystis* species and their mammalian hosts, indicating a pattern of co-phylogeny (Demanche et al. 2001, Guillot et al. 2001, Hugot et al. 2003). Estimates of *Pneumocystis* speciation times based on genetic variation suggest the divergence between *P. carinii* and *P. jirovecii* occurred approximately 90–100 MYA, aligning with the divergence of primates from rodents (Keely et al. 2003). Speciation dating for *Pneumocystis* from rodent Murinae (*P. carinii* and *P. murina*) suggests divergence around 51-71 MYA, consistent with the rat-mouse phylogenetic divergence estimate (Keely et al. 2003). A similar analysis for *P. carinii* and *P. wakefieldiae* indicates divergence around 15-22 MYA (Cushion et al. 2004, Fischer et al. 2006).

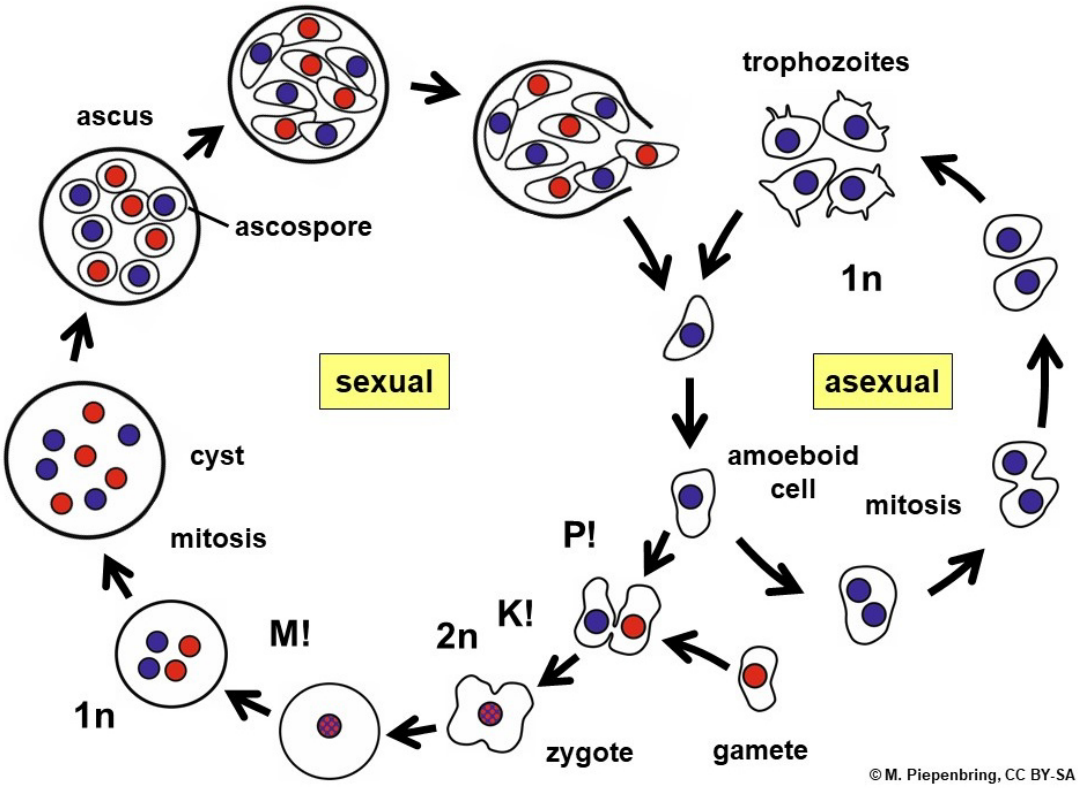


Figure 290 – Sexual and asexual life cycles of *Pneumocystidales* (From Mycological teaching diagrams by Meike Piepenbring 2023). Abbreviations: 1n = haploid, 2n = diploid, P! = plasmogamy, K! = karyogamy, M! = meiosis. Black and white circles represent haploid nuclei of different mating types, circles of both colors represent diploid nuclei.

Justification of order and problems

Initially, the *Pneumocystis* species were misclassified due to their unusual morphology. They were considered to be protozoans rather than fungi. However, later multiple molecular studies have consistently demonstrated that *Pneumocystis* should be classified within the ascomycete genus, with *Schizosaccharomycetales* being the most likely closest relatives (Meade & Stringer 1991, Edlind et al. 1992, Liu et al. 1992, Ypma-Wong et al. 1992).

Eriksson & Hawksworth (1993b) accepted 45 orders within ascomycetes, and at that time, *Pneumocystis* was placed among "*incertae sedis*," and its exact classification was uncertain. While *Pneumocystis* shared similarities with fission yeasts of *Schizosaccharomycetales* in aspects such as its life cycle and 18S rDNA, it was deemed too early to definitively categorize it within *Schizosaccharomycetales* (Eriksson 1994a). Although 18S rDNA sequences suggested that *Pneumocystis* taxa are closely related to basal ascomycetes, the statistical support for this relationship was not very strong. Also, various molecular markers did not consistently point to a close relationship (Eriksson 1994a). A notable difference was found in the calmodulin gene, which exhibited significant dissimilarity between *Pneumocystis* and *Schizosaccharomyces* (Eriksson 1994a). Consequently, it was decided to establish a separate order and family to accommodate *Pneumocystis*. This taxonomic decision was formalized by Eriksson (1994a) when *Pneumocystidales* and *Pneumocystidaceae* were established to accommodate *Pneumocystis*.

Significance

Ecological and economic roles

Pneumocystidales is a diverse group of opportunistic fungal organisms having an extracellular parasitic life cycle, known for their affinity to pneumocytes in various mammalian hosts (Dei-Cas 2000). These adaptable organisms have evolved to thrive and reproduce within the lungs of both immunocompromised and healthy mammals, making them potential reservoirs for infections (Chabé

et al. 2004, Aliouat-Denis et al. 2008). *Pneumocystis* can be transmitted through airborne routes, and even the lungs of healthy individuals are often colonized by this fungus (Riebold et al. 2012). However, in individuals with weakened immune systems, *Pneumocystis* species can cause severe and life-threatening pneumonia (Thomas & Limper 2007). In addition to humans, *Pneumocystis* infections have been documented in a wide range of wild and domestic animal species. These include monkeys, mice, shrews, rats, rabbits, ferrets, horses, goats, pigs, wild boars, red foxes, raccoon dogs, domestic dogs and cats (Laakkonen et al. 1993, Shah et al. 1996, Wazir & Ansari 2004, Danesi et al. 2016, Kureljušić et al. 2016, Weissenbacher-Lang et al. 2016, Weissenbacher-Lang et al. 2018, Danesi et al. 2019, Riebold et al. 2020, Kureljušić et al. 2022). The medical significance of *Pneumocystidales* drives research efforts to understand its biology, develop diagnostic tools, and explore treatment options (Krajicek et al. 2009, Nakamura et al. 2009). These indirectly contribute to the pharmaceutical and healthcare industries. Controlling and managing pneumonia caused by *Pneumocystis* spp. in immunocompromised populations is vital for public health (Sokulska et al. 2015). Effective treatment and prevention strategies are essential to reduce the economic burden of pneumonia caused by *Pneumocystis* spp. on healthcare systems (Goldie & Freedberg 1999, Walzer 2013).

Chemical diversity

The chemical diversity and secondary metabolites of *Pneumocystis* spp. have not been extensively explored or characterized in comparison to other fungal genera. Nonetheless, it has been reported that *Pneumocystis* species exhibit responsiveness to anti-parasitic medications such as pentamidine and cotrimoxazole. These drugs are used in the treatment of *Pneumocystis* infections (Catherinot et al. 2010).

An interesting distinction is found in the composition of *Pneumocystis* spp. cell walls, as they contain cholesterol instead of ergosterol. This unique composition is a key factor in explaining why amphotericin B, an antifungal medication that typically targets ergosterol in fungal cell membranes, is ineffective against *Pneumocystis* spp. (Catherinot et al. 2010). It has been reported that *Pneumocystis* produce a range of glycoproteins and proteases that are believed to play crucial roles in their interactions with host cells and the host immune system (Fishman 2020). The surface of *Pneumocystis* species can be coated with a variety of host proteins. This coating may include specific and nonspecific immunoglobulins, albumin, surfactant proteins, as well as extracellular matrix proteins such as laminin and fibronectin. This interaction with host proteins can have several effects, including helping the organism evade the host immune system and facilitating adherence to host cells (Fishman 2020).

Other relevant data and future recommendations

The environmental source of *Pneumocystis* remains a mystery, which has made it challenging to conduct epidemiological studies. Whereas, genome analysis has been a valuable tool for investigating disease outbreaks in geographical variations (Edman et al. 1988, Stringer et al. 1989, Liu et al. 1992, Gigliotti et al. 2014, Ma et al. 2016, Fishman 2020, Latinne et al. 2021). *Pneumocystis* species demonstrate high host-specificity, each often associated with a specific animal species, and the precise molecular mechanisms responsible for this specificity are not well-understood (Fishman 2020, Riebold et al. 2020, Cissé et al. 2021). The inability to culture *Pneumocystis* species *in vitro* is a significant challenge in studying this organism (Porollo et al. 2012). However, researchers are overcoming this limitation by conducting more specific molecular studies, including epidemiological research, to gain insights into *Pneumocystis* biology and genetics (Porollo et al. 2012, Ma et al. 2018). Additionally, the secondary metabolites or chemical diversity of *Pneumocystis* have not been extensively explored when compared to some other fungal groups. This suggests that there may be untapped potential for discovering unique bioactive compounds or chemical processes associated with *Pneumocystis* that could have broader implications in various fields of research.

***Schizosaccharomycetes* O.E. Erikss. & Winka, Myconet 1: 10 (1997)**
***Schizosaccharomycetales* O.E. Erikss., Systema Ascomycetum 11: 146 (1994)**

Subphylum : *Taphrinomycotina*
Class : *Schizosaccharomycetes*
Subclass : *Schizosaccharomycetidae*

Introduction

Schizosaccharomycetales currently comprises the monotypic family *Schizosaccharomycetaceae*, which includes *Schizosaccharomyces* (Wijayawardene et al. 2020). These are commonly known as "fission yeasts" due to their distinctive method of cell division through medial fission, which sets them apart from budding yeasts (Chang & Nurse 1996). Fission yeasts are unicellular organisms with a saprobic lifestyle (Eriksson 1993, Bullerwell et al. 2003). Their classification within the *Ascomycota* is based on fundamental characteristics like the formation of ascospores, non-centric mitosis, life cycle characteristics, and phylogenetic evidence (Sipiczki 1995). *Schizosaccharomyces* was originally typified by *S. pombe*, a yeast strain that was isolated from millet beer in East Africa (Lindner 1893, Vorderman 1894). *Schizosaccharomyces* is recognized to encompass five species *viz*. *S. cryophilus* (Helston et al. 2010), *S. japonicus* (Yukawa & Maki 1931), *S. octosporus* (Beijerinck 1894), *S. osmophilus* (Brysch-Herzberg et al. 2019), and *S. pombe* (Lindner 1893).

History

Schizosaccharomyces pombe, the type species of *Schizosaccharomycetales*, was isolated and identified by Lindner (1893) from East African millet beer. The formal classification of *Schizosaccharomycetales* can be traced back to the early 20th century, with the establishment of the order for the fission yeasts by Eriksson (1993). Leupold (1970) suggested the genetic basis of homothallism in *S. pombe*, which was a critical aspect of its reproductive biology. In the mid-1970s, there was a significant breakthrough in understanding the cell cycle regulation in *S. pombe*. Hartwell et al. (1974) and Nurse et al. (1976) conducted pioneering research that identified key cell cycle control genes in fission yeast. *Schizosaccharomyces pombe* genome sequence and annotation were published, making it the sixth eukaryotic model organism to have its genome fully sequenced and annotated (Wood et al. 2002). This achievement provided researchers with valuable genetic information and resources for studying this important yeast species. With time, *Schizosaccharomyces cryophilus*, *S. japonicus*, *S. octosporus* and *S. osmophilus* were introduced (Beijerinck 1894, Yukawa & Maki 1931, Helston et al. 2010, Brysch-Herzberg et al. 2019). Research on *Schizosaccharomycetales* continued to advance, with ongoing studies in areas such as genomics, genetics, cell biology, and biotechnology (Takegawa et al. 2009, Jeffares et al. 2015, Löbs et al. 2017, Vyas et al. 2021).

General description

Schizosaccharomyces species are characterized by their unique features, including fission cells, true hyphae, and the production of variously-shaped (spherical, ovoidal or reniform), smooth or warty, liberated ascospores. They primarily reproduce vegetatively through cell elongation and binary fission (Minet et al. 1979, Kreger-van Rij 1984).

When they reproduce asexually, cells elongate at their tips and then divide by binary fission. This means that a single cell can give rise to two identical daughter cells without the involvement of mating or meiosis (Minet et al. 1979, Kreger-van Rij 1984). Some fission yeast species have the capability to develop true hyphae, which are elongated, thread-like structures. These hyphae can branch and often fragment into specialized structures known as arthrospores (Kurtzman 1998).

Though the fission yeasts typically reproduce asexually as haploids, they also have the ability to switch to sexual reproduction when facing nitrogen starvation. Sexual reproduction involves cell elongation, formation of conjugation tubes, and union between haploid cells of opposite mating types (Hirata & Tanaka 1982, Leupold 1987, Kurtzman 1998). This results in the formation of a diploid

zygote, which undergoes meiosis to produce four haploid nuclei encapsulated by spore walls. In some species, a second mitotic division occurs, generating eight spores (Tanaka & Hirata 1982) (Fig. 292).

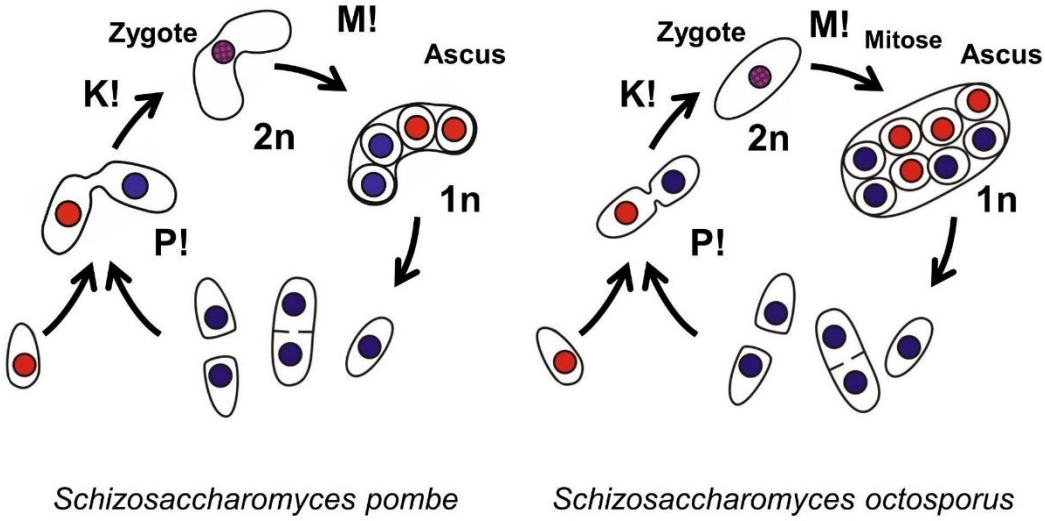


Figure 291 – Life cycles of *Schizosaccharomycetales* (From Mycological teaching diagrams by Meike Piepenbring (2023)). a. *Schizosaccharomyces pombe*. b. *S. octosporus*. Abbreviations: 1n = haploid, P! = plasmogamy, K! = karyogamy, 2n = diploid, M! = meiosis Black and white circles represent haploid nuclei of different mating types; circles of both colors represent diploid nuclei.

Families included in *Schizosaccharomycetales*

Schizosaccharomycetaceae Beij. ex Klöcker

Evolution

Schizosaccharomyces is one of the representative genera in the early diverging *Ascomycota* lineage. These fungi have been classified as "*Archiascomycetes*" or placed within the subphylum "*Taphrinomycotina*" (Berbee & Taylor 1994, Taylor 1994, Nishida & Sugiyama 1994, Sugiyama et al. 2006). *Archiascomycetes* are considered to be the most ancestral lineage of the ascomycetes (Bullerwell et al. 2003). Multiple phylogenetic analyses, including Bayesian methods and multi-locus gene sequences, have confirmed the monophyly of these subphyla and the basal position of *Taphrinomycotina* within *Ascomycota* (Sugiyama et al. 2006). It has been discovered that, the budding yeast, *Saccharomyces cerevisiae* and the fission yeast *Schizosaccharomyces pombe* evolutionarily diverged from each other by approximately 350-400 MYA (Sipiczki 2000, Wood et al 2002). However, to address contentious questions regarding the origin, monophyly, and evolution of the *Taphrinomycotina*, additional integrated phylogenetic analyses which involve sequences from a more extensive set of genes encompassing a broader taxonomic sampling, particularly from the early diverging *Ascomycota* are necessary (Sugiyama et al. 2006).

Justification of order and problems

Historically, budding and fission yeasts were thought to belong in *Hemiascomycetes* (Kurtzman 1994). However, molecular research demonstrated that budding and fission yeasts are distinct groups and do not belong to a single order (Kurtzman 1994). Therefore, the creation of two orders, *Endomycetales* and *Schizosaccharomycetales*, was proposed. This division was consistent with prior biochemical comparisons (Kurtzman 1994).

Previously, *Schizosaccharomyces* was associated with either a separate family or subfamily of t*Endomycetales* (Kurtzman & Robnett 1994). However, due to the significant phylogenetic distance between *Schizosaccharomyces* and budding yeasts, *Schizosaccharomyces* was reassigned to *Schizosaccharomycetales* (Kurtzman & Robnett 1991, Kurtzman 1994). Further research was conducted by Eriksson (1993), who gathered and compared the DNA sequences of *Saccharomyces*

cerevisiae and *Schizosaccharomyces pombe*. Their findings supported the establishment of two distinct orders, *Saccharomycetales* and *Schizosaccharomycetales*. The order *Schizosaccharomycetales* was specifically established for the fission yeasts (Eriksson 1993).

Kurtzman & Robnett (1994) conducted a study to determine the placement of various genera within families and orders of ascosporogenous yeasts and yeast-like fungi. They utilized the divergence in partial nucleotide sequences from large and small subunit ribosomal RNAs for this purpose. Their research finally led to the conclusion that ascosporogenous yeasts should not be considered reduced versions of filamentous fungi (Kurtzman & Robnett 1994).

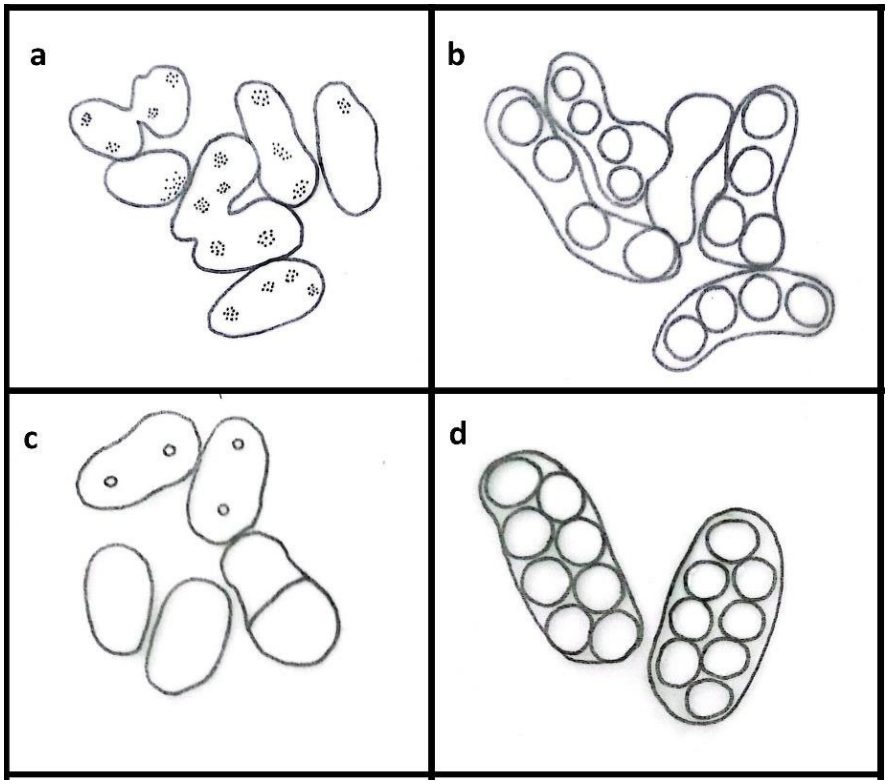


Figure 292 – Morphology of *Schizosaccharomycetales* (redrawn from Seike & Niki (2022)). a Vegetative cell of *Schizosaccharomyces pombe*. b Asci of *S. pombe*. c Vegetative cells of *S. octosporus.* Asci of *S. octosporus*.

Significance

Ecological and economic roles

Fission yeasts can be considered as integral components of natural microbial communities that actively engage in the fermentation of botanical sugars across diverse geographic regions (Jeffares 2018). According to research by Brysch-Herzberg et al. (2022), *Schizosaccharomyces pombe* and *S. octosporus* are primarily associated with bee honey as their main habitat. Additionally, these species have been frequently found on dried fruits like raisins, mangoes, or pineapples, potentially introduced by honeybees during ripening or drying (Brysch-Herzberg et al. 2022). *Schizosaccharomyces pombe* has been isolated from grape mash and fermented raw cacao beans, while *S. octosporus* has not been found in fresh fruit (Brysch-Herzberg et al. 2022). *Schizosaccharomyces osmophilus* is predominantly linked to solitary bee bread and is less commonly found in raisins (Brysch-Herzberg et al. 2022). *Schizosaccharomyces japonicus* is commonly found in forest substrates but also appears on fruits and in fruit fermentations (Brysch-Herzberg et al. 2022).

Fission yeasts have been identified in various traditional alcoholic fermentations, such as palm wine, a beverage produced by fermenting palm sap (Theivendirarajah & Chrystopher 1987, Amanchukwu et al. 1989, Ouoba et al. 2012). They have also been detected in natural fermentations of key agricultural products like coffee (*Coffea arabica*) and cocoa (*Theobroma cacao*) (Silva et al.

2000, Schwan & Wheals 2004). They have also found applications in brewing processes, highlighting their relevance in various industrial fermentation contexts (Benito 2019, Vyas et al. 2021). It has been found that the co-fermentation of mandarin wine with both *Saccharomyces cerevisiae* and *Schizosaccharomyces pombe* offers several advantages in terms of producing a distinctive taste and flavor when compared to fermentation only with *S. cerevisiae* (Luo et al. 2023). According to Millarini et al. (2020), the polysaccharides derived from *Schizosaccharomyces japonicus* have been found to have a beneficial effect on the heat stability of wine proteins and they are capable of reducing protein haze in wine, which is undesirable from an aesthetic and quality standpoint.

Schizosaccharomyces pombe is a crucial model organism in biological research (Wood et al. 2002, Hoffman et al. 2015, Fantes & Hoffman 2016, Hayles & Nurse 2018). Another fission yeast, *S. japonicus*, has also emerged as a model organism for cell biology research (Sipiczki 2000, Klar 2013, Russell et al. 2017). They have played pivotal roles in advancing our understanding of fundamental cellular processes, including cell cycle regulation, DNA repair, chromosome segregation, and more (Nurse 1994, Martin & Koonin 2006). These studies have contributed valuable insights into fundamental biological mechanisms relevant to both normal cell function and diseases like cancers (Bähler et al. 1998, Vyas et al. 2021).

Schizosaccharomyces pombe is utilized as a probiotic feed supplement in animal husbandry, particularly in poultry and livestock. When incorporated into animal feed, it can improve gut health and enhance nutrient absorption, leading to better overall animal health, growth and production (Chen 2023).

Chemical diversity

Schizosaccharomyces pombe plays a role in biotechnological production of coenzyme Q_{10} (CoQ_{10}), which is a benzoquinone acting as a vital antioxidant with health benefits such as energy production and anti-oxidative properties. The unique metabolic pathways of *S. pombe* enable substantial CoQ10 synthesis, making it suitable for harvesting and using as a human nutritional supplement (Kawamukai 2009, Lee et al. 2017).

Research has found that, *S. pombe* can be used for the bioethanol production using agricultural wastes with specific physico-chemical conditions of the substrates and fermenting organisms. This can be applied in biofuel production (Choi et al. 2010, Abubaker et al. 2012, Ebabhi & Adekunle 2016). Additionally, it has been found that *Schizosaccharomyces* spp. (*S. pombe* and *S. japonicus*) release a notably high quantity of cell wall-origin polysaccharides right from the beginning of alcoholic fermentation (Domizio et al. 2017). Certain *Schizosaccharomyces* strains also demonstrate the ability to produce significant levels of pyruvic acid, which is known to be important for wine color stability (Domizio et al. 2017). Therefore, the release of polysaccharides, including galactomannoproteins, by these yeasts would suggest them particularly interesting for the industrial production of exogenous polysaccharide preparations (Domizio et al. 2017).

Other relevant data and future recommendations

Until now, *Schizosaccharomycetales* comprises only *Schizosaccharomyces* which has only five accepted species (Lindner 1893, Beijerinck 1894, Yukawa & Maki 1931, Helston et al. 2010, Brysch-Herzberg et al. 2019). While molecular data are abundant for *S. pombe*, information about other species is limited. Despite substantial knowledge about the biology of *S. pombe*, its evolution and ecology are poorly understood (Jeffares et al. 2015). Defining the species within *Schizosaccharomyces* is challenging. Various methods have been used to define the species within *Schizosaccharomyces*, but none of these approaches has provided a fully satisfactory species concept (Brysch-Herzberg et al. 2019). Relying solely on mating experiments may not be sufficient for confirming species affiliations. Therefore, when describing new species within *Schizosaccharomyces*, it is crucial to consider all available information from molecular genetics, physiology, morphology, and ecology (Brysch-Herzberg et al. 2019). It is also important to include a diverse set of strains from closely related species originating from various geographic locations (Brysch-Herzberg et al. 2019). In addition, a comprehensive understanding of *S. pombe* metabolism

holds the potential for wide-ranging applications in various fields and may unveil novel practical uses (Chen 2023).

***Taphrinales* Gäum. & C.W. Dodge, Comparative Morphology of Fungi: 159 (1928)**

Subphylum : *Taphrinomycotina*
Class : *Taphrinomycetes*
Subclass : *Taphrinomycetidae*

Introduction

Taphrinales was introduced by Gäumann & Dodge (1928) comprising two families; *Taphrinaceae* and *Protomycetaceae*, distinguished by the number of ascospores and the way they are formed. Considering that *Taphrinales* consists of about 120 currently recognized species (Wijayawardene et al. 2022a), it is the biggest order of *Taprinomycotina*, a morphologically and ecologically heterogeneous (Sugiyama et al. 2006) species-poor (Kurtzman & Sugiyama 2015, Spatafora et al. 2017), assemblage of early diverging *Ascomycota* lineages. *Taphrinales*, the single order of *Taphrinomycetes*, accommodates dimorphic fungi with a biotrophic, plant-parasitic (Fig. 93), filamentous teleomorphic state. Furthermore, a cultivable, anamorphic yeast-like state (Fig. 294) is known for *Protomyces* and *Taphrina* (Kramer 1973). *Taphrinaceae* was described by Gäumann & Dodge (1928) and contains a single genus *Taphrina*, introduced by Fries (1815), currently accommodating nearly 100 species (Wijayawardene et al. 2022a). *Protomycetaceae* as (*Protomyceae*) was introduced by Gray (1821) and at that time he assigned several divergent genera, including basidiomycetes, to that family. Currently six genera; *Buerenia*, *Protomyces*, *Protomycopsis*, *Saitoella*, *Taphridium* and *Volkartia* are assigned to *Protomycetaceae* (Kurtzman & Sugiyama 2015, Wijayawardene et al. 2022a) with *Protomyces* as the type (Tubaki 1957).

Species of *Taphrina*, the single genus assigned to *Taphrinaceae* that infect primarily the fern species, *Rosales* and *Fagales* (Sugiyama et al. 2006), while the host range of *Buerenia*, *Protomyces*, *Protomycopsis*, *Taphridium* and *Volkartia* (*Protomycetaceae*) is restricted to the *Apiaceae* (*Umbelliferae*) and *Asteraceae* (*Compositae*) families (Reddy & Kramer 1975). Recently, Wang et al. (2016a) have reported the isolation of *Protomyces* strains from *Arabidopsis thaliana* (*Brassicaceae*) which is outside the previously documented host range of *Protomyces*, and described them as a novel species, *P. arabidopsidicola* (Wang et al. 2021a). In terms of morphological characteristics, haustoria were reported in some *Taphrina* species (Kramer 1973, Webster & Weber 2007). Due to the presence of carotenoids, the yeast cultures of *Protomyces* generally show reddish, salmon-like color, while *Taphrina* species often have lighter shades of red, lavender or yellow (Kurtzman 2011).

The species of *Taphrinales* occur mainly in temperate zones, rarely in tropics (Gäumann & Dodge 1928), while one species, *T. antarctica*, was recovered from Antarctica (Selbmann et al. 2014). They are most frequently isolated from hosts with characteristic symptoms, however, sometimes also from symptom-free plants, including non-hosts (Babjeva & Reshetova 1998, Inácio et al. 2004, Golonka & Vilgalys 2013, Selbmann et al. 2014, Christita et al. 2022). *Taphrina* species were reported also from forest litter (Wuczkowski et al. 2005) and one species, *T. antarctica*, was isolated from rock (Selbmann et al. 2014). The occurrence of *T. deformans* exhibiting moderate esterase activity on plasticized PVC exposed to air was reported by Webb et al. (2000). Christita et al. (2023) suggested that "in a sense" *Taphrina* species can be regarded as opportunistic plant pathogens, because they cause disease only occasionally under very specific conditions.

History

Taphrina, the type of *Taphrinaceae* and the most well-known genus of the order *Taphrinales* was described (as *Taphria*) more than two centuries ago (Fries 1815). Not much later *Protomyces*, the type of *Protomycetaceae* was introduced (Unger 1833). Three additional genera in *Protomycetaceae*; *Protomycopsis*, *Taphridium* and *Volkartia* were also described more than 100 years ago (Magnus 1905, Juel 1902, Maire 1907, respectively), while *Buerenia* (as *Burenia*) was

proposed in 1975 (Reddy & Kramer 1975). The order *Taphrinales* was proposed by Gäumann & Dodge (1928) to accommodate the families *Taphrinaceae* and *Protomycetaceae*. The assignment of these families to *Taphrinales* has not been initially unequivocally supported. While it was accepted by Arx et al. (1982), others argued for the placement of *Protomycetaceae* in the order *Protomycetales* (Kramer 1973, Reddy & Kramer 1975, Heath et al. 1987, Eriksson & Winka 1997), because of the differences in morphology, in the karyological characters of the parasitic hyphae, in the way of ascus and ascospore formation and in the mitotic systems. However, as phylogenetic analyses clearly confirmed the close relationship of *Protomyces* and *Taphrina* species (Kurtzman 1993, Nishida et al. 1993, Nishida & Sugiyama 1994, Sjamsuridzal et al. 1997, Sugiyama et al. 2006, Čadež et al. 2021), the placement of *Protomycetaceae* and *Taphrinaceae* in the order *Taphrinales* has become widely accepted (Kirk et al. 2008a, Wijayawardene et al. 2022a). Eijk & Roeymans (1982) studied the distribution of carotenoids and sterols in 37 strains representing 28 *Taphrina* and three *Protomyces* species. All strains produced variable amounts of carotenoids. The majority of them produced brassicasterol as the principal sterol, while many of them did not produce detectable amount of ergosterol. Three of the four strains that did not produce brassicasterol were later found to be misidentified and not representing *Taphrinomycotina* (Sjamsuridzal et al. 1997). The cell wall carbohydrate composition of numerous *Protomyces* and *Taphrina* species were studied by Prillinger at al. (1990). Tavares et al. (2004) successfully applied PCR and fluorescent *in situ* hybridization (FISH) techniques for direct detection of *T. deformans* in asymptomatic leaves and buds of infected peach trees.

A comprehensive monograph of the genus *Taphrina* discussing 97 species was published by Mix (1949). He interpreted as conspecific those forms which were morphologically similar and occurred on related hosts. The most important morphological features considered were the habit of mycelium, shape and size of asci, presence or absence as well as shape and size of stalk cells and size of ascospores. Moore (1990) proposed *Lalaria* for the anamorphic yeast phase of 23 previously recognized *Taphrina* species for which isolates were available in culture collections. He also provided an identification key based on the ability of these species to utilize different carbon-sources. Tavares et al. (2004) and Fonseca & Inácio (2011) questioned the reliability of the separation of the *Lalaria* species based on physiological characters, arguing that the yeast state of *Taphrina* species can effectively be discriminated by molecular methods only. Tavares et al. (2004) also provided an emended description of *Lalaria*, while Fonseca & Inácio (2011) reduced the genus to only five species which were represented by strains isolated from substrates other than plant material infected by a known *Taphrina* species and/or the yeast state isolates for which connection to a *Taphrina* teleomorph could not unequivocally be established. Fonseca & Rodrigues (2011) discussed in detail those 28 *Taphrina* species for which authentic strains were available. Selbmann et al. (2014) emended the diagnosis of the genus *Taphrina* to accommodate the asexual saprobic yeast state without known teleomorphic counterpart and transferred the extant *Lalaria* species to *Taphrina*.

Büren (1915) conducted a detailed study on the morphology and biology of some species of genera currently assigned to *Protomycetaceae*; *Protomyces*, *Protomycopsis*, *Taphridium* and *Volkartia*. Based on morphological and karyological observations Kramer (1958) transferred *Taphrina osmundae*, causing spots on the leaves of the fern *Osmunda japonica*, to the newly erected genus *Mixia*, which he tentatively placed in the family *Protomycetaceae*. Later, recognizing the differences between *Mixia* and the other genera of *Protomycetaceae* he established the family *Mixiaceae* (*Protomycetales*) to accommodate the genus (Kramer 1987). However, Nishida et al. (1995), considering the placement of *Mixia osmundae* based on SSU rRNA gene sequence and morphological characters concluded that it is actually a basidiomycete and transferred it from *Ascomycota* to *Basidiomycota*. Reddy & Kramer (1975) in their taxonomic revision reexamined all available material of the genera assigned to *Protomycetaceae* and proposed a new genus *Buerenia*. They provided a key to the five genera (*Buerenia*, *Protomyces*, *Protomycopsis*, *Taphridium* and *Volkartia*) based on morphological traits, like location of the ascogenous cells in the host tissue and their position on the hyphae (terminal or intercalary) and surface ornamentation, their requirement of rest period before germination and whether vesicula is formed or not. In the latest edition of the

monographic series The Yeasts: A Taxonomic Study, Kurtzman (2011) treated six *Protomyces* species available in culture of the ca. 10 recognized ones.

General description

Species assigned to *Taphrinales* are parasitic fungi which infect flowering plants and ferns, causing lesions, galls, color changes, hypertrophied and deformed leaves and fruits as well as leaf spots, or close clusters of twigs, witches' brooms (Gäumann & Dodge 1928, Kramer 1973). Species assigned to *Protomycetaceae* mainly induce the formation of distinct galls or swellings, while *Taphrina* species often cause leaf curl, witches' brooms, tongue-like outgrowths from female catkins, leaf spots or deformed fruits (Bacigálová et al. 2005). Their mycelium can be intercellular, subcuticular or develops in the wall of the epidermal cells. Some hyphal cells growing in plants give rise to thick-walled cells which germinate to an ascus. Ascospores are formed in a protoplasmic layer, adjacent to the wall of the ascus. The mycelium, annual or perennial, is diploid in *Protomycetaceae* and dikaryotic in *Taphrinaceae* (Gäumann & Dodge 1928, Kramer 1973). Neither ascocarp nor differentiated ascogenous hyphae are formed (Webster & Weber 2007, Kurtzman & Sugiyama 2015).

In *Protomycetaceae* hyphal cells give rise to thick-walled resting spores (chlamydospores) which are distributed throughout the host tissue or form a subepidermal layer. The resting spores may germinate by rupture or extension of the outer wall to form an enlarged spore sac, an ascus. As a result of the fusion of the vacuoles to a large central vacuole, the multinucleate protoplasm becomes oriented in a peripheral layer and the nuclei, present in an indefinite number, undergo reduction division, forming four ascospores ("endospores") per nucleus. The several hundred "endospores" accumulate at the top of the sporangium and at the rupture of the sporangium they are forcibly discharged. In case of *Protomyces*, following the ejection, the uninucleate spores bud and can be cultivated on artificial media in the yeast state. Prior to infection of the host the "endospores" or blastospores conjugate to form diploid mycelium (Gäumann & Dodge 1928, Kramer 1973). In *Taphrinaceae* the dikaryotic hyphal cells form a subcuticular or subepidermal layer of slightly thickened walled cells (chlamydospores or ascogenous cells). Karyogamy takes place in the binucleate ascogenous cells, then, during germination, the endosporium with the protoplasm burst out of the outer layer of the wall of the ascogenous cell or the wall of the ascogenous cells elongate to form thin-walled sacs.



Figure 293 – Common symptoms caused by *Taphrina* species. a Leaf curl caused by *T. deformans* on peach. b Witches' broom on hornbeam caused by *T. carpini*.

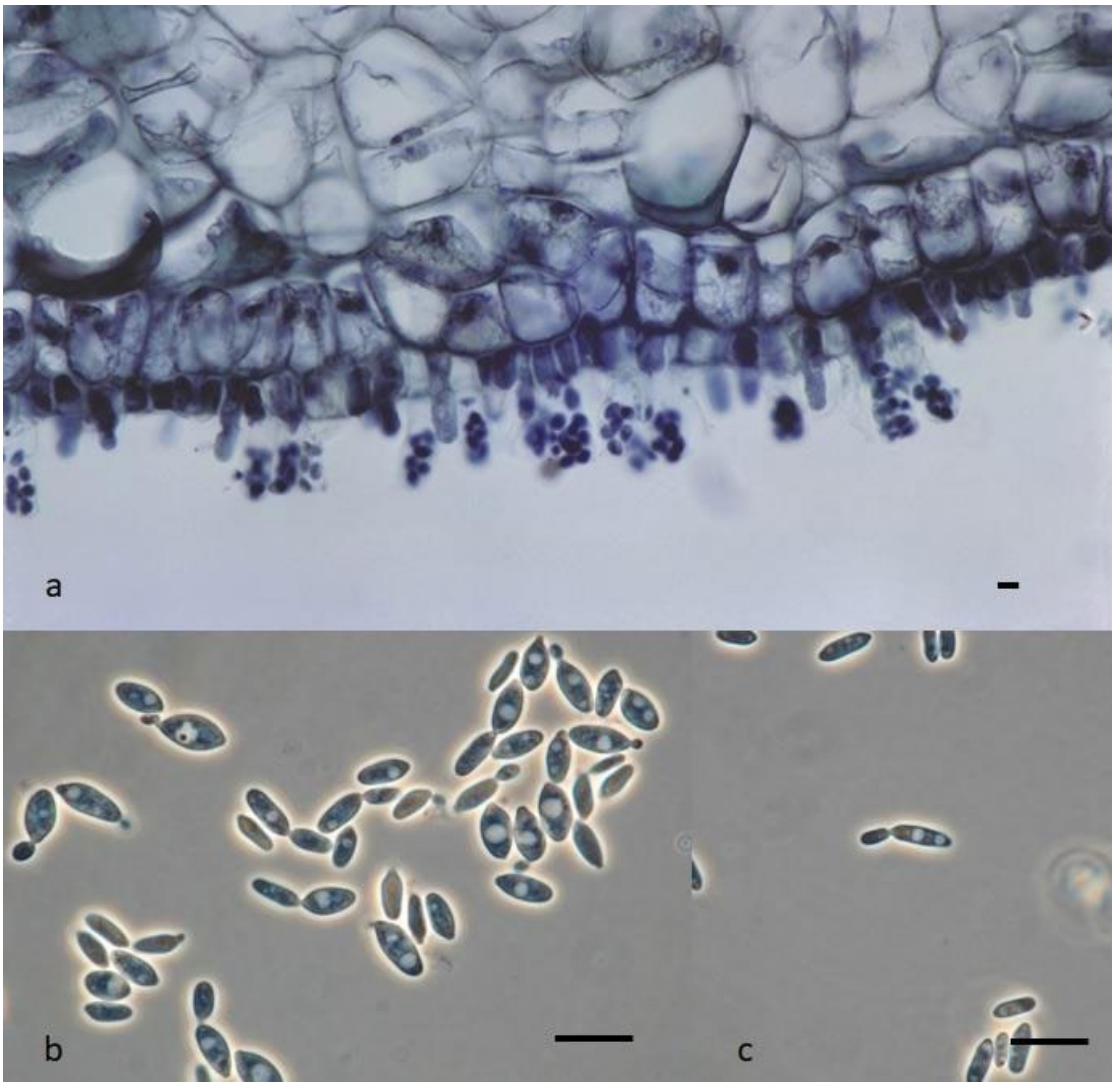


Figure 294 – Parasitic and saprobic stages of *Taphrinaceae.* a Asci and ascospores of *T. deformans* on the host plant (image supplied by M. I. Walker/SCIENCE SOURCE). b Yeast stage of *T. deformans*. c Yeast stage of *Protomyces pachydermus*. Scale bars: a, b = 10 µm.

These sac-like cells divide and the apical cells become asci while the basal cells are called stipe or stalk cells. Stalk cells may sometimes be lacking. Meiosis takes place in young asci and is often followed by one or more mitoses. As a result, four, eight or more ascospores are formed. The uninucleate ascospores propagate by budding, either within the ascus or outside of it. Ascospores and/or blastospores are forcibly discharged from the ascus by rupturing its wall at the apex. Blastospores can be cultivated on artificial media in the yeast state. The dikaryotic condition is usually restored by the division of the haploid nuclei of the yeast cells, however, in one species, *T. epiphylla*, ascospores or blastospores conjugate in pairs to form dikaryotic mycelium (Gäumann and Dodge 1928, Mix 1949, Kramer 1973). The yeast state of *Taphrina* and *Protomyces* species possess the rare combination of a two-layered cell wall and enteroblastic budding (Sjamsuridzal et al. 1997, Kurtzman & Sugiyama 2001, 2015).

Sexual morph: *Mycelium* biotrophic, subcuticular or subepidermal, septate, dikaryotic or diploid. *Haustoria* present or absent. *Ascomata* absent. Interascal tissue absent. *Ascogenous cells* terminal or intercalary, often thick walled, smooth or ornamented. *Asci* cylindrical to ellipsoid, four to multi-spored. *Ascospores* hyaline, aseptate, globose or ellipsoid, ejected simultaneously in a mass. Asexual morph: Pigmented haploid yeast-like cells, enteroblastic, mostly polar budding (Fig. 293, 294).

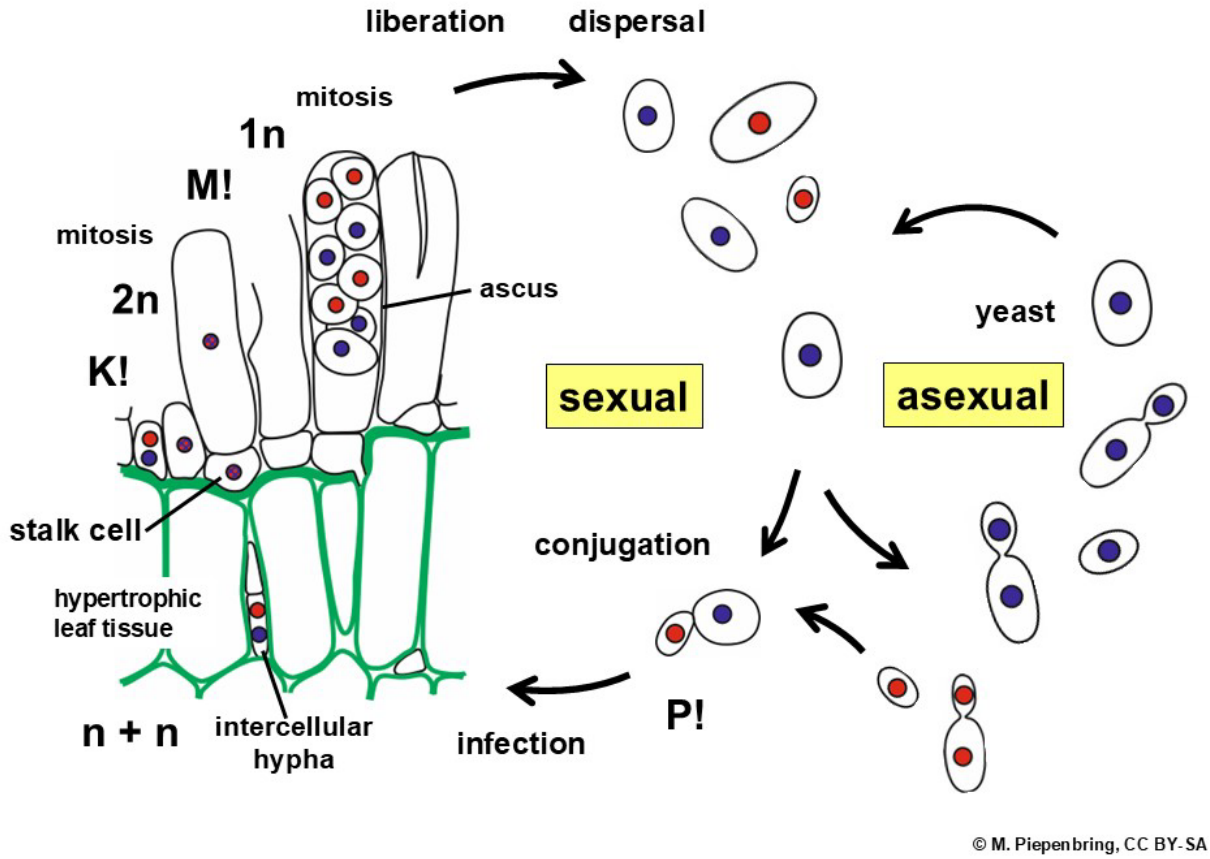


Figure 295 – Sexual and asexual life cycles of *Taphrinales* (*Taphrina deformans*) (From Mycological teaching diagrams by Meike Piepenbring (2023)). Abbreviations: 1n = haploid, 2n = diploid, P! = plasmogamy, K! = karyogamy, M! = meiosis. Blue and red circles represent haploid nuclei of different mating types, circles of both colors represent diploid nuclei. (Conjugation is rare in *T. deformans*).

Families included in *Taphrinales*

Protomycetaceae Gray
Taphrinaceae Gäum. & C.W. Dodge

Taphrinales genus *incertae sedis*
Savitreella Nutaratat, Boontham & Khunnamw.

Evolution

Phylogenetic analyses of the ribosomal RNA coding region indicate the monophyly of the genera *Protomyces* and *Taphrina*, except for *T. vestergrenii*, which occupies an intermediate position between the two genera (Rodrigues & Fonseca 2003). Furthermore, other studies confirmed that the two genera also appear monophyletic (Sjamsuridzal et al. 1997, Rodrigues & Fonseca 2003, Fonseca & Rodrigues 2011, Kurtzman 2011, Selbmann et al. 2014). Unfortunately, cultures of only a portion of *Taphrina* and *Protomyces* species are available (Fonseca & Rodrigues 2011, Kurtzman 2011) and neither cultures nor sequence data are available for genera *Buerenia*, *Protomycopsis*, *Taphridium* and *Volkartia* (Christita et al. 2023), hindering their reliable phylogenetic placement. Rodrigues & Fonseca (2003) found correlation between clustering of some *Taphrina* species in the phylogenetic tree comprising the internal transcribed spacer regions (ITS) and the host plant genera and/or families they parasitize. From this observation they concluded that this evidence constitutes a strong indication of the importance of co-evolution in the speciation of *Taphrina* species. Berbee (2001)

suggested that "the lack of molecular diversity and the dicot host preferences of confirmed *Taphrina* and *Protomyces* species point to a radiation long after the origin of angiosperms rather than phylogenetic tracking during angiosperm origins". Based on genome sequencing and comparative genomics of different *Taphrina* species with distinct host ranges, Wang et al. (2020b) came to the conclusion that "recent ecological divergence and speciation of *Taphrina* pathogens is driven by host-specificity and coevolution with their host plants".

Justification of order and problems

Despite the differences in morphology, karyological state of the parasitic hyphae, the mode of ascus and ascospore formation and the mitotic systems (Kramer 1973, Reddy & Kramer 1975, Heath et al. 1987, Eriksson & Winka 1997), the close relationship of the *Protomycetaceae*, represented by *Protomyces* species, and *Taphrinaceae*, represented by *Taphrina* species, was demonstrated e.g., by the phylogenetic analyses conducted by Kurtzman (1993), Nishida et al. (1993), Nishida & Sugiyama (1994), Sjamsuridzal et al. (1997), Rodrigues & Fonseca (2003), Bacigálová et al. (2003) Sugiyama et al. (2006), Fonseca & Rodrigues (2011), Kurtzman (2011), Selbmann et al. (2014), Čadež et al. (2021), Nutaratat et al. (2022), as well as by our current genome-scale phylogenetic analysis (Fig. 296) including the *Taphrina* and *Protomyces* species having accessible whole genome sequences in GenBank. Although the genus *Saitoella* Goto, Sugiy., Hamam. & Komag. is currently assigned to *Taphrinales* (Sugiyama & Hamamoto 2011, Kurtzman & Sugiyama 2015, Wijayawardene et al. 2022a), we exclude it from the order, because several phylogenetic analyses, e.g., Sjamsuridzal et al. (1997), Čadež et al. (2021), Groenewald et al. (2023) and the analysis conducted in the present study, indicate that it is not closely related to the species assigned to *Taphrinales*, rather, among the currently recognized taxa it is most closely related to *Neolecta*, a fungus forming macroscopic fruiting body. Therefore, we suggest placing it pro tem in *Taphrinomycotina incertae sedis*.

Significance

Ecological and economic roles

Taphrina species infect primarily ferns, *Rosales* and *Fagales* species (Sugiyama et al. 2006), while *Buerenia*, *Protomyces*, *Protomycopsis*, *Taphridium* and *Volkartia* species infect *Apiaceae* (*Umbelliferae*) and *Asteraceae* (*Compositae*) (Reddy & Kramer 1975). *Taphrina deformans* the causal agent of peach leaf curl (Fig. 293 – 1a), is the most serious pathogen among *Taphrinales* and occurs wherever peach trees grow (Webster & Weber 2007). In the infested areas of the leaves host cells increase in size, lose their chlorophyll, and often accumulate a red pigment in their enlarged vacuoles (Fitzpatrick 1934). Auxin and cytokinin production were detected in the investigated *Taphrina* species (Kern & Naef-Roth 1975), however, the role of these hormones in their pathogenicity has not been confirmed (Christita et al. 2021). Numerous additional *Taphrina* species are known to infect different plants and cause different symptoms. For example, *T. pruni* causes pocket plums making the plum wrinkled and shriveled and the fruit to have cavity in the center instead of stone (Webster & Weber 2007). *Taphrina carpini*, *T. wiesneri* and *T. betulina* induce the formation of witches' broom in twigs of European hornbeam (*Carpinus betulus*) (Fig. 293 – 1b) (Gäumann & Dodge 1928), Japanese cherry tree (*Cerasus yedoensis*) (Kurtzman & Sugiyama 2001) and birch (*Betula pendula*) (Christita et al. 2023), respectively. *Taphrina alni* produces tongue-like outgrowths from female catkins of grey alder (*Alnus incana*) (Bacigálová et al. 2003). These infections are usually considered to have less serious consequences than the leaf curl on peach caused by *T. deformans*, but e.g., the witches' broom caused by *T. betulina* can cause significant loss to birch forestry production (Christita et al. 2023).

Chemical diversity

Numerous *Taphrina* and *Protomyces* species produce variable amounts of carotenoids and brassicasterol (Eijk & Roeymans 1982). Several *Taphrina* species, including *T. deformans* produce indoleacetic acid (Yamada et al. 1990).

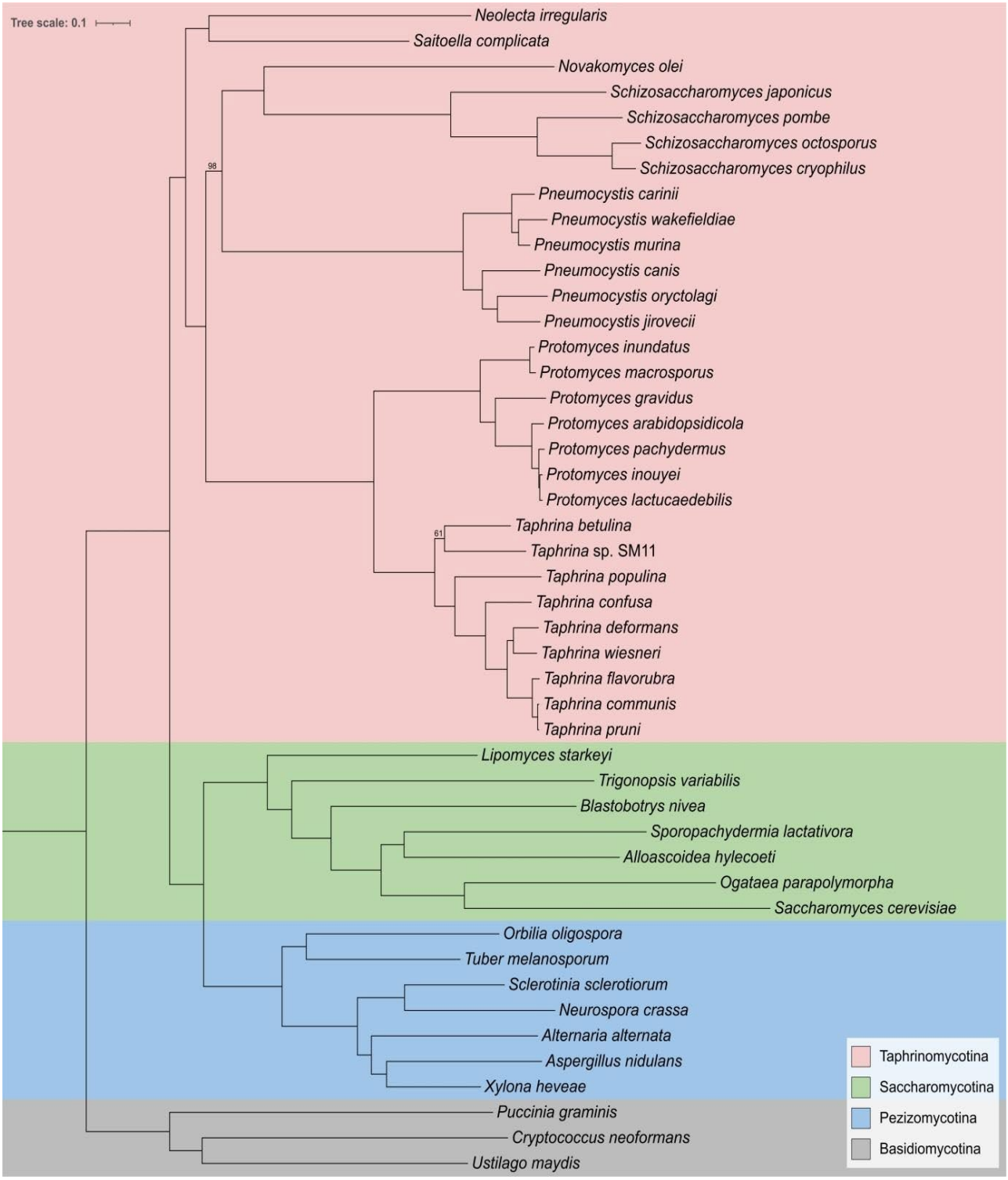


Figure 296 – Genome-scale phylogeny of *Protomyces* and *Taphrina* species. Maximum likelihood analysis with the Q.yeast model on a data matrix of 1035 concatenated orthologous proteins of 46 taxa. Bootstrap values are given only for branches where they were less than 100 %.

Other relevant data and future recommendations

Isolation of *Buerenia*, *Protomycopsis*, *Taphridium* and *Volkartia* strains, given that they are cultivable, would be a major step in understanding the biology, ecology and the taxonomy of these species. Genome sequencing and mining of the species assigned to *Taphrinales* will provide an unprecedented opportunity to reconstruct the phylogeny of this order and to identify potential biotechnologically interesting features of these species.

DISCUSSION

Ascomycota and *Basidiomycota*, the two largest phyla of fungi, encompass the majority of all known fungal species (Pem et al. 2024). *Ascomycota*, in particular, stands out with its highest species richness, a result of its faster evolutionary rate compared to *Basidiomycota* (Wang et al. 2010b). This phylum is a key player in the study of fungal diversity (Hibbett et al. 2018). Within *Ascomycota*, the classes *Dothideomycetes*, *Lecanoromycetes* and *Sordariomycetes* boast the richest species diversity (Wang et al. 2010b). In this study, these three classes accommodate the highest number of orders with 57, 21 and 52 orders. The traditional classification of ascomycetes was initiated with the ascoma type (Fries 1823). Later, ascomatal development types were used which resulted in two major groups, including *Ascohymeniales* and *Ascoloculares* (Nannfeldt 1932). However, numerous studies on the classification showed that the morphological diversity of these groups has a heterogeneous nature. Molecular techniques have shed light on the advances in fungal taxonomy and the polyphasic approach has been recommended as the reliable technique to study species diversity (Maharachchimbukura et al. 2021a).

In the ordinal classification provided by Eriksson & Winka (1997), 20 orders (*Calosphaeriales*, *Coryneliales*, *Gyalectales*, *Laboulbeniales*, *Lahmiales*, *Lichinales*, *Medeolariales*, *Meliolales*, *Ostropales*, *Patellariales*, *Pertusariales*, *Phyllachorales*, *Pyrenulales*, *Rhytismatales*, *Spathulosporales*, *Teloschistales*, *Triblidiales*, *Trichosphaeriales*, *Trichotheliales* and *Verrucariales*) were treated with uncertain phylogenetic position. However, among these orders, 17 orders were transferred to *Dothideomycetes*, *Eurotiomycetes*, *Laboulbeniomycetes*, *Lecanoromycetes*, *Leotiomycetes,* *Lichinomycetes* and *Sordariomycetes* with the aid of morphological and phylogenetic evidence. *Triblidiales* has been treated as a synonym of *Rhytismatale*s (Magnes 1997). *Trichosphaeriaceae* (*Trichosphaeriales*) has been recently recognized under family *incertae sedis* in *Diaporthomycetidae* (Hongsanan et al. 2017a), whereas *Trichotheliaceae* (*Trichotheliales*) is accepted under *Gyalectales* in *Lecanoromycetes* (Kraichak et al. 2018b). Further, Eriksson & Winka (1997) treated 17 orders in seven classes within *Pezizomycotina* and four orders in four classes within *Taphrinomycotina* whereas a single order and a class within *Saccharomycotina* were accepted. Based on the phylogenetic classification of Hibbett et al. (2007), ten classes were accepted within *Pezizomycotina* whereas four classes and four orders were accepted within *Taphrinomycotina* and the classification of *Saccharomycotina* remained the same. In the study of Lumbsch & Huhndorf (2010), eleven classes were accepted under *Pezizomycotina* whereas four classes were accepted under *Taphrinomycotina*, while a single class was accepted under *Saccharomycotina* (Lumbsch & Huhndorf 2010). The count has increased by accepting 13 classes in *Pezizomycotina* and five classes in *Taphrinomycotina* while *Saccharomycotina* remained unchanged (Wijayawardene et al. 2017a). The classification within and among classes in *Pezizomycotina* has undergone several changes following the advent of molecular technology (Tedersoo et al. 2018). Combining both available literatures as well as molecular phylogeny, we accept 171 orders with 16 classes within *Pezizomycotina* and 6 orders within *Taphrinomycotina*. However, molecular data for *Lahmiales* is not available, which is also discussed under the particular order. *Oncopodiellales* is a recently introduced order which has not been included in the study, including in the phylogeny. However, we also accept this order under *Dothideomycetes* following Sun et al. (2025). Further studies are needed to understand its potential phylogenetic relationship with the members of *Pezizomycotina.*

Saccharomycotina is the second largest subphylum in *Ascomycota* that accommodates important opportunistic pathogens and biotechnologically important species. The traditional classification of the subphylum was mainly based on micro-morphological features of asexual and sexual reproduction, and physiological and biochemical characteristics. However, molecular phylogenetic analyses lead to numerous changes within this group with the inclusion of 16 families within a single class *Saccharomycetes* and an order *Saccharomycetales* with more than 1200 species. However, recent studies (Shen et al. 2018, 2020b, Li et al. 2021a) questioned the higher-level classification of *Saccharomycotina*, leading to the revision of the subphylum. Consequently, based on relative evolutionary divergence and genome content analyses, Groenewald et al. (2023)

introduced seven classes (*Alloascoideomycetes*, *Dipodascomycetes*, *Lipomycetes*, *Pichiomycetes*, *Saccharomycetes*, *Sporopachydermiomycetes*, and *Trigonopsidomycete*) and 12 orders (*Alaninales*, *Alloascoideales*, *Ascoideales*, *Dipodascales*, *Lipomycetales*, *Phaffomycetales*, *Pichiales*, *Saccharomycetales*, *Saccharomycodales*, *Serinales*, *Sporopachydermiales*, and *Trigonopsidales*). The establishment of orders is supported by genomic studies and several biological factors such as morphology, physiology, behaviors, or ecology that are well detailed in Groenewald et al. (2023).

We conducted multigene phylogenetic analyses based on SSU, LSU, 5.8S, TEF and RPB2 sequence data to investigate the phylogenetic placement of orders within *Ascomycota* (Fig. 1). All the classes of *Pezizomycotina* and *Taphrinomycotina* formed a monophyletic clade except the class *Leotiomycetes.* Our results place *Dothideomycetes* in the crown clade, following *Arthoniomycetes* and *Laboulbeniomycetes*. The crown clade primarily comprises *Pleosporomycetidae*, which includes the orders *Pleosporales*, *Hysteriales*, *Gloniales*, and *Mytilinidiales*. The orders previously classified under *Dothideomycetidae* were recovered in the basal clades, along with several newly established orders such as *Arthrocatenales*, *Endophytiales*, *Endosporiales*, and *Phaeosclerales*. Both the crown and basal clades largely accommodate orders that were traditionally assigned to their respective subclasses. *Arthoniomycetes* was nested within *Dothideomycetes*, which is not a surprising since both classes are known as *Dothideomyceta* and formed a monophyletic clade (Schoch & Grube 2015). However, one lichenized lineage of *Dothideomycetes*, *Trypetheliales*, formed a long-branch sister relationship with *Arthoniomycetes*, with low support. The clade comprising *Arthoniales*, *Lichenostigmatales*, and *Trypetheliales* was also reported in previous phylogenetic studies (Ertz et al. 2014). Most members of *Arthoniales* are lichenized, though some species are non-lichenized or lichenicolous fungi. *Lichenostigmatales*, represented by a single family, *Phaeococcomycetaceae*, primarily consists of lichenicolous fungi, with some species inhabiting rocks. Several *Lichenostigma* strains also showed a close phylogenetic affinity with the rock-inhabiting order *Lichenotheliales* within *Dothideomycetes* (Ertz et al. 2014, 2015). In *Trypetheliales*, most species in the family *Trypetheliaceae* are lichenized, whereas members of *Polycoccaceae* entirely accommodate lichenicolous fungi. A close phylogenetic relationship between lichenized and non-lichenized members was also observed in *Strigulales* and *Monoblastiales*. The phylogenetic position of *Neodactylariales* was surprising, as it initially formed a close phylogenetic association with *Pleosporales* during the establishment of the order (Qiao et al. 2020). However, in this study, it was recovered in the basal lineage of *Dothideomycetes* and *Arthoniomycetes*. The generic type, *Neodactylaria*, had an uncertain phylogenetic placement during the establishment of the genus and was placed in *Dothideomycetes, Incertae sedis* (Crous et al. 2017b). This asexually reproducing monotypic order could be treated under *Dothideomycetes* orders *incertae sedis*, which is also accepted by Hyde et al. (2024b).

The orders classified under *Dothideomycetes* orders *incertae sedis* were mostly recovered between the clades of *Pleosporomycetidae* and *Dothideomycetidae*, with a few exceptions, including *Aureoconidiellales* and *Catinellales*. *Aureoconidiellales* was established within *Dothideomycetidae* and initially formed a close phylogenetic association with *Asterinales* and *Cladoriellales* (Hernández-Restrepo et al. 2020). However, this study showed a closer phylogenetic relationship with *Cladoriellales* and was recovered in a sister clade with other *incertae sedis* orders. This asexually reproducing order, reported on living leaves, also shares similar morphological characteristics with the asexually typified order *Cladoriellales*. The sexually typified monotypic order *Catinellales* was established within *Dothideomycetes incertae sedis* (Hongsanan et al. 2020a) and was recovered in the basal lineage of *Dothideomycetidae* with low bootstrap support.

The clade starting from *Holmiellales* to *Superstratomycetales* showed a closer phylogenetic relationship to *Pleosporomycetidae* than to *Dothideomycetidae*. All of these orders have been classified under *Dothideomycetes* orders *incertae sedis* in recent studies (Hongsanan et al. 2020a, Hyde et al. 2024b). The orders traditionally placed in *Dothideomycetidae* also grouped together in a distinct clade (from *Cladosporiales* to *Dothideales*). Within this *Dothideomycetidae* clade, *Dothideales* was recovered as a basal lineage, while *Myriangiales*, *Endophytiales*, *Endosporiales*,

and *Phaeosclerales* formed a separate group. These orders are known to include many rock-inhabiting fungi.

Laboulbeniomycetes formed a sister clade to *Dothideomyceta*, and all the orders within *Laboulbeniomycetes* formed a well-resolved monophyletic clade. However, *Vezdaeales* was also recovered within *Laboulbeniomycetes*, an order that had previously been placed in *Pezizomycotina* orders *incertae sedis* in earlier studies. This order was also nested within *Asterinales* when a different taxon sampling was used (data not shown). Members of *Vezdaeales* are poorly developed lichens and were previously assumed to be part of *Lecanoromycetes* (Lücking et al. 2017). However, molecular data are available for only a few strains, making it difficult to conclude their higher-level classification and further investigation is needed.

The next clade includes *Candelariales* (*Candelariomycetes*), *Symbiotaphrinales*, *Xylonales* (*Symbiotaphrinales*), *Geoglossales* (*Geoglossomycetes*), *Sareales* (*Sareomycetes*), and *Thelocarpales*, and the order was previously placed in *Sordariomycetes* as an order *incertae sedis*. *Thelocarpales* formed a polyphyletic clade and showed a close phylogenetic relationship to *Symbiotaphrinales* and *Geoglossales*. *Thelocarpales* is a highly diverse order in terms of morphology, with the majority of species being lichenized, while some are lichenicolous fungi. Many species in this order lack molecular data and have not been extensively studied in phylogenetic analyses. Reeb et al. (2004) previously noted the uncertain phylogenetic placement of *Thelocarpon*, suggesting it could be quite basal within *Pezizomycotina*. In the phylogenetic analysis conducted by Wijayawardene et al. (2022a), the order formed a close phylogenetic association with *Vezdaeales* and was recovered as polyphyletic. Both orders were subsequently treated under *Pezizomycotina incertae sedis* (Wijayawardene et al. 2022a). The phylogenetic uncertainty for both *Thelocarpales* and *Vezdaeales*, is also found in this study, highlighting the need for broader sampling from fresh collections for accurate phylogenetic placement.

In a recent study, Hashimoto et al. (2021) synonymized *Sareales* under *Xylonales* and *Sareomycetes* under *Xylonomycetes* based on morphological characteristics and a multigene phylogenetic analysis using SSU, LSU, RPB1, RPB2, and mtSSU gene sequence data. *Sarea difformis* and *S. resinae* were grouped with members of *Xylonomycetes*, while *Symbiotaphrinales* formed a close phylogenetic association with *Geoglossales* (Hashimoto et al. 2021). Consequently, *Symbiotaphrinales* was treated under *Pezizomycotina incertae sedis* due to distinct phylogenetic, morphological, and ecological characteristics (Hashimoto et al. 2021). Meanwhile, Mitchell et al. (2021) expanded the generic concept of *Sareomycetes* by including *Atrozythia*, *Sarea*, and *Zythia* within the order, a perspective overlooked by Hashimoto et al. (2021). The phylogenetic analysis, conducted by Díaz-Escandón et al. (2022), also showed a close phylogenetic association between *Sarea* and *Xylona*, and together they formed a sister clade to *Symbiotaphrinales*. Our current phylogenetic analysis concurs with the findings of Hashimoto et al. (2021), but we could not fully incorporate the broader taxon sampling required for these orders.

The next clade grouped together to form the class *Eurotiomycetes*, with all orders within the class forming a well-resolved monophyletic clade supported by stable bootstrap values. The lichenized orders *Pyrenulales* and *Verrucariales* showed a close phylogenetic relationship with *Phaeomoniellales* and *Chaetothyriales*. All these orders are well integrated into their respective subclasses: *Chaetothyriomycetidae* (*Phaeomoniellales*, *Chaetothyriales*, *Pyrenulales*, *Verrucarials*), *Eurotiomycetidae* (*Arachnomycetales*, *Eurotiales*, *Onygenales*), *Cryptocaliciomycetidae* (*Cryptocaliciales*), *Coryneliomycetidae* (*Coryneliales*), *Sclerococcomycetidae* (*Sclerococcales*) and *Myccaliciomycetidae* (*Mycocaliciales*) except *Tuberculiformales*. The asexually reproducing monotypic order *Turquoiseomycetales* was initially placed in *Lecanoromycetes* based on LSU sequence data (Crous et al. 2019a) and was later accepted within *Lecanoromycetes* as order *incertae sedis* (Wijayawardene et al. 2022a, Hyde et al. 2024b). This order formed a sister clade to *Xylobotryales* (*Xylobotryomycetes*), which includes the two families *Cirrosporiaceae* and *Xylobotryaceae*. The inclusion of these families is discussed in the corresponding entry (*Xylobotryales*). Notably, *Xylobotryaceae* is known only from its sexual morph, while *Cirrosporiaceae* is exclusively known from its asexual morph. In this study, *Cirrosporiaceae* showed a closer phylogenetic relationship to

Turquoiseomycetales than *Xylobotryaceae*. The close phylogenetic association between *Turquoiseomyces* with *Mycocaliciales* was also discussed during the establishment of the genus, yet it was not placed in *Eurotiomycetes* due to its unusual morphology (Réblová & Seifert 2012), and Voglmayr et al. (2019b) placed it within *Xylobotryales*. Given the distinct morphological features observed between *Cirrosporiaceae* and *Xylobotryaceae*, both *Cirrosporiaceae* and *Turquoiseomycetaceae* could be merged under *Turquoiseomycetales*, or *Turquoiseomycetales* could be considered a part of *Xylobotryomycetes*.

The next clade represents *Lecanoromycetes*, with all the orders recovered as well-resolved monophyletic clades. The orders previously placed under the subclass *Lecanoromycetidae* are well resolved, except for *Rhizocarpales* and *Sporastatiales*. These two orders were treated separately based on a temporal approach (Kraichak et al. 2017), where they formed sister clades. However, Lücking et al. (2017) and Lücking (2019) retained both *Rhizocarpaceae* and *Sporastatiaceae* within *Rhizocarpales*, synonymizing *Sporastatiales*. In this study, both orders were recovered as separate clades without strong statistical support as well as sister clades with different taxon sampling (data not shown). Therefore, these orders could be treated as separate orders due to morphological differences. Based on shared evolutionary origin, *Sarrameanales* and *Schaereriales* were suggested to be combined. However, in our study, both orders formed distinct lineages, and the morphological differences and justifications for each order are provided in the *Schaereriales* section. Within *Ostropomycetidae*, all previously accepted orders formed a monophyletic clade. However, the inclusion of *Micropeltidales* under *Ostropomycetidae* is surprising, as it formed an unstable clade sister to *Thelenellales*, *Odontotrematales*, *Graphidales*, *Gyalectales*, and *Ostropales*. *Umbilicariales* (*Umbilicariomycetidae*) formed a close clade to *Sarrameanales* and was previously recovered in the basal clade of *Lecanoromycetidae* (Miadlikowska et al. 2014). However, the higher-level classification of this order has not been widely studied since the establishment of its own subclass, *Umbilicariomycetidae*.

Within *Sordariomycetes*, all the clades formed monophyletic groups. The crown clade accommodates the orders typically classified within *Diaporthomycetidae*, while the basal clade of this subclass includes orders *Amplistromatales* and *Catabotryales* that were traditionally classified within *Xylariomycetidae*. *Amplistromatales* was originally introduced to accommodate *Amplistromataceae* and *Catabotrydaceae* within *Sordariomycetes* order *incertae sedis* (Maharachchikumbura et al, 2015). However, Hyde et al. (2017a) placed *Amplistromatales* under *Diaporthomycetidae* based on molecular clock analyses, suggesting the exclusion of *Catabotrydaceae*. Later, *Catabotryales* was established to accommodate *Catabotrydaceae*, based on sequence data from one species (Hyde et al. 2020d). Consequently, both *Amplistromatales* and *Catabotryales* were recovered as sister clades and accepted within *Sordariomycetes* order *incertae sedis*. The placement of *Amplistromatales* within *Diaporthomycetidae* has also been reported in previous studies (Hongsanan et al. 2017a, Wijayawardene et al. 2017a). Based on the available data, these two orders can be placed within *Diaporthomycetidae*. The next clade entirely represents *Sordariomycetidae*, including the newly established orders *Pinibarreniales* and *Planisphaeriales*. *Pisorisporiales* (*Pisorisporiomycetidae*) formed a distinct clade within the class. The subsequent clade represents *Hypocreomycetidae*, where all orders are monophyletic, and the placement of *Xenodactylariales* within the subclass is confirmed, as reported by Bao et al. (2023). The orders *Conioscyphales*, *Fuscosporellales*, and *Pleurotheciales*, previously placed in *Savoryellomycetidae*, formed a single group. The basal clade represents *Amphisphaeriales*, *Delonicicolales*, and *Xylariales* of *Xylariomycetidae*.

Lulworthiomycetidae was established to accommodate *Koralionastetales* and *Lulworthiales*. However, the polyphyletic nature of *Lulworthiales* is well detailed in the corresponding section. In this study, *Lulworthiales* are intermixed with *Spathulosporales*. The inclusion of *Spathulospora* within *Lulworthiales* has also been noted in several phylogenetic studies (Inderbitzin et al. 2004, Dayarathne et al. 2025). If more data becomes available, *Spathulosporales* could be merged under *Lulworthiales*, and in this study, it is accepted within *Lulworthiomycetidae*. However,

Koralionastetales is retained as a separate order within the subclass and broad taxon sampling from fresh collections is important to resolve the taxonomic boundaries within *Lulworthiomycetidae*.

The orders of *Leotiomycetes* exhibited non-monophyly. *Lauriomycetales* and *Umbellidiales* formed distinct clades, separate from each other and closely related to *Sordariomycetes*. Both orders are anamorphic and were recently recovered in the basal clades of *Leotiomycetes* (Barreto et al. 2023), with *Sordariales* used as an outgroup. *Medeolariales* was considered part of *Helotiales* and was found to be more closely related to *Leotiales* in this study and the inclusion of *Lichinodium* within *Leotiales* is also supported. Due to a lack of molecular data, the phylogenetic placement of *Lahmiales* (*Leotiomycetes*) remains uncertain. However, all other orders traditionally accepted within *Leotiomycetes* formed monophyletic clades. *Orbiliales* (*Orbiliomycetes*) and *Pezizales* (*Pezizomycetes*) were recovered in the basal clades of *Pezizomycotina*, with both orders forming well-supported monophyletic clades. The synonymization of the classes *Candelariomycetes*, *Coniocybomycetes*, *Geoglossomycetes*, *Sareomycetes*, and *Xylonomycetes* under *Lichinomycetes* by Díaz-Escandón et al. (2022) is not supported in this study. Given their distinct morphological characteristics, lifestyles, and phylogenetic variation, these classes should be treated separately.

Taphrinomycotina was recovered in the basal lineage of *Ascomycota*. Each class within this subphylum accommodates a single order, and all orders form monophyletic clades. *Schizosaccharomycetales* and *Novakomycetales* formed a close phylogenetic association and were recovered in the basal clade of this subphylum, while the remaining orders, including *Neolectales*, *Taphrinales*, *Archaeorhizomycetales*, and *Pneumocystales*, grouped together.

Saccharomycotina formed a close phylogenetic relationship with the subphylum *Pezizomycotina*. Within *Saccharomycotina*, the classes *Lipomycetes*, *Trigonopsidomycetes*, *Dipodascomycetes*, *Alloascoideomycetes*, and *Sporopachydermiomycetes* each accommodate a single order, all of which form monophyletic clades. *Pichiomycetes* contains three orders: *Alaninales*, *Pichiales*, and *Serinales*, while *Saccharomycetes* includes four orders: *Ascoideales*, *Phaffomycetales*, *Saccharomycetales*, and *Saccharomycodales*. The orders from both classes are nested together. However, due to the limited taxon sampling selected for this subphylum and the recent taxonomic revision by Groenewald et al. (2023), we retain this subphylum without discussing its taxonomic changes.

This study provides the first detailed study of orders that are currently accepted in *Ascomycota*. Among the accepted orders within *Pezizomycotina* as well as within *Ascomycota*, *Dothideomycetes* contains the highest number of orders, with 57, followed by *Sordariomycetes* with 52 orders. *Lecanoromycetes* includes 21 orders, while *Eurotiomycetes* and *Leotiomycetes* each comprise 12 orders. *Laboulbeniomycetes* consists of 3 orders, whereas *Arthoniomycetes* and *Xylonomycetes* each accommodate 2 orders, while *Thelocarpales* and *Vezdaeales* are treated as *incertae sedis* within *Pezizomycotina*. *Candelariomycetes*, *Coniocybomycetes*, *Geoglossomycetes*, *Lichinomycetes*, *Orbiliomycetes*, *Pezizomycetes*, *Sareomycetes* and *Xylobotryomycetes* accommodates only a single order within each class. However, recent studies conducted on *Sareomycetes* raised questions about treating *Sareales* as a separate order and whether it should be a synonym of *Xylonales* (Mitchel et al. 2021) under *Xylonomycetes* (Hashimoto et al. 2021). The issues have also been discussed under each section in this study and further studies are needed to resolve the taxonomy. *Vezdaeales* is being treated under *Pezizomycotina* orders *incertae sedis*. Among the accepted classes within *Taphrinomycotina*, only a single order has been accepted under each class.

In this study, we provide a lifecycle teaching diagram of 16 orders of *Pezizomycotina; Asterinales* (Fig. 17), *Helotiales* (Fig. 161), *Hypocreales* (Figs. 220, 221), *Laboulbeniales* (Fig. 127), *Meliolales* (Fig. 230), *Mycosphaerellales* (Fig. 64), *Ophiostomatales* (Fig. 236), *Pezizales* (Fig. 180), *Pleosporales* (Fig. 85), *Phyllachorales* (Fig. 247), (Fig. 172), *Sordariales* (Fig. 253), *Venturiales* (Fig. 103) and *Xylariales* (Fig. 275) (*Pezizomycotina*), as well as three orders (*Pneumocystidales* (Fig. 290), *Schizosaccharomycetales* (Fig. 291) and *Taphrinales* (Fig. 295) of *Taphrinomycotina* (*Taphrinomycotina*). Each diagram is explained with a representative genus/genus of their sexual and asexual cycles of each order.

Fungi produce both sexually and asexually and the asexual morphs have been frequently reported among the members, unlike most higher eukaryotes (Hyde et al. 2011, Wallen & Perlin 2018). The sexual process involves meiosis (meiospores), whereas the asexual morph involves only mitosis (mitospores) (Carris et al. 2012). *Ascomycota* are generally known as "sac fungi" which form meiotic spores called ascospores enclosed in a special sac called an ascus. Sexual reproduction occurs in three stages including plasmogamy, karyogamy and meiosis in *Ascomycota*. The initial stage is plasmogamy in which two haploid cells are fused and form a dikaryotic stage where two haploid nuclei (+ and −) coexist in a single cell. In the second stage (karyogamy), two haploid cells fused to form a diploid zygote nucleus. In the last stage (meiosis), the diploid zygote nuclei produce haploid nuclei. These haploid nuclei form haploid spores by mitosis and cell division within the ascus (Wallen & Perlin 2018, Senanayake et al. 2022). Senanayake et al. (2022) provided the latest treatment of sexually producing ascomycetes, which is predicted to range from 1.37 to 2.56 million. However, the reported ratio is 1:22 due to a lack of studies, documentation and nomenclatural issues and limited approaches to defining species.

Coelomycetes and hyphomycetes, the main groups of asexually producing fungi that form conidiomata (Wijayawardene et al. 2012b, 2016, 2022a, Li et al. 2020, Liu et al. 2024). Most plant pathogens produce an asexual morph, adding to the complexity in identification work (Wijayawardene et al. 2022a). The occurrence of pleomorphic fungi as both sexual and asexual morphs, sometimes in the same host at the same time or only one at a time, further complicates the research. The concept of synanamorph or syn asexual morph, showing more than one asexual morph, adds another layer of complexity. Wijayawardene et al. (2022a) estimated that 540,000–860,000 fungi can reproduce asexually, but only 30,000 species are known. The use of polyphasic approaches, including morphological, biological, and phylogenetic species concepts, is instrumental in navigating this complexity and documenting and classifying these fungi (Maharachchikumbura et al. 2021a, Pem et al. 2021).

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REFERENCES

Aamri LE, Hafidi M, Scordino F, Krasowska A et al. 2020 – *Arthrographis curvata* and *Rhodosporidium babjevae* as new potential fungal lipase producers for biotechnological applications. Brazilian Archives of Biology and Technology 63, p.e20180444.

Abarca GH, Ruiz RF, Mota RM, Hérnandez CI et al. 2011 – A new species of *Heliocephala* from México with an assessment of the systematic positions of the anamorph genera *Heliocephala* and *Holubovaniella*. Mycologia 103(3), 631–640.

Abbott SP, Sigler L, Currah RS. 1996 – Delimitation, typification and taxonomic placement of the genus *Arachnomyces*. Systema Ascomycetum 14, 70–85.

Abbott SP, Sigler L, Currah RS. 1998 – *Microascus brevicaulis* sp. nov., the teleomorph of *Scopuariopsis brevicaulis*, supports placement of *Scopulariopsis* with the *Microascaceae*. Mycologia 90 (2), 297–302.

Abdel-Lateff A, Elkhayat ES, Fouad MA, Okino T. 2009 – Aureobasidin, new antifouling metabolite from marine-derived fungus *Aureobasidium* sp. Natural Product Communications 4(3), 389–94.

Abdel-Mageed HM, Barakat AZ, Bassuiny RI, Elsayed AM et al. 2022 – Biotechnology approach using watermelon rind for optimization of α-amylase enzyme production from *Trichoderma virens* using response surface methodology under solid-state fermentation. Folia Microbiologica 67(2), 253–265.

Abdel-Raheem A, Shearer CA. 2002 – Extracellular enzyme production by freshwater ascomycetes. Fungal Diversity 11(5), 1–19.

Abdel-Wahab MA, Abdel-Aziz FA, Mohamed SS, Abdel-Aziz AE. 2011 – *Annulatascus nilensis* sp. nov., a new freshwater ascomycete from the River Nile, Egypt. IMA Fungus 2, 1–6.

Abdel-Wahab MA, Dayarathne MC, Suetrong S, Guo SY et al. 2017 – New saprobic marine fungi and a new combination. Botanica Marina 60(4), 469–488.

Abdel-Wahab MA, El-Samawaty AE, El Gorban AM, Yassin MA et al. 2018 – *Khaleijomyces marinus* gen. et sp. nov. (*Juncigenaceae*, *Torpedosporales*) a new lignicolous marine fungus from Saudi Arabia. Phytotaxa 340, 277–285.

Abdel-Wahab MA, El-Sharouney H, Jones EBG. 2001 – Two new intertidal lignicolous *Swampomyces* species from Red Sea mangroves in Egypt. Fungal Diversity 8, 35–40.

Abdel-Wahab MA, Hodhod MS, Bahkali AHA, Jones EBG. 2014 – Marine fungi of Saudi Arabia. Botanica Marina 57, 323–335.

Abdel-Wahab MA, Jones EBG, Bahkali AH, Elgorban AM. 2019 – Marine fungi from Red Sea mangroves in Saudi Arabia with *Fulvocentrum rubrum* sp. nov. (*Torpedosporales*, *Ascomycota*). Nova Hedwigia 108, 365–377.

Abdel-Wahab MA, Jones EBG, Bahkali AH. 2020 – Marine fungi recorded from *Avicennia marina* (Forsk.) Vierh. and their secondary product potential. Nova Hedwigia 111, 357–390.

Abdel-Wahab MA, Jones EBG, El Gorban AM, Bahkali AH. 2022 – *Torpedospora yanbuensis* sp. nov. (*Torpedosporales*, *Sordariomycetes*), a new marine fungus from the Red Sea mangroves, Saudi Arabia. Nova Hedwigia 115, 393–404.

Abdel-Wahab MA, Pang KL, Nagahama T, Abdel-Aziz FA et al. 2010 – Phylogenetic evaluation of anamorphic species of *Cirrenalia* and *Cumulospora* with the description of eight new genera and four new species. Mycological Progress 9, 537–558.

Abdel-Wahab MA. 2000 – Diversity of fungi in subtropical mangroves. Ph.D. thesis, Faculty of Science at Sohag, South Valley University, Egypt.

Abdel-Wahab MA. 2005 – Diversity of marine fungi from Egyptian Red Sea mangroves. Botanica Marina 48, 348–355.

Abdollahzadeh J, Groenewald JZ, Coetzee MP, Wingfield MJ et al. 2020 – Evolution of lifestyles in *Capnodiales*. Studies in Mycology 95(1), 381–414.

Abeywickrama PD, Qian N, Jayawardena RS, Li Y et al. 2023 – Endophytic fungi in green manure crops; friends or foe?. Mycosphere 14(1), 1–106.

Abou-Mansour E, Couche E, Tabacchi R. 2004 – Do fungal naphthalenones have a role in the development of esca symptoms. Phytopathologia Mediterranea 43, 75–82.
Abraúl M, Alves A, Hilário S, Melo T et al. 2023 – Evaluation of lipid extracts from the marine fungi *Emericellopsis cladophorae* and *Zalerion maritima* as a source of anti-Inflammatory, antioxidant and antibacterial compounds. Marine Drugs 21(4), 199.
Abreo E, Martínez S, Bettucci L, Lupo S. 2011 – *Phaeomoniella chlamydospora* and *Phaeoacremonium* spp. in grapevines from Uruguay. Phytopathologia Mediterranea 50, S77–S85.
Abubaker HO, Sulieman AME, Elamin HB. 2012 – Utilization of *Schizosaccharomyces pombe* for production of ethanol from cane molasses. Journal Microbiology Research 2(2), 36–40.
Acharius E. 1803 – Methodus qua omnes detectos Lichenes. F.D.D. Ulrich, Stockholm.
Acharius E. 1806 – *Arthonia*, novum genus lichenum. Neues Journal für die Botanik. [Edited by Schrader]. Erfurt 1, 1–23.
Acharius E. 1808a – Förteckning pa de i Sverige växande arter af Lafvarnes famille. Nova Acta Reg. Acad. Sci. Holmiae 29, 228–237.
Acharius E. 1808b – Förteckning på de i Sverige växande arter af Lafvarnas familj. K. Sven. Vetenskapsakad. Akad. Förhandl 29, 125–132.
Acharius E. 1814 – Synopsis methodica Lichenum. Svanborg, Lundae.
Acharius E. 1815 – Afhandling om de cryptogamiske vexter, som komma under namn af Calicioidea. Fo¨ rsta stycket. Kungliga Svenska Vetenskapsakademiens Handlinger 1815, 246–271.
Acharius E. 1816a – Afhandling om de cryptogamiske vexter, som komma under namn af Calicioidea. Andra Stycket. Kungliga Svenska Vetenskapsakademiens Handlinger 4, 285.
Acharius E. 1816b – Afhandling om de cryptogamiske vexter, som komma under namn af Calicioidea.; Andra Stycket. Kungliga Svenska Vetenskapsakademiens Handlinger 1816, 106–125, 260–291.
Acharius E. 1817a – Afhandling om de cryptogamiske vexter, som komma under namn af Calicioidea. Tredje Stycket. Kungliga Svenska Vetenskapsakademiens Handlinger 1817, 220–244.
Acharius E. 1817b – *Trypethelium*, genus lichenum, monographice descriptum, adjectis Iconibus omnium hactenus detectarum specierum. Memoires de la Société Imperiale des Naturalistes de Moscou 5, 162–173.
Acharius E. 1817c – Species novae e Trypethelii genere. Memoires de la Société Imperiale des Naturalistes de Moscou 5, 174–178.
Acosta HDG. 1995 – El ge´nero *Micropeltis* Montagne (*Micropeltaceae*, *Ascomycotina*) en las Antillas Mayores. Rev Jard Bot Nac 16, 29–46.
Agardh CA. 1817 – Synopsis algarum Scandinaviae. Berling, Lund.
Aguirre-Hudson B, Kokubun T, Spooner BM, Tibell L. 2007 – Taxonomy of *Calicium victorianum* (F. Wilson) Tibell (*Caliciaceae*, *Lecanorales*), a lichenized ascomycete new to Europe. The Lichenologist 39(5), 401–407.
Aguirre-Hudson B. 1991 – A taxonomic study of the species referred to the ascomycete genus *Leptorhaphis*. Bulletin of the British Museum (Natural History), Botany 21, 85–192.
Ahamed A, Vermette P. 2008 – Culture-based strategies to enhance cellulase enzyme production from *Trichoderma reesei* RUT-C30 in bioreactor culture conditions. Biochemical Engineering Journal 40(3), 399–407.
Ahmad S, Johnson RJ, Hillier S, Shelton WR et al. 1985 – Fungal Peritonitis Caused by *Lecythophora mutabilis*. Journal of Clinical Microbiology 22(2), 18286.
Ahmed SA, González GM, Tirado-Sánchez A, Moreno-López LM et al. 2018 – *Nigrograna mackinnonii*, not *Trematosphaeria grisea* (syn., *Madurella grisea*), is the main agent of black grain eumycetoma in Latin America. Journal of Clinical Microbiology 56, e01723–17.
Ahti T, Stenroos S. 2013 – *Cladoniaceae*. In: Ahti T, Stenroos S, Moberg R (eds) Nordic Lichen Flora, vol 5. Museum of Evolution, Uppsala University, Uppsala.

Ahti T. 1982 – Evolutionary trends in cladoniiform lichens. The Journal of the Hattori Botanical Laboratory 52, 331–341.
Ahti T. 2000 – *Cladoniaceae*. Flora Neotropica Monogr 78, 1–363.
Ai C, Dong Z, Yun J, Zhang Z, Xia J, Zhang X. 2024 – Phylogeny, taxonomy and morphological characteristics of *Apiospora* (*Amphisphaeriales*, 6). Microorganisms 12, 1372.
Ai CC, Ma J, Zhang K, Castañeda-Ruíz RF et al. 2019 – *Cordana meilingensis* and *C. lushanensis* spp. nov. from Jiangxi, China. Mycotaxon 134, 329–334.
Ai H, Wang W, Zhang X, Feng T et al. 2018 − Preparation of compound E1011 from potato endophytic fungi fermentation product. Chinese patent (CN1091180635).
Aime MC, Miller AN, Aoki T, Bensch K et al. 2021 – How to publish a new fungal species, or name, version 3.0. IMA Fungus 12, 1–5.
Ainsworth GC. 1961 – Ainsworth and Bisby's dictionary of the fungi. 5th edition, Commonwealth Mycological Inst., Kew, Kew, Surrey, England, UK.
Ainsworth GC. 1971 – Ainsworth & Bisby's Dictionary of Fungi. 6th Ed. Commonwealth Mycological Institute, Kew, Surrey, UK.
Akata I, Kaya A, Uzun Y. 2016 – Two new genus records for Turkish *Helotiales*. Kastamonu Uni, Orman Fakültesi Dergisi 16, 131–134.
Akulov A. 2013 – Morphological features, distribution and ecological preferences of *Albertiniella polyporicola* (Jacz.) Malloch et Cain (In Ukrainian). Chornomorsk Botanical Journal. 9, 553–558.
Albertini JB von, Schweinitz LD von. 1805 – Conspectus fungorum in Lusatiae Superioris agro Niskiensi crescentium, e methodo Persooniana. Sumtibus Kummerianis, Lipsiae.
Alexopoulos CJ, Mims CW. 1979 – Introductory Mycology. 3rd Edition. Wiley, New York.
Alexopoulos CJ. 1962 – Introductory mycology. John Wiley and Sons, Inc., New York.
Al-Hedaithy SSA. 2001 – First report of human infection due to the fungus *Triadelphia pulvinata*. Journal of Clinical Microbiology 39, 3386–3389.
Alias SA, Zainuddin N, Jones EBG. 2010 – Biodiversity of marine fungi in Malaysian mangroves. Botanica Marina 53, 545–554.
Aliouat-Denis CM, Chabé M, Demanche C, Viscogliosi E et al. 2008 – *Pneumocystis* species, co-evolution and pathogenic power. Infection, Genetics and Evolution 8(5), 708–726.
Alkan N, Meng X, Friedlander G, Reuven E et al. 2013 – Global aspects of pacC regulation of pathogenicity genes in *Colletotrichum gloeosporioides* as revealed by transcriptome analysis. Molecular Plant-Microbe Interactions 26(11), 1345–1358.
Al-Khayri JM, Rashmi R, Toppo V, Chole PB et al. 2023 – Plant Secondary Metabolites: The Weapons for Biotic Stress Management. Metabolites 13, 716.
Allen JL, McMullin RT. 2015 – *Chaenotheca balsamconensis*, a new calicioid lichen on *Trichaptum abietinum* from North America that is benefiting from widespread conifer fatalities. The Bryologist 118, 54 –58.
Alongi G, Catra M, Cormaci M. 1999 – First record of *Haloguignardia cystoseirae Ascomycota* parasitic on *Cystoseira elegans Fucophyceae* from the Mediterranean Sea. Botanica Marina 42, 33–35.
Alvarez LV, Groenewald JZ, Crous PW. 2016 – Revising the *Schizoparmaceae*: *Coniella* and its synonyms *Pilidiella* and *Schizoparme*. Studies in Mycology 85, 1–34.
Alves BVB, Borges LJ, Hanna SA, Soares MBP et al. 2025 – Pigment Production by *Pseudofusicoccum* sp.: extract production, cytotoxicity activity, and diketopiperazines identified. Microorganisms 13, 277.
Alves E, Dias M, Lopes D, Almeida A et al. 2020 – Antimicrobial lipids from plants and marine organisms: An overview of the current state-of-the-art and future prospects. Antibiotics 9, 441.
Alves JL, Barreto RW, Pereira OL. 2010 – Additions to the mycobiota of the invasive weed *Miconia calvescens* (*Melastomataceae*). Mycologia 102, 69–82.
Alvin KL, Muir MD. 1970 – An epiphyllous fungus from the Lower Cretaceous. Biological Journal of the Linnean Society 2(1), 55–59.

Amanchukwu SC, Obafemi A, Okpokwasili GC. 1989 – Hydrocarbon degradation and utilization by a palm-wine yeast isolate. FEMS Microbiology Letters 57(2), 151–154.
Amano N. 1983 – Saprobic loculoascomycetous fungi from Japan 1. Hysteriaceous Fungi. Transactions of the Mycological Society of Japan 24, 283–297.
Ambrico M. 2016 – *Melanin*, a long lasting history bridging natural pigments and organic bioelectronics. Polymer International 65, 1249–1250.
Ametrano CG, Grewe F, Crous PW, Goodwin SB et al. 2019a – Genome-scale data resolve ancestral rock-inhabiting lifestyle in *Dothideomycetes* (*Ascomycota*). IMA Fungus 10, 19.
Ametrano CG, Knudsen K, Kocourková J, Grube M et al. 2019b – Phylogenetic relationships of rock-inhabiting black fungi belonging to the widespread genera *Lichenothelia* and *Saxomyces*. Mycologia 111(1), 127–160.
Amtoft A, Lutzoni F, Miadlikowska J. 2008 – *Dermatocarpon* (*Verrucariaceae*) in the Ozark highlands, North America. Bryologist 111, 1–40.
Ananda K, Sridhar KR. 2004 – Diversity of filamentous fungi on decomposing leaf and woody litter of mangrove forests in the southwest coast of India. Current Science 87(10), 1431–1437.
Anderson AC. 2005 – Targeting DHFR in parasitic protozoa. Drug Discovery Today 10, 121–128.
Anderson MG, Jarman TB, Rickards RW. 1995 – Structures and absolute configurations of antibiotics of the oligosporon group from the nematode-trapping fungus *Arthrobotrys oligospora*. Journal of Antibiotics 48(5), 391–398.
Andersson K, Eriksson OE, Landvik S. 1995 – *Boliniaceae* transferred to *Sordariales* (*Ascomycota*). Syst Ascomycetum 14, 1–16.
Andi S, Taguchi G, Fujikawa T, Taga N et al. 2001 – Effect of the disruption of glycerol-3-phosphate dehydrogenase gene on the production of material metabolites in *Colletotrichum gloeosporioides*. Journal of Bioscience and Bioengineering 91(1), 36–42.
Ando Y, Masuya H, Motohashi K, Linnakoski R et al. 2016 – Phylogenetic relationship of Japanese isolates belonging to the *Grosmannia piceiperda* complex (*Ophiostomatales*). Mycoscience 57, 123–135.
Andolfi A, Mugnai L, Luque J, Surico G et al. 2011 – Phytotoxins produced by fungi associated with grapevine trunk diseases. Toxins 3, 1569–1605.
Andrade DS, Aptroot A, Lücking R, Barbosa BMC et al. 2020 – Crustose *Caliciaceae* in *Restinga vegetation* in Brazil with a new species of *Gassicurtia* and two identification keys. The Bryologist 123(1), 75–83.
Anke H, Stadler M, Mayer A, Sterner O. 1996 – Secondary metabolites with nematicidal and antimicrobial activity from nematophagous fungi and *Ascomycetes*. Canadian Journal of Botany 73(S1), 932–939.
Anke H, Zähner H, König WA. 1978 – Metabolic products of microorganisms. 170. On the antibiotic activity of cladosporin. Archives of Microbiology 116, 253–257.
Ansil PA, Rajeshkumar KC, Lücking R, Sharma B. 2023 – Phylogenetic placement of *Phlyctis atomella* (*Phlyctidaceae*) from the Western Ghats, India. Czech Mycology 75(2).
Aouali S. 2021 – Two new *Geoglossaceae* for Algeria. Annales de la Recherche Forestière en Algérie 11(2), 68–74.
Apinis AE. 1967 – *Dactylomyces* and *Thermoascus*. Transactions of the British Mycological Society 50, 573–582.
Apinis AE. 1968 – Relationships of certain keratinophilic *Plectascales*. Mycopathologia et Mycologia Applicata 35, 97–104.
Apt KE. 1988 – Morphology and development of hyperplasia on *Cystoseira osmundacea* (*Phaeophyta*) associated with *Haloguignardia irritans* (*Ascomycotina*). American journal of botany 75, 979–984.
Aptroot A, Cáceres MES, Johnston MK, Lücking R. 2016 – How diverse is the lichenized fungal family *Trypetheliaceae* (*Ascomycota*: *Dothideomycetes*)? A quantitative prediction of global species richness. The Lichenologist 48, 983–994.
Aptroot A, Lücking R, Cáceres ME. 2023 – New species and records of *Graphidaceae* and

Gomphillaceae (lichenized fungi) from Brazil. Plant and Fungal Systematics 68(2), 249–261.
Aptroot A, Lücking R, Sipman H, Umaña L et al. 2008a – Pyrenocarpous lichens with bitunicate asci: A first assessment of the lichen biodiversity inventory in Costa Rica. Bibliotheca Lichenologica 97, 1–162
Aptroot A, Lücking R. 2016 – A revisionary synopsis of the *Trypetheliaceae* (*Ascomycota*: *Trypetheliales*). The Lichenologist 48, 763–982.
Aptroot A, Menezes AA, De Lima EL, Xavier-Leite AB et al. 2013a – New species of *Polymeridium* from Brazil expand the range of known morphological variation within the genus. The Lichenologist 45, 545 –552.
Aptroot A, Parnmen S, Luecking R, Baloch E et al. 2014 – Molecular phylogeny resolves a taxonomic misunderstanding and places *Geisleria* close to *Absconditella* s. str. (*Ostropales*: *Stictidaceae*). The Lichenologist 46(1), 115–128.
Aptroot A, Schumm F. 2010 – Chimeras occur on the pantropical Lichinomycete *Phyllopeltula corticola*. The Lichenologist 42, 307–310.
Aptroot A, Seaward MR. 1999 – Annotated checklist of Hongkong lichens. Tropical Bryology 57–102.
Aptroot A, Sipman HJM, Barreto FMO, Nunes AD et al. 2019 – Ten new species and 34 new country records of *Trypetheliaceae*. The Lichenologist 51, 27–43.
Aptroot A, Sipman HJM, Cáceres MES. 2013b – Twenty-one new species of *Pyrenula* from South America, with notes on overmature ascospores. The Lichenologist 45, 169–198.
Aptroot A, Sparrius LB, LaGreca S, Bungartz F. 2008b – *Angiactis*, a new crustose lichen genus in the *Roccellaceae*, with species from Bermuda, the Galápagos Islands and Australia. Bryologist 111, 510–516.
Aptroot A, Sparrius LB. 2003 – New microlichens from Taiwan. Fungal Diversity 14, 1–50.
Aptroot A, Sparrius LB. 2008 – Crustose *Roccellaceae* in the Galapagos Islands, with the new species *Schismatomma spierii*. Bryologist 111, 659–666.
Aptroot A. 1991a – A monograph of the *Pyrenulaceae* (excluding *Anthracothecium* and *Pyrenula*) and the *Requienellaceae*, with notes on the *Pleomassariaceae*, the *Trypetheliaceae* and *Mycomicrothelia* (lichenized and non–lichenized *Ascomycetes*). The Lichenologist 44, 1–178.
Aptroot A. 1991b – *Monoblastia pellucida*: a remarkable new lichen species from tropical coastal areas, with comments on the *Monoblastiaceae*. Bryologist 404–406.
Aptroot A. 2006 – *Mycosphaerella* and its anamorphs 2. Conspectus of *Mycosphaerella*. CBS Biodiversity Series 5, 1–231.
Aptroot A. 2012 – A world key to the species of *Anthracothecium* and *Pyrenula*. The Lichenologist 44, 2–53.
Aptroot A. 2013 – Ecology of the lichen family *Trypetheliaceae* in Brazil. Livro de Resumos do Sexto Encontro do Grupo Brasileiro de Liquenólogos 1, 16.
Aptroot A. 2022 – World key to the species of *Pyrenulaceae* and *Trypetheliaceae*. Archive for Lichenology 29, 1–90.
Arauzo S, Iglesias P. 2014 – La familia *Geoglossaceae* en la penî nsula Ibe rica y la Macaronesia. Errotari (11), 166–259.
Archana O, Nagadesi PK. 2022 – Endophytic, non-endophytic fungal alkaloids and its applications. Saudi Journal of Pathology and Microbiology 7, 4–19.
Archer AW. 2001 – The lichen genera *Phaeographis* and *Phaeographina* (*Graphidaceae*) in Australia 3: *Phaeographis*–new reports and new species. Telopea 9(3), 663–677.
Ariyawansa HA, Hawksworth DL, Hyde KD, Jones EBG et al. 2014 – Epitypification and neotypification: guidelines with appropriate and inappropriate examples. Fungal Diversity 69, 57–91.
Ariyawansa HA, Phillips AJ, Chuang WY, Tsai I. 2018 – *Tzeananiaceae*, a new pleosporalean family associated with *Ophiocordyceps macroacicularis* fruiting bodies in Taiwan. MycoKeys 37, 1–17.

Ariyawansa HA, Thambugala K, Manamgoda D, Jayawardena R et al. 2015 – Towards a natural classification and backbone tree for *Pleosporaceae*. Fungal Diversity 71, 85–139.
Armaleo D, Clerc P. 1991 – Lichen chimeras: DNA analysis suggests that one fungus forms two morphotypes. Experimental Mycology 15(1), 1–10.
Armand A, Hyde KD, Huanraluek N, Wang Y, Jayawardena RS. 2023 – Identification and characterization of *Colletotrichum* species associated with durian fruit in northern Thailand. Mycosphere 14(2), 107–129.
Arnaud G, Les Asterinees V. 1930 − Etude sur les Champignons parasites: *Caliciacees*. *Hemisphaeriacees*, etc. Aannales des Epiphyties 16, 235–302.
Arnaud G. 1918 – Le´s Asterine´es. Ann E´ c natl agric Montp 16, 1–288.
Arnold AE, Lutzoni F. 2007 – Diversity and host range of foliar fungal endophytes: are tropical leaves biodiversity hotspots? Ecology 88(3), 541–549.
Arnold AE, Mejia LC, Kyllo D, Rojas EI et al. 2003 – Fungal endophytes limit pathogen damage in a tropical tree. Proceedings of the National Academy of Sciences USA 100, 15649–15654.
Arnold AE, Miadlikowska J, Higgins KL, Sarvate SD et al. 2009 – A phylogenetic estimation of trophic transition networks for ascomycetous fungi: are lichens cradles of symbiotrophic fungal diversification? Systematic Biology 58, 283–297.
Arnold AE. 2007 – Understanding the diversity of foliar endophytic fungi: Progress, challenges, and frontiers. Fungal Biology Reviews 21, 51–66.
Arnold G. 1972 – Über einige neue Taxa und Kombinationen der *Sphaeriales*. Zeitschrift für Pilzkunde 37, 187–198.
Aronsson G. 1991 – Lindskål, Holwaya mucida, i Sverige. Sven. Bot. Tidskr 85, 9–18.
Arora D. 1986 – Mushrooms demystified: a comprehensive guide to the fleshy fungi.
Arora P. 2012 – Geoglossaceous fungi in Slovakia III. The genus *Geoglossum*. Biologia 67, 654–658.
Artanti N, Tachibana S, Kardono LB. 2014 – Effect of media compositions on a-glucosidase inhibitory activity, growth and fatty acid content in mycelium extracts of *Colletotrichum* sp. TSC13 from *Taxus sumatrana* (Miq.) de Laub. Pakistan Journal of Biological Sciences 17, 884–890.
Artjariyasripong S, Mitchell JL, Hywel-Jones NL, Jones EBG. 2001 – Relationships of the genus *Cordyceps* and related genera, based on parsimony and spectral analysis of partial 18S and 28S ribosomal gene sequences. Mycoscience 42, 503–517.
Arunpanichlert J, Rukachaisirikul V, Sukpondma Y, Phongpaichit S et al. 2010 – Azaphilone and isocoumarin derivatives from the endophytic fungus *Penicillium sclerotiorum* PSU-A13. Chem Pharm Bull (Tokyo) 58, 1033–1036.
Arunrattiyakorn P, Kuno M, Aree T, Laphookhieo S et al. 2018 – Biotransformation of β-mangostin by an endophytic fungus of *Garcinia mangostana* to furnish xanthenes with an unprecedented heterocyclic skeleton. Journal of Natural Products 81(10), 2244–50.
Arup U, Søchting U, Frödén P. 2013 – A new taxonomy of the family *Teloschistaceae*. Nordic journal of Botany 31(1), 016–083.
Arx JA von, van der Walt JP, Liebenberg NVDM. 1982 – The classification of *Taphrina* and other fungi with yeastlike cultural states. Mycologia 74, 285–296.
Arx JA von. 1987 – Plant-pathogenic Fungi. J. Cramer, Berlin, Germany.
Arzanlou M, Groenewald JZ, Gams W, Braun U et al. 2007 – Phylogenetic and morphotaxonomic revision of *Ramichloridium* and allied genera. Studies in Mycology 58 (1), 57–93.
Arzanlou M, Torbati M, Jafary H. 2012 – Fruit rot of olive (*Olea europaea*) caused by *Truncatella angustata*. Plant Pathology & Quarantine 2, 117–123.
Asgari B, Zare R, Gams W. 2007 – *Coniochaeta ershadii*, a new species from Iran, and a key to well documented *Coniochaeta* species. Nova Hedwig 84, 175–187.
Asgari B, Zare R. 2006 – Two new *Coniochaeta* species from Iran. Nova Hedwig 82, 227–236.
Assefa A, Abate D, Stenlid J. 2014 – Characterization of *Corynelia uberata* Fr., a putative fungal pathogen of *Podocarpus falcatus* in Ethiopian forests. Forest Pathology 44, 45–55.

Assimakopoulou A, Elena K. 2010 – Is there an influence of inorganic nutrition on the susceptibility of the pistachio to *Camarosporium pistaciae*? Options Mediterraneennes, Serie A 94, 181–185.
Aumentado HD, Armand A, Phukhamsakda C, Hyde KD et al. 2024 – Polyphasic identification of two novel *Colletotrichum* species causing leaf spots on mangroves in Thailand. European Journal of Plant Pathology 169, 1–27.
Aveskamp MM, Gruyter J de, Crous PW. 2008 – Biology and recent developments in the systematics of *Phoma*, a complex genus of major quarantine significance. Fungal Diversity 31, 1–18.
Aveskamp MM, Gruyter J de, Woudenberg JHC, Verkley GJM et al. 2010 – Highlights of the *Didymellaceae*: a polyphasic approach to characterise *Phoma* and related pleosporalean genera. Studies in Mycology 65, 1–60.
Avila-Diaz I, Garibay-Orijel R, Magna-Lemus RE, Oyama K. 2013 – Molecular evidence reveals fungi associated within the epiphytic orchid *Laelia speciosa* (HBK) Schltr. Botanical Sciences 91 (4), 523–529.
Awasthi DD, Singh KP. 1975 – Three new taxa of lichens from Palni Hills, India. Geophytology 5 (1), 39–42.
Ayers TT. 1941 – *Biatorella resinae*: The Perfect Stage of *Zythia resinae*. Mycologia 33, 130–135.
Aylward J, Wingfield BD, Dreyer LL, Roets F et al. 2017 – Contrasting carbon metabolism in saprotrophic and pathogenic microascalean fungi from *Protea* trees. Fungal Ecology 30, 88–100.
Ayres MP, Wilkens RT, Ruel JJ, Lombardero MJ et al. 2000 – Nitrogen budgets of phloem-feeding bark beetles with and without symbiotic fungi. Ecology 81, 2198–2210.
Azevedo E, Barata M, Marques MI, Caeiro MF. 2017 – *Lulworthia atlantica*: a new species supported by molecular phylogeny and morphological analysis. Mycologia 109, 287–295.
Baba T, Janošík L, Koukol O, Hirose D. 2021 – Genetic variations and in vitro root-colonizing ability for an ericaceous host in *Sarcoleotia globosa* (*Geoglossomycetes*). Fungal Biology 125(12), 971–979.
Babjeva I, Reshetova I. 1998 – Yeast resources in natural habitats at polar circle latitude. Food Technology and Biotechnology 36(1), 1–5.
Bacigálová K, Lopandic K, Rodrigues MG, Fonseca Á et al. 2003 – Phenotypic and genotypic identification and phylogenetic characterisation of *Taphrina* fungi on alder. Mycological Progress 2(3), 179–196.
Bacigálová K, Mułenko W, Wołczańska A. 2005 – Parasitic microfungi of the Tatra Mountains. 1. *Taphrinales*. Polish Botanical Journal 50(2), 185–207.
Bae H, Roberts DP, Lim H, Strem MD et al. 2011 – Endophytic *Trichoderma* isolates from tropical environments delay disease onset and induce resistance against *Phytophthora capsici* in hot pepper using multiple mechanisms. Molecular Plant-Microbe Interactions 24(3), 336–351.
Baert F, Stubbe D, D'hooge E, Packeu A et al. 2020 – Updating the taxonomy of dermatophytes of the BCCM/IHEM collection according to the new standard: a phylogenetic approach. Mycopathologia 185(1), 161–168.
Baghdadi VV. 1968 – De speciebus novis Penicilli Fr. e terris Syriae isolatis notula. Novosti Sistematiki Nizshikh Rastenii 5, 96–114
Bähler J, Wu JQ, Longtine MS, Shah NG et al. 1998 – Heterologous modules for efficient and versatile PCR-based gene targeting in *Schizosaccharomyces pombe*. Yeast 14(10), 943–951.
Bakhshi M, Arzanlou M, Babai-Ahari A, Groenewald JZ et al. 2015 – Is morphology in *Cercospora* a reliable reflection of generic affinity? Phytotaxa 213, 22–34.
Baldrian P, Kolařík M, Štursová M, Kopecký J et al. 2012 – Active and total microbial communities in forest soil are largely different and highly stratified during decomposition. Soil Biology and Biochemistry 46, 107–115.
Baldrian P, Valášková V. 2008 – Degradation of cellulose by basidiomycetous fungi. FEMS Microbiological Reviews 32, 501–521.

Balis E, Velegraki A, Fragou A, Pefanis A et al. 2006 – Lung mass caused by *Phoma exigua.* Scandinavian Journal of Infectious Diseases 38, 552–555.
Baloch E, Gilenstam G, Wedin M. 2013 – The relationships of *Odontotrema* (*Odontotremataceae*) and the resurrected *Sphaeropezia* (*Stictidaceae*) – new combinations and three new *Sphaeropezia* species. Mycologia 105, 384–397.
Baloch E, Lücking R, Lumbsch HT, Wedin M. 2010 – Major clades and phylogenetic relationships between lichenized and non-lichenized lineages in *Ostropales* (*Ascomycota*: *Lecanoromycetes*). Taxon 59(5), 1483–1494.
Bánki O, Roskov Y, Döring M, Ower G et al. 2023 – Catalogue of Life Checklist (Version 2023-10-16). Catalogue of Life.
Bao DF, Bhat DJ, Boonmee S, Hyde KD et al. 2022 – Lignicolous freshwater ascomycetes from Thailand: Introducing *Dematipyriforma muriformis* sp. nov., one new combination and two new records in *Pleurotheciaceae*. MycoKeys 93, 57–79.
Bao DF, Hyde KD, Maharachchikumbura SS, Perera RH et al. 2023 – Taxonomy, phylogeny and evolution of freshwater *Hypocreomycetidae* (*Sordariomycetes*). Fungal Diversity 121(1), 1–94.
Bao DF, Hyde KD, McKenzie EHC, Jeewon R et al. 2021 – Biodiversity of lignicolous freshwater hyphomycetes from China and Thailand and description of sixteen species. Journal of Fungi 7(8), 1–42.
Bao DF, Luo ZL, Liu JK, Bhat DJ et al. 2018 – Lignicolous freshwater fungi in China III: Three new species and a new record of *Kirschsteiniothelia* from northwestern Yunnan Province. Mycosphere 9, 755–768.
Bao DF, McKenzie EHC, Bhat DJ, Hyde KD et al. 2020 – *Acrogenospora* (*Acrogenosporaceae*, *Minutisphaerales*) appears to be a very diverse genus. Frontier in Microbiology 11, 1606.
Baral HO, Carter A. 2013 – *Patinella hyalophaea* Sacc. Rediscovered in New Brunswick, Canada. Ascomycete 5, 91–96.
Baral HO, Haelewaters D, Partel K. 2015 – A new attempt to classify the families of the *Helotiales*. In: The second international workshop on ascomycete systematics. CBS symposium 22724 April, Amsterdam.
Baral HO, Kutorga E. 2010 – *Helicogonium fusisporum* sp. nov., an intrahymenial parasite in *Orbilia eucalypti*. Mycotaxon 113, 331–336.
Baral HO, Weber E, Gams W, Hagedorn G et al. 2018a – Generic names in the *Orbiliaceae* (*Orbiliomycetes*) and recommendations on which names should be protected or suppressed. Mycological Progress 17, 5–31.
Baral HO, Weber E, Marso G, Quijada L et al. 2018b – A new connection between wood saprobism and beetle endosymbiosis: the rarely reported saprobic discomycete *Tromeropsis* is congeneric with the symbiotic yeast *Symbiotaphrina (Symbiotaphrinales, Xylonomycetes*) and two asexual morphs misplaced in *Hyphozyma*. Mycological Progress 17, 215–254.
Baral HO, Weber E, Marson G. 2020 – Monograph of *Orbiliomycetes* (*Ascomycota*) based on vital taxonomy; National Museum of Natural History: Luxembourg, Volume Part I and II, 1–1752.
Baral HO. 1999 – A monograph of *Helicogonium* (= *Myriogonium*, *Leotiales*), a group of nonascocarpous intrahymenial mycoparasites. Nova Hedwigia 69(1–2), 1–71.
Baral HO. 2015 – Nomenclatural novelties *Arachnopezizaceae*, *Chaetomellaceae*, *Chlorociboriaceae*, *Godroniaceae*, *Helicogoniaceae*, *Marthamycetaceae*, *Tympanidaceae*. Index Fungorum 225.
Baral HO. 2016 – Inoperculate *Discomycetes*. In: Syllabus of Plant families. A. Engler's Syllabus der Pflanzenfamilien. Vol. 1(2), *Ascomycota* (Jaklitsch W, Baral HO, Lücking R, Lumbsch T, eds): 55–221. 13 edn. Stuttgart: Borntraeger Science Publishers.
Baranyay JA. 1966 – Fungi from dwarf mistletoe infections in western hemlock. Canadian Journal of Botany 44, 597–604.
Barata M. 2002 – Fungi on the halophytes *Spartina maritima* in salt marshes. In: Hyde KD (Eds.), Fungi in marine environments. Fungal Diversity Research Series, Hong Kong 179–193.

Barbosa FR, Gusmao LFP, Raja HA, Shearer CA. 2013 – New species and new records of freshwater ascomycetes from Brazil and Costa Rica. Mycologia 105, 335–343.
Barbosa FR, Maia LC, Gusmão LFP. 2009 – Conidial fungi associated to leaf litter of *Clusia melchiorii* Gleason and *C. nemorosa* G. Mey (*Clusiaceae*) in a fragment of Atlantic rainforest, Bahia State, Brazil. Acta Botanica Brasilica 23, 79–84.
Barbosa MA, Costa PMO, Malosso E, Castañeda-Ruiz RF. 2016 – *Codinaea leomaiae* sp. nov. from the Brazilian Atlantic Forest. Mycotaxon 131, 423–428.
Bargagli R, Borghini F, Celesti C. 2000 – Elemental composition of the lichen *Umbilicaria decussata*. Italian Journal of Zoology, Supplement 1, 157–162.
Barghoorn ES, Linder DH. 1944 – Marine fungi: their taxonomy and biology. Farlowia 1, 395–467
Bärlocher F, Boddy L. 2016 – Aquatic fungal ecology - How does it differ from terrestrial? Fungal Ecology 19, 5e13.
Bärlocher F. 2006 – Fungal endophytes in submerged roots. In: Schulz BJE, Boyle CJC, Sieber TN (eds) Microbial root endophytes. Springer Berlin Heidelberg, Berlin, Heidelberg 179–190.
Barnes CJ, van der Gast CJ, Burns CA, McNamara NP et al. 2016 – Temporally variable geographical distance effects contribute to the assembly of root-associated fungal communities. Frontiers in Microbiology 7, 195.
Barr M, Huhndorf SM. 2001 – *Loculoascomycetes*. *In*: D.J. McLaughlin, E.G. McLaughlin, P. A. Lemke (eds.), The Mycota, a comprehensive treatise on fungi as experimental systems for basic and applied research, vol. VII, Systematics and evolution, part A, 283–305. Springer, New York, New York, USA.
Barr ME, Blackwell M. 1980 – A new genus in the *Lophiaceae*. Mycologia 72, 1224–1227.
Barr ME. 1956 – The development of the ascocarp in *Phaeotrichum hystricinum.* Canadian Journal of Botany 34(4), 563–568.
Barr ME. 1968 – The *Venturiaceae* in North America. Canadian Journal of Botany 46, 799–864.
Barr ME. 1970 – Some amerosporous ascomycetes on *Ericaceae* and *Empetraceae*. Mycologia 62(2), 377–394.
Barr ME. 1976 – Perspectives in the *Ascomycotina*. Memoirs of the New York Botanical Garden 28, 1–8.
Barr ME. 1978 – The *Diaporthales* in North America, with emphasis on *Gnomonia* and its segregates. Mycol Mem 7, 1–232.
Barr ME. 1979a – A classification of *Loculoascomycetes*. Mycologia 71, 935–957.
Barr ME. 1979b – On the *Massariaceae* in North America. Mycotaxon 9, 17–37.
Barr ME. 1982 – On the *Pleomassariaceae* (*Pleosporales*) in North America. Mycotaxon 15, 349–383.
Barr ME. 1983a – Muriform ascospores in class *Ascomycetes*. Mycotaxon 18, 149–157.
Barr ME. 1983b – The ascomycete connection. Mycologia 75, 1–13.
Barr ME. 1985 – Notes on the *Calosphaeriales*. Mycologia 77(4), 549–565.
Barr ME. 1987a – New taxa and combinations in the *Louculoascomycetes*. Mycotaxon 29, 501–505.
Barr ME. 1987b – Prodromus to class *Loculoascomycetes*. Amherst, Mass.: M.E. Barr Bigelow 1–168.
Barr ME. 1990a – *Melanommatales* (*Loculoascomycetes*). North American Flora, Series II, Part 13, 1–129.
Barr ME. 1990b – Podromus to nonlichenized, pyrenomycetous members of class HymenoAscomycetes. Mycotaxon 39, 43–184.
Barr ME. 1993a – Notes on the *Pleomassariaceae*. Mycotaxon 49, 129–142.
Barr ME. 1993b – Redisposition of some taxa described by JB Ellis. Mycotaxon 46, 45–76.
Barr ME. 1994 – Notes on the *Amphisphaeriaceae* and related families. Mycotaxon 51, 191–224.
Barr ME. 1996 – *Planistromellaceae*, a new family in the *Dothideales*. Mycotaxon 60, 433–442.
Barr ME. 2000 – Notes on coprophilous bitunicate *Ascomycetes*. Mycotaxon 76, 105–112.
Barrasa JM, Checa J, Martinez AT. 1993 – *Crassoascus*, a new nonstromatic genus in the *Clypeospaeriaceae*. Mycotaxon 46, 299–305.

Barreto GG, Bezerra JD, Costa-Rezende DH, Gusmão LF. 2023 – A multigene phylogeny of *Umbellidion* revealed a novel lineage in *Leotiomycetes*. Mycological Progress 22(7), 48.
Barreto GG, Souza-Motta CM, Silva GA, Groenewald JZ et al. 2024 – Meristematic and meristematic-like fungi in *Dothideomycetes*. Fungal Systematics and Evolution 14, 77–88.
Barreto RW, Evans H. 1998 – Fungal pathogens of *Euphorbia heterophylla* and *E. hirta* in Brazil and their potential as weed biocontrol agents. Mycopathologia 141, 21–36.
Barreto RW, Johnston PR, Crous PW, Evans HC. 2012 – A new species of the lenticel fungal genus *Claviradulomyces* (*Ostropales*) from the Brazilian Atlantic forest tree *Xylopia sericea* (*Annonaceae*). IMA fungus 3(2), 135–141.
Barrus MF, Horsfall JG. 1928 – Preliminary note on snowberry anthracnose. Phytopathology 18, 797–803.
Bateman C, Huang YT, Simmons DR, Kasson MT et al. 2017 – Ambrosia beetle *Premnobius cavipennis* (Scolytinae: Ipini) carries highly divergent ascomycotan ambrosia fungus, *Afroraffaelea ambrosiae* gen. nov. et sp. nov. (*Ophiostomatales*). Fungal Ecology 25, 41–49.
Batista AC. 1959 – Monografia dos fungos *Micropeltaceae*. Publicac ¸o ˜es Inst Micol Univ Recife 56, 1–519
Batista TM, Hilario HO, de Brito GA, Moreira RG et al. 2020 – Whole-genome sequencing of the endemic Antarctic fungus *Antarctomyces pellizariae* reveals an ice-binding protein, a scarce set of secondary metabolites gene clusters and provides insights on *Thelebolales* phylogeny. Genomics 112, 2915–2921.
Batzer JC, Arias MMD, Harrington TC, Gleason ML. 2008 – Four species of *Zygophiala* (*Schizothyriaceae*, *Capnodiales*) are associated with the sooty blotch and flyspeck complex on apple. Mycologia 100, 246–258.
Bayman P, Baker JL, Doster MA, Michailides TJ et al. 2002 – Ochratoxin production by the *Aspergillus ochraceus* group and *Aspergillus alliaceus*. Applied and Environmental Microbiology 68(5), 2326–9.
Beatrice Schol-Schwarz M. 1968 – *Rhinocladiella*, its synonym *Fonsecaea* and its relation to *Phialophora*. Antonie van Leeuwenhoek 34, 119–152.
Beck A. 1999 – Photobiont inventory of a lichen community growing on heavy-metal-rich rock. The Lichenologist 31, 501–510.
Becker K, Pfütze S, Kuhnert E, Cox RJ et al. 2021 – Hybridorubrins A−D, novel azaphilone heterodimers from stromata of *Hypoxylon fragiforme* and insights into the biosynthetic machinery for azaphilone diversification. Chemistry – A European Journal 27(4), 1438–1450.
Becker K, Stadler M. 2021 – Recent progress in biodiversity research on the *Xylariales* and their secondary metabolism. The Journal of Antibiotics 74(1), 1–23.
Becker K, Wessel AC, Luangsa-Ard JJ, Stadler M. 2020a – Viridistratins A−C, antimicrobial and cytotoxic benzo[j]fluoranthenes from stromata of *Annulohypoxylon viridistratum* (*Hypoxylaceae*, *Ascomycota*). Biomolecules 10(5), 805
Becker K, Wongkanoun S, Wessel A, Bills GF et al. 2020b – Phylogenetic and chemotaxonomic studies confirm the affinities of *Stromatoneurospora phoenix* to the coprophilous *Xylariaceae*. Journal of Fungi 6(3), 144.
Behera PK, Nayaka S, Upreti DK. 2020 – Lichens on monuments of Odisha - Are they causing biodeterioration? NeBIO, An International Journal of Environment and Biodiversity, Official publication of North East Centre for Environmental Education (NECEER), Imphal.
Beijerinck MW. 1894 – *Schizosaccharomyces octosporus*, eine achtsporige Alkoholhefe. Zentralblatt Bakteriologie Parasitenkunde 16, 49–58.
Beimforde C, Feldberg K, Nylinder S, Rikkinen J et al. 2014 – Estimating the Phanerozoic history of the *Ascomycota* lineages: combining fossil and molecular data. Molecular Phylogenetics and Evolution 78, 386–398.
Beimforde C, Schmidt AR, Rikkinen J, Mitchell JK. 2020 – *Sareomycetes* cl. nov., A new proposal for placement of the resinicolous genus *Sarea* (*Ascomycota*, *Pezizomycotina*). Fungal Systematics and Evolution 6, 25–37.

Belete T, Boyraz N. 2017 – Critical review on apple scab (*Venturia inaequalis*) biology, epidemiology, economic importance, management and defense mechanisms to the causal agent. Journal of Plant Physiology & Pathology 5, 2.
Bellemère A, Hafellner J. 1982 – L'ultrastructure des asques de genre *Dactylospora* (*Discomycetes*) et son interet taxonomique. Cryptogamie, Mycologie 3, 71–93.
Bellemère A. 1994a – Asci and ascospores in ascomycete systematics. In: Hawksworth DL (ed) Ascomycete Systematics: Problems and Perspectives in the Nineties. Plenum Press, New York, pp 111–126.
Bellemére A. 1994b – Documents et commentaires sur l'ultrastructure des asques *polysporés* des *Acarospora*, de quelques genres de la famille des *Acarosporaceae* et de genres similaires. Bulletin of the Linnean Society of Provence 45, 355– 388.
Belnap J, Büdel B, Lange OL. 2001 – Biological Soil Crusts: Characteristics and Distribution. In Belnap, J.; Lange, O.L. (eds.). Biological Soil Crusts: Structure, Function, and Management. Ecological Studies. Vol. 150. Berlin, Heidelberg: Springer Berlin Heidelberg 3–30.
Bender HB. 1932 – The genera of fungi imperfecti. Mycologia 24(4), 410–412.
Bendiksby M, Timdal E. 2013 – Molecular phylogenetics and taxonomy of *Hypocenomyce sensu lato* (*Ascomycota*: *Lecanoromycetes*): extreme polyphyly and morphological/ecological convergence. Taxon 62(5), 940–956.
Benito M, Alexopoulou E, Ferreira AV, Nakas JP. 2015 – Characterization of fungal populations isolated from wheat straw during composting. Applied and Environmental Microbiology 81(7), 2297–2308.
Benito S. 2019 – The impacts of *Schizosaccharomyces* on winemaking. Applied Microbiology and Biotechnology 103(11), 4291–4312.
Benjamin CR. 1955 – Ascocarps of *Aspergillus* and *Penicillium*. Mycologia 47, 669–687.
Benjamin RK, Shanor L. 1952 – Sex of host specificity and position specificity of certain species of *Laboulbenia* on *Bembidion picipes*. American Journal of Botany 39(2), 125–131.
Bennett RJ, Turgeon BG. 2016 – Fungal sex: the *Ascomycota*. Microbiology spectrum 4(5), 10–1128.
Benny GL, Kimbrough JW. 1980 – A synopsis of the orders and families of *Plectomycetes* with keys to genera. Mycotaxon 12(1), 1–91.
Benny GL, Samuelson DA, Kimbrough JW. 1985 – Studies in the *Coryneliales*. II. Taxa parasitic on *Podocarpaceae: Corynelia*. Botanical Gazette 146, 238–251.
Bensch K, Braun U, Groenewald JZ, Crous PW. 2012 – The genus *Cladosporium*. Studies in Mycology 72, 1–401.
Bensch K, Groenewald JZ, Braun U, Dijksterhuis J et al. 2015 – Common but different: the expanding realm of *Cladosporium*. Studies in Mycology 82, 23–74.
Bensch K, Groenewald JZ, Dijksterhuis J, Starink-Willemse M et al. 2010 – Species and ecological diversity within the *Cladosporium cladosporioides* complex (*Davidiellaceae, Capnodiales*). Studies in Mycology 67, 1–94.
Benton MJ. 1988 – Mass extinctions and the fossil record of reptiles: paraphyly, patchiness and periodicity. Systematics Association special 34, 269–294.
Bera M, Khan MA, Hazra T, Acharya K et al. 2022 – A novel fossil-species of *Meliolinites* Selkirk (fossil *Meliolaceae*) and its life cycle stages associated with an angiosperm fossil leaf from the Siwalik (Mio-Pliocene) of Bhutan sub-Himalaya. Fungal Biology 126, 576–86.
Berbee ML, Taylor JW. 1992a – 18s Ribosomal RNA gene sequence characters place the pathogen *Sporothrix schenckii* in the genus *Ophiostoma*. Experimental Mycology 16, 87–91.
Berbee ML, Taylor JW. 1992b – Detecting the morphological convergence in true fungi using 18S RNA sequence data. BioSystems 28, 117–125.
Berbee ML, Taylor JW. 1993 – *Ascomycetes* relationships: dating the origin of asexual lineages with 18S ribosomal RNA gene sequence data. In: Reynolds DR, Taylor JW (eds) The fungal holomorph: mitotic, meiotic and pleomorphic speciation in fungal systematics. CAB International, Wallingford 67–78.

Berbee ML, Taylor JW. 2001 – Fungal molecular evolution: Gene trees and geologic time. In: McLaughlin, D.J., McLaughlin, E.G., Lemke, P.A. (eds) Systematics and Evolution. The Mycota, vol 7B. Springer, Berlin, Heidelberg.

Berbee ML. 2001 – The phylogeny of plant and animal pathogens in the *Ascomycota*. Physiological and Molecular Plant Pathology 59(4), 165–187.

Berbee ML. Taylor JW. 1994 – 18S ribosomal DNA sequence data and dating, classifying, and ranking the fungi. In Ascomycete systematics: problems and perspectives in the nineties (pp. 213–223). Boston, MA: Springer US.

Berbee, ML, Taylor JW. 1992c – Convergence in ascospore discharge mechanism among pyrenomycete fungi based on 18S ribosomal DNA sequence. Molecular Phylogenetics and Evolution 1, 59–71.

Berlese AN. 1900 – Icones Fungorum ad usum Sylloges Saccardianae adcommodatae. 3. *Sphaeriaceae allantosporae*. Cramer, Padova 3, 1–120.

Bermúdez-Cova MA, Cruz-Laufer AJ, Piepenbring M. 2022 – Hyperparasitic fungi on black mildews (*Meliolales*, *Ascomycota*): Hidden fungal diversity in the tropics. Frontiers in Fungal Biology 3, 88527923.

Bessey CE. 1907 – A synopsis of plant phyla. University of Nebraska Studies 7, 275–373.

Bessey CE. 1914 – Revisions of some plant phyla.

Bevan RJ, Greenhalgh GN. 1976 – *Rhytisma acerinum* as a biological indicator of pollution. Environmental Pollution 10(4), 271–285.

Bezarra JDP, Nascimento CCF, Barbosa RN, da Silva et al. 2015 – Endophytic fungi from medicinal plant *Bauhinia forficata*: diversity and biotechnological potential. Brazilian Journal of Microbiology 46, 49–57.

Bezerra JD, Oliveira RJ, Paiva LM, Silva GA et al. 2017a – *Bezerromycetales* and *Wiesneriomycetales* ord. nov. (Class *Dothideomycetes*), with two novel genera to accommodate endophytic fungi from Brazilian cactus. Mycological Progress 16, 297–309.

Bezerra JD, Sandoval-Denis M, Paiva LM, Silva GA et al. 2017b – New endophytic *Toxicocladosporium* species from cacti in Brazil, and description of *Neocladosporium* gen. nov. IMA Fungus 8, 77–97.

Bhattacharya D, Lutzoni F, Reeb V, Simon D et al. 2000 – Widespread occurrence of spliceosomal introns in the rDNA genes of *Ascomycetes*. Molecular Biology and Evolution17(12), 1971–1984.

Bhattacharya D, Reeb V, Simon DM, Lutzoni F. 2005 – Phylogenetic analyses suggest reverse splicing spread of group I introns in fungal ribosomal DNA. BMC Evolutionary Biology 5, 68.

Bhunjun CS, Phukhamsakda C, Hyde KD, McKenzie EH et al. 2024 – Do all fungi have ancestors with endophytic lifestyles? Fungal Diversity 125, 73–98.

Bhunjun CS, Phukhamsakda C, Jeewon R, Promputtha I et al. 2021 – Integrating different lines of evidence to establish a novel ascomycete genus and family (*Anastomitrabeculia*, *Anastomitrabeculiaceae*) in *Pleosporales*. Journal of Fungi 7, 94.

Biasetto CR, Somensi A, Abdalla VD, Abreu LM et al. 2019 – Phytotoxic constituents from endophytic fungus *Xylaria cubensis* associated with *Eugenia brasiliensis*. Química Nova 42(5), 485–8.

Biazrov LG, Pelgunova LA. 2015 – Composition and proportion of elements on surface of crustose lichens. Arid Ecosystems 21(2), 62–70.

Biedermann PH, Müller J, Grégoire JC, Gruppe A et al. 2019 – Bark beetle population dynamics in the Anthropocene: challenges and solutions. Trends in ecology & evolution 34, 914–924.

Biedermann PH, Vega FE. 2020 – Ecology and evolution of insect–fungus mutualisms. Annual Review of Entomology 65, 431–455.

Bielczyk U, Jedrzejczyk-Korycinska M, Kiszka J. 2009 – Lichens of abandoned zic-lead mines. Acta Mycologica 44(2).

Bielczyk U, Kiszka J. 2001 – The genus *Absconditella* (*Stictidaceae*, *Ascomycota* lichenisati) in Poland. Polish Botanical Journal 46(2), 175–181.
Billar de Almeida A, Concas J, Campos MD, Materatski P et al. 2020 – Endophytic fungi as potential biological control agents against grapevine trunk diseases in Alentejo region. Biology 9(12), 420.
Billings RF, Gehring EH, Cameron RS, Gunter JT. 2001 – Current practices in managing oak wilt: federal cost share programs, trenching, chemical injection, and the Texas suppression program. In Shade tree wilt diseases. Proceedings from Wilt Diseases of Shade Trees: a National Conference, St. Paul, Minnesota, USA, 25–28 August, 1999 (pp.117–129). American Phytopathological Society (APS Press).
Bills GF, Gloer JB, An Z. 2013 – Coprophilous fungi: antibiotic discovery and functions in an underexplored arena of microbial defensive mutualism. Current Opinion in Microbiology 16(5), 549–565.
Bills GF, González-Menéndez V, Martín J, Platas G et al. 2012 – *Hypoxylon pulicicidum* sp. nov. (*Ascomycota*, *Xylariales*), a pantropical insecticide-producing endophyte. PLoS ONE 7, e46687.
Bitancourt AA, Jenkins AE. 1936a – *Elsinoë fawcettii* the perfect stage of the Citrus scab fungus. Phytopathology 26, 393–395.
Bitancourt AA, Jenkins AE. 1936b – Perfect stage of the sweet orange fruit scab fungus. Mycologia 28, 489–492.
Blackwell M, Haelewaters D, Pfister DH. 2020 – *Laboulbeniomycetes*: Evolution, natural history, and Thaxter's final word. Mycologia 112(6), 1048–1059.
Blackwell M, Malloch D. 1989a – *Pyxidiophora*: a link between the *Laboulbeniales* and hyphal *Ascomycetes*. Memoirs of the New York Botanical Garden 49, 23–32.
Blackwell M, Malloch D. 1989b – *Pyxidiophora*: life histories and arthropod associations of two species. Canadian Journal of Botany 67, 2552–2562.
Blackwell M, Malloch D. 1990 – Discovery of a *Pyxidiophora* with *Acariniola*-type ascospores. Mycological Research 94, 415–417.
Bladt TT, Frisvad JC, Knudsen PB, Larsen TO. 2013 – Anticancer and antifungal compounds from *Aspergillus, Penicillium* and other filamentous fungi. *Molecules* 18, 11338–11376.
Blanchette RA. 1995 – Degradation of the lignocellulose complex in wood. Canadian Journal of Botany 73, 999–1010.
Boedijn KB. 1931 – Notes on some sooty moulds. Bulletin du Jardin Botanique de Buitenzorg 11, 220–231.
Boedijn KB. 1961 – *Myriangiales* from Indonesia. Persoonia 2, 63–75.
Boedijn KB. 1962 – The *Sordariaceae* of Indonesia. Persoonia 2, 305–320.
Boeger WA, Pie MR, Ostrensky A, Patella L. 2005 – Lethargic crab disease: multidisciplinary evidence supports a mycotic etiology. Memórias do Instituto Oswaldo Cruz 100, 161–167.
Boehm EWA, Mugambi G, Miller AN, Huhndorf S et al. 2009a – A phylogenetic reappraisal of the *Hysteriaceae*, *Mytilinidiaceae* & *Gloniaceae* with keys to world species. Studies in Mycology 64, 49–83.
Boehm EWA, Mugambi GK, Miller AN, Huhndorf SM et al. 2009b – A molecular phylogenetic reappraisal of the *Hysteriaceae*, *Mytilinidiaceae* and *Gloniaceae* (*Pleosporomycetidae*, *Dothideomycetes*) with keys to world species. Studies in Mycology 64, 49–83.
Boehm EWA, Schoch CL, Spatafora JW. 2009c – On the evolution of the *Hysteriaceae* and *Mytilinidiaceae* (*Pleosporomycetidae*, *Dothideomycetes*, *Ascomycota*) using four nuclear genes. Mycological Research 113, 461–479.
Boerema GH, de Gruyer J, Noordeloos ME, Hamers MEC. 2004 – *Phoma* identification manual. Differentiation of specific and infra-specific taxa in culture CABI Publishing, Wallingford, UK.

Boerema GH, de Gruyter J, Kesteren HA. 1994 – Contributions towards a monograph of *Phoma* (*Coelomycetes*) – III-1. Section Plenodomus: Taxa often with a *Leptosphaeria* teleomorph. Persoonia 15, 431–487.
Bohman G. 1969 – Chemical studies on lichens 22. Anthraquinones from the Lichen *Lasallia papulosa* var. *rubiginosa* and the fungus *Valsaria rubricosa*. Acta Chem Scand 23, 2241–2244.
Boistel A. 1903 – Nouvelle Flore des Lichens, II. P. Dupont. Paris.
Bold HC. 1957 – The Morphology of Plants. Harper Row, New York.
Bonorden HF. 1864 – Abhandlungen aus dem Gebiete der Mykologie. Abhandlungen der Naturforschenden Gesellschaft zu Halle 8, 1–168.
Bonthond G, Sandoval-Denis M, Groenewald JZ, Crous PW. 2018 – *Seiridium* (*Sporocadaceae*): an important genus of plant pathogenic fungi. Persoonia 40, 96–118.
Boonmee S, D'souza MJ, Luo ZL, Pinruan U et al. 2016 – *Dictyosporiaceae* fam. nov. Fungal Diversity 80, 457–482.
Boonmee S, Ko TWK, Chukeatirote E, Chen H et al. 2012 – Two new *Kirschsteiniothelia* species with *Dendryphiopsis* anamorphs cluster in *Kirschsteiniotheliaceae* fam. nov. Mycologia 104, 698–714.
Boonmee S, Phookamsak R, Hongsanan S, Doilom M et al. 2017 – Mycosphere notes 51–101. Revision of genera in *Perisporiopsidaceae* and *Pseudoperisporiaceae* and other *Ascomycota* genera *incertae sedis*. Mycosphere 8(10), 1695–1801.
Boonmee S, Rossman AY, Liu JK, Li WJ et al. 2014 – *Tubeufiales*, ord. nov., integrating sexual and asexual generic names. Fungal Diversity 68, 239–298.
Boonmee S, Wanasinghe DN, Calabon MS, Huanraluek N et al. 2021 – Fungal diversity notes 1387–1511: taxonomic and phylogenetic contributions on genera and species of fungal taxa. Fungal Diversity 111, 1–335.
Boonmee S, Zhang Y, Chomnunti P, Chukeatirote E et al. 2011 – Revision of lignicolous *Tubeufiaceae* based on morphological reexamination and phylogenetic analysis. Fungal Diversity 51, 63–102.
Boonyuen N, Chuaseeharonnachai C, Nuankaew S, Kwantong P et al. 2021 – Novelties in *Fuscosporellaceae* (*Fuscosporellales*): Two new *Parafuscosporella* from Thailand revealed by morphology and phylogenetic analyses. Diversity 13, 517.
Boonyuen N, Chuaseeharonnachai C, Suetrong S, Sri-Indrasutdhi V et al. 2011 – *Savoryellales* (*Hypocreomycetidae*, *Sordariomycetes*): a novel lineage of aquatic ascomycetes inferred from multiple-gene phylogenies of the genera *Ascotaiwania*, *Ascothailandia* and *Savoryella*. Mycologia 103 (6), 1351–1350.
Borgato L, Ertz D, Van Rossum F, Verbeken A. 2022 – The diversity of lichenized trentepohlioid algae (*Ulvophyceae*) communities is driven by fungal taxonomy and ecological factors. Journal of Phycology 58, 582–602.
Bosch-Roig P, Barca D, Crisci GM, Lalli C. 2013 – Lichens as bioindicators of atmospheric heavy metal deposition in Valencia, Spain. Journal of Atmospheric Chemistry 70(4), 373–388.
Boudier É. 1885 – Nouvelle classification naturelle des *Discomycetes* echarnus connus generalement sous le nom de *Pezizales*. Bulletin de la Société Mycologique de France 1, 91–120.
Boudier JLE. 1907 – Histoire et classification des Discomycètes d'Europe, edition anastatica. A. Asher, Amsterdam, Netherlands.
Bovio E, Garzoli L, Poli A, Prigione V et al. 2018 – The culturable mycobiota associated with three Atlantic sponges, including two new species: *Thelebolus balaustiformis* and *T. spongiae*. Fungal Systematics and Evolution 1, 141–167.
Bowen JK, Mesarich CH, Bus VG, Beresford RM et al. 2011 – *Venturia inaequalis*: the causal agent of apple scab. Molecular plant pathology 12, 105–122.
Bowman EA, Arnold AE. 2021 – Drivers and implications of distance decay differ for ectomycorrhizal and foliar endophytic fungi across an anciently fragmented landscape. The ISME Journal 15, 3437–3454.

Brackel W von. 2008 – *Zwackhiomyces echinulatus* sp. nov. And other lichenicolous fungi from Sicily, Italy. Herzogia 21, 181–198.
Braconcini M, Gorrasi S, Fenice M, Barghini P et al. 2024 – *Rambellisea gigliensis* and *Rambellisea halocynthiae*, gen. *et* spp. nov. (*Lulworthiaceae*) from the marine tunicate *Halocynthia papillosa*. Journal of Fungi 10, 127.
Bradwell T. 2009 – Lichenometric dating: a commentary, in the light of some recent statistical studies. Geografiska Annaler: Series A, Physical Geography 91(2), 61–69.
Brahmanage RS, Lu YZ, Bhat DJ, Wanasinghe DN et al. 2017 – Phylogenetic investigations on freshwater fungi in *Tubeufiaceae* (*Tubeufiales*) reveals the new genus *Dictyospora* and new species *Chlamydotubeufia aquatica* and *Helicosporium flavum*. Mycosphere 8(7), 917–933.
Brandriff H. 1936 − The development of the ascocarp of *Acrospermum compressum*. Mycologia 28, 228–235.
Brasch J, Beck-Jendroscheck V, Voss K, Yurkov A et al. 2017 – *Xanthothecium peruvianum* isolated from human stratum corneum: A case report, characterisation and short review that suggest emendation of *Arachnomyces peruvianus*. Mycoses 60(7), 469–476.
Brasier C. 2000 – The rise of the hybrid fungi. Nature 405, 134–135.
Brasier CM, Kirk SA. 2010 – Rapid emergence of hybrids between the two subspecies of *Ophiostoma novo-ulmi* with a high level of pathogenic fitness. Plant Pathology 59, 186–99.
Brasier CM. 2001 – Rapid evolution of introduced plant pathogens via interspecific hybridization: hybridization is leading to rapid evolution of Dutch elm disease and other fungal plant pathogens. Bioscience 51, 123–33.
Braun U, Crous PW, Dugan F, Groenewald JZ et al. 2003 – Phylogeny and taxonomy of *Cladosporium*-like hyphomycetes, including *Davidiella* gen. nov., the teleomorph of *Cladosporium* s. str. Mycological Progress 2, 3–18.
Braun U, Nakashima C, Crous PW, Groenewald JZ et al. 2018 – Phylogeny and taxonomy of the genus *Tubakia* s. lat. Fungal Systematics and Evolution 1, 41–99.
Brefeld O. 1891 – Unters. Gesammtgebiet Mykol. x, 190–191.
Breitenbach VF. 1963 – The Indigenous Trees of Ethiopia, 2nd edn. Addis Ababa, Ethiopia: Ethiopian Forestry Association.
Bretag TW, Keane PJ, Price TV. 2006 – The epidemiology and control of ascochyta blight in field peas: a review. Australian Journal of Agricultural Research 57, 883–902.
Breton A, Faurel L. 1967 – Etude des affinites du genre *Mycorhynchus* Sacc. et description de plusieurs especes nouvelles. Revue de Mycologie 38, 229–258.
Briggs LH, Castaing DR, Denyer AN, Orgias EF et al. 1972 – Chemistry of fungi. Part VIII. Constituents of *Valsaria rubricosa* and the identification of papulosin with *valsarin*. Journal of the Chemical Society, Perkin Transactions 1, 1464–1466.
Briggs LH, Castaing DR, Valsarin C. 1965 – Constituents of the New Zealand Fungus, *Valsaria rubricosa*. In Proceedings, no. 28, p. 71. National Institute of Sciences of India.
Bright DE, Torres JA. 2006 – Studies on West Indian *Scolytidae* (*Coleoptera*) 4: A review of the *Scolytidae* of Puerto Rico, USA with descriptions of one new genus, fourteen new species and notes on new synonymy (*Coleoptera*: *Scolytidae*). Koleopterologische Rundschau 76, 389–428.
Brinkmann V, Billich A, Baumruker T, Heining P et al. 2010 – Fingolimod (FTY720): discovery and development of an oral drug to treat multiple sclerosis. Nature reviews Drug discovery 9(11), 883–897.
Broders K, Iriarte-Broders G, Bergstrom GC, Byamukama E et al. 2022 – *Phyllachora* species infecting maize and other grass species in the Americas represents a complex of closely related species. Ecology and Evolution 12, e8832.
Brodo IM. 1984 – Lichenes Canadenses Exsiccati: Fascicle III. The Bryologist 87, 97–111.
Brouard JS. 1979 – Zone lines in Scots pine needles associated with *Lophodermium*. BSc (Hons) Thesis, University of Aberdeen.

Brown G, Schultz M, Robinson MD. 2002 – Saxicolous and terricolous lichens from the foothills of northern Oman. Nova Hedwigia 75, 177–188.
Bruce A, Verrall S, Hackett CA, Wheatley RE. 2004 – Identification of volatile organic compounds (VOCs) from bacteria and yeast causing growth inhibition of sapstain fungi, Holzforschung 193–198.
Brummelen J. van. 1998 – Reconsideration of relationships within the *Thelebolaceae* based on ascus ultrastructure. Persoonia 16, 119–125.
Bruner SC, Jenkins AE. 1933 – Identity and host relations of the *Elsinoë* of lima bean. Journal of Agricultural Research 47, 783–789.
Bruns TD, Chung JA, Carver AA, Glassman SI. 2020 – A simple pyrocosm for studying soil microbial response to fire reveals a rapid, massive response by *Pyronema* species. PLoS ONE 15, e0222691.
Brusse F. 1988 – *Acarosporaceae lithoglypha*, a new lichen genus from clarens sandstone. Bothalia 18(1), 89–90.
Brysch-Herzberg M, Jia GS, Seidel M, Assali I et al. 2022 – Insights into the ecology of *Schizosaccharomyces* species in natural and artificial habitats. Antonie Van Leeuwenhoek 115(5), 661–695.
Brysch-Herzberg M, Tobias A, Seidel M, Wittmann R et al. 2019 – *Schizosaccharomyces osmophilus* sp. nov., an osmophilic fission yeast occurring in bee bread of different solitary bee species. FEMS yeast research 19(4), p. foz038.
Bucher VVC, Hyde KD, Pointing SB, Reddy CA 2004a – Production of wood decay enzymes, mass loss and lignin solubilization in wood by marine ascomycetes and their anamorphs. Fungal Diversity 15, 1–14.
Bucher VVC, Pointing SB, Hyde KD, Reddy CA. 2004b – Production of wood decay enzymes, loss of mass, and lignin solubilization in wood by diverse tropical freshwater fungi. Microbial Ecology 48, 331–337.
Büdel B, Becker U, Porembski S, Barthlott W. 1997a – Cyanobacteria and cyanobacterial lichens from inselbergs of the Ivory Coast, Africa. Botanica Acta 110, 458–465.
Büdel B, Elix JA. 1997 – *Peltula langei* Büdel et Elix spec. nov. from Australia, with remarks on its chemistry and the ascoma of *Peltula clavata* (Krempelh.) Wetm. Bibliotheca Lichenologica 67, 3–9.
Büdel B, Karsten U, Garcia-Pichel F. 1997b – Ultraviolet-absorbing scytonemin and mycosporine-like amino acid derivatives in exposed, rock-inhabiting cyanobacterial lichens. Oecologia 165–172.
Büdel B, Lange OL. 1991 – Water status of green and blue-green phycobionts in lichen thalli after hydration by water vapor uptake: do they become turgid. Botanica Acta 104, 361–366.
Büdel B, Schultz M. 2003 – A way to cope with high irradiance and drought: inverted morphology of a new cyanobacterial lichen, *Peltula inversa* sp. nova, from the Nama Karoo, Namibia. Bibliotheca Lichenologica 86, 225–232.
Büdel B. 1982 – Phycobionten der Lichinaceen. Diplom-Thesis. Universität Marburg, Marburg.
Büdel B. 1986 – Peltulaceae Büdel fam. nov. In Notes on ascomycete systematics, nos. 1–224. Eriksson OE, Hawksworth DL (Eds). Systema Ascomycetum 5, 149.
Büdel B. 1987a – Zur Biologie und Systematik der Flechtengattungen *Heppia* und *Peltula* im südlichen Afrika. Bibliotheca Lichenologica 23, 1–105.
Büdel B. 1987b – Taxonomy and biology of the lichen genus *Peltula* Nyl. Bibliotheca Lichenologica 25, 209–217.
Büdel B. 1992 – Taxonomy of lichenized procaryotic blue-green algae. In Algae and Symbiosis, Reisser W (Ed). Biopress Limited, Bristol 301–324.
Bugni TS, Ireland CM. 2004 – Marine-derived fungi: a chemically and biologically diverse group of microorganisms. Natural Product Reports 21(1), 143– 63.
Bullerman LB. 2003 – Spoilage fungi in food – An Overview. Caballero, B. 2003. Encyclopedia of Food Sciences and Nutrition (Second Edition), 5511–5522.

Bullerwell CE, Leigh J, Forget L, Lang BF. 2003 – A comparison of three fission yeast mitochondrial genomes. Nucleic Acids Research 31(2), 759–768.
Bulman LS. 1993 – *Cyclaneusma* needle-cast and *Dothistroma* needle blight in NZ pine plantations. New Zealand Forestry 38, 21–24.
Bundhun D, Senanayake I, Jayawardena RS, Cheewangkoon R. 2021a – First reports of the sexual morphs of *Diaporthe forlicesenica* nom. nov. and *Diaporthe goulteri* (*Diaporthaceae*, *Diaporthales*) revealed by molecular phylogenetics. Phytotaxa 516(1), 1–27.
Bundhun D, Wanasinghe DN, Maharachchikumbura SS, Bhat DJ et al. 2021b – *Yuxiensis granularis* gen. et sp. nov., a novel quellkörper-bearing fungal taxon added to *Scortechiniaceae* and inclusion of *Parasympodiellaceae* in *Coronophorales* based on phylogenetic evidence. Life 11, 1011.
Büren G von. 1915 – Die schweizerischen Protomycetaceen mit besonderer Berücksichtigung ihrer Entwicklungsgeschichte und Biologie. Bern: Druck und Verlag von K. J. Wyss.
Burgess KMN, Ibrahim A, Sørensen D, Sumarah MW. 2017 – TrienylfuranolA and trienylfuranone A-B: metabolites isolated from endophytic fungus, *Hypoxylon submoniticulosum*, in the raspberry Rubus idaeus. The Journal of Antibiotics 70, 721–5.
Buschbom J, Mueller G. 2004 – Resolving evolutionary relatonships in the lichen-forming genus *Porpidia* and related allies (*Porpidiaceae*, *Ascomycota*). Molecular Phylogenetics and Evolution 32, 66–82.
Bussaban B, Lumyong S, Lumyong P, Seelanan T et al. 2005 – Molecular and morphological characterization of Pyricularia and allied genera. Mycologia 97(5), 1002–1011.
Bylin A, Arnerup J, Högberg N, Thor G. 2007 – A phylogenetic study of *Fuscideaceae* using mtSSU rDNA. Bibliotheca Lichenologica 96, 49–60.
Byrne PJ, Jones EBG. 1974 – Lignicolous marine fungi. Veroff Ins Meeresforschung, Bremerhaven Supplement 5, 301–320.
Čadež N, Dlauchy D, Tome M, Péter G. 2021 – *Novakomyces olei* sp. nov., the first member of a novel *Taphrinomycotina* lineage. Microorganisms 9(2), 301.
Cai L, Hyde KD, Tsui CKM. 2006a – Genera of freshwater fungi. Fungal Diversity 18, 1–261.
Cai L, Jeewon R, Hyde K. 2006b – Phylogenetic investigations of *Sordariaceae* based on multiple gene sequences and morphology. Mycological Research 110, 137–150.
Cai L, McKenzie EHC, Hyde KD. 2004 – New species of *Cordana* and *Spadicoides* from decaying bamboo culms in China. Sydowia 56, 222–228.
Cai L, Tsui CK, Zhang KQ, Hyde KD. 2002 – Aquatic fungi from Lake Fuxian, Yunnan, China. Fungal Diversity 9, 57–70.
Cai L, Zhang K, McKenzie EHC, Hyde KD. 2003 – Freshwater fungi from bamboo and wood submerged in the Liput River in the Philippines. Fungal Diversity 13, 1–12.
Cain RF. 1956a – Studies on coprophilous *Ascomycetes*. II. *Phaeotrichum*, a new cleistocarpous genus in a new family, and its relationships. Canadian Journal of Botany 34, 675–684.
Cain RF. 1956b – Studies on soil fungi. *Saturnomyces* a new genus of the *Aspergillaceae*. Canadian Journal of Botany 34(1), 135–141.
Calabon M, Hyde K, Jones E, Bao D et al. 2023a – Freshwater fungal biology. Mycosphere 14, 195–413.
Calabon MS, Al-Otibi FO, Hyde KD. 2025 – Morpho-molecular phylogenetic evidence confirms *Natipusilla* as a synonym of *Ascominuta*. New Zealand Journal of Botany 1–14.
Calabon MS, Hyde KD, Jones EBG, Luo ZL et al. 2022 – Freshwater fungal numbers. Fungal Diversity 114, 3–235.
Calabon MS, Jones EB, Boonmee S, Doilom M et al. 2021a – Five novel freshwater ascomycetes indicate high undiscovered diversity in Lotic habitats in Thailand. Journal of Fungi 7, 117.
Calabon MS, Jones EBG, Promputtha I, Hyde KD. 2021b – Fungal biodiversity in salt marsh ecosystems. Journal of Fungi 7(8), 648.
Calabon MS, Jones EG, Pang KL, Abdel-Wahab MA et al. 2023b – Updates on the classification and numbers of marine fungi. Botanica Marina 66(4), 213–238.

Calatayud V, Barreno E. 2003 – A new *Lichenostigma* on vagrant *Aspicilia* species. The Lichenologist 35(4), 279–285.
Calatayud V, Etayo J, Diederich P. 2001 – *Paralethariicola aspiciliae* (*Ostropales*, *Odontotremataceae*), a new genus and species of lichenicolous fungi. The Lichenologist 33(6), 477–482.
Calatayud V, Triebel D, Pérez-Ortega S. 2007 – *Zwackhiomyces cervinae*, a new lichenicolous fungus (*Xanthopyreniaceae*) on *Acarospora*, with a key to the known species of the genus. The Lichenologist 39(02), 129–134.
Calcott MJ, Ackerley DF, Knight A, Keyzers RA et al. 2018 – Secondary metabolism in the lichen symbiosis. Chemical Society Reviews 47(5), 1730–60.
Calhim S, Halme P, Petersen JH, Læssøe T et al. 2018 – Fungal spore diversity reflects substrate-specific deposition challenges. Scientific Reports 8(1), 5356.
Campbell CK, Johnson EM, Warnock DW. 1997 – Nail infection caused by *Onychocola canadensis*: report of the rst four British cases. Journal of Medical and Veterinary Mycology 35, 423–425.
Campbell J, Ferrer A, Raja HA, Sivichai S et al. 2007 – Phylogenetic relationships among taxa in the *Jahnulales* inferred from 18S and 28S nuclear ribosomal DNA sequences. Canadian Journal of Botany 85, 873–882.
Campbell J, Inderbitzin P, Kohlmeyer J, Volkmann-Kohlmeyer B. 2009 – *Koralionastetales*, a new order of marine *Ascomycota* in the *Sordariomycetes*. Mycological research 113, 373–380.
Campbell J, Shearer CA. 2004 – *Annulusmagnus* and *Ascitendus*, two new genera in the *Annulatascaceae*. Mycologia 96, 822–833.
Campbell J, Volkmann-Kohlmeyer B, Gräfenhan T, Spatafora JW et al. 2005 – A re-evaluation of *Lulworthiales*: relationships based on 18S and 28S rDNA. Mycological Research 109, 556–568.
Campbell R, Sutton BC. 1977 – Conidial ontogeny in *Echinocatena arthrinioides* gen. et sp. nov. (*Deuteromycotina*: *Hyphomycetes*). Transactions of the British Mycological Society 69, 125–131.
Cannon P, Coppins B, Fletcher A, Sanderson N et al. 2022 – *Caliciales*: *Leprocaulaceae*, including the genera *Halecania* and *Leprocaulon*. Revisions of British and Irish Lichens 23, 1–8.
Cannon P, Coppins B, Orange A, Sanderson N et al. 2021 – Raman spectroscopy of the *Candelaria* and *Pyxine* lichen. Revisions of British and Irish Lichens 21, 1–8.
Cannon PF, Damm U, Johnston PR, Weir BS. 2012 – *Colletotrichum* – Current status and future directions. Studies in Mycology 73(1), 181–213.
Cannon PF, Hawksworth DL. 1983 – *Arxiomyces*, a new name for *Phaeostoma* von Arx & E. Müller. Transactions of the British Mycological Society 81(3), 644–645.
Cannon PF, Kirk PM. 2007 – Fungal families of the world. CABI Bioscience, Wallingford 1–456.
Cannon PF, Minter DW. 1986 – The *Rhytismataceae* of the Indian subcontinent. Mycological Papers 155, 1–123.
Cannon PF. 1988 – Proposal to merge the *Phyllachorales* with the *Diaporthales*, with a new family structure. Systema Ascomycetum 7, 23–43.
Cannon PF. 1991 – Revision of *Phyllachora* and some similar genera on the host family *Leguminosae*. Mycological Papers 163, 1–302.
Cannon PF. 1994 – The newly recognized family *Magnaporthaceae* and its interrelationships. Systema Ascomycetum 13, 25–42.
Cannon PF. 1996 – Systematics and diversity of the *Phyllachoraceae* associated with *Rosaceae*, with a monograph of *Polystigma*. Mycological Research 100, 1409–1427.
Cannon PF. 1997 – Diversity of the *Phyllachoraceae* with special reference to the tropics. In: Hyde K (ed), Biodiversity of Tropical Microfungi 255–278.
Cano J, Guarro J. 2002 – The genus *Aphanoascus*. Mycological Research 94(3), 355–377.
Cao S, Clardy J. 2011 – New naphthoquinones and a new δ-lactone produced by endophytic fungi from Costa Rica. Tetrahedron letters 52(17), 2206–2208.

Cao S, Zhang F, Liu C, Hao Z et al. 2015 – Distribution patterns of haplotypes for symbionts from *Umbilicaria esculenta* and *U. muehlenbergii* reflect the importance of reproductive strategy in shaping population genetic structure. BMC Microbiology 15, 1–2.
Cao XX, Wei JG, Hou JG, Fan CL et al. 2021 – First report of *Chaetomella raphigera* causing brown spot on *Eucalyptus urophylla× E. grandis* in China. Journal of Plant Pathology 103, 403–403.
Carini A. 1910 – Formas de eschizogonia do Trypanosoma lewisi. Bol. Soc. de Med. E Cir de Sao Paulo 18, 204.
Carlucci A, Cibelli F, Lops F, Phillips AJL et al. 2015 – *Pleurostomophora richardsiae* associated with trunk diseases of grapevines in southern Italy. Phytopathologia Mediterranea 54, 109–123.
Carneiro de Almeida DA, Pascholati Gusmão LF, Miller AN. 2016 – Brazilian semi-arid *Ascomycetes* II: New and interesting records of *Bertiaceae*, *Nitschkiaceae* and *Scortechiniaceae* (*Coronophorales*, *Sordariomycetes*). Nova Hedwigia 102, 513–522.
Carpenter SE. 1988 – *Leotiales*, a name to replace *Helotiales* (*Ascomycotina*). Mycologia 80(1), 127–130.
Carreto JI, Carignan MO. 2011 – Mycosporine-like amino acids: relevant secondary metabolites. Chemical and ecological aspects. Marine Drugs 9, 387–446.
Carrino-Kyker SR, Kluber LA, Petersen SM, Coyle KP et al. 2016 – Mycorrhizal fungal communities respond to experimental elevation of soil pH and P availability in temperate hardwood forests. FEMS Microbiology Ecology 92, 1–19.
Carris LM, Little CR, Stiles CM. 2012 – Introduction to Fungi. The Plant Health Instructor.
Carroll G, Munk A. 1964 – Studies on lignicolous *Sordariaceae*. Mycologia 56, 77–98.
Carroll GC, Carroll FE. 1978 – Studies on the incidence of coniferous needle endophytes in the Pacific Northwest. Canadian Journal of Botany 56(24), 3034–3043.
Carvalho CD, Ferreira-D'Silva A, Wedge DE, Cantrell CL et al. 2018 – Antifungal activities of cytochalasins produced by *Diaporthe miriciae*, an endophytic fungus associated with tropical medicinal plants. Canadian Journal of Microbiology 64, 835–843.
Casadevall A, Steenbergen JN, Nosanchuk JD. 2003 – "Ready made" virulence and "dual use" virulence factors in pathogenic environmental fungi–the *Cryptococcus* neoformans paradigm. Current Opinion in Microbiology 6(4), 332–337.
Castañeda RF, Fabre DE, Parra M, Perez M et al. 1996 – Some airborne conidial fungi from Cuba. Mycotaxon 60, 283–290.
Castañeda Ruíz RF, Kendrick B. 1990 – Conidial fungi from Cuba: I. University of Waterloo Biology Series 32, 1–53.
Castañeda-Ruiz RF, Heredia G, Arias-Mota RM, Stadler M et al. 2012 – Two new fungi from Mexico: *Anaseptoidium* gen. nov. and *Cylindrosympodium sosae* sp. nov. Mycotaxon 119, 141–148.
Castello M. 2003 – Lichens of the Terra Nova Bay area, northern Victoria Land.
Castlebury LA, Rossman AY, Jaklitsch WJ, Vasilyeva LN. 2002 – A phylogeny overview of the *Diaporthales* based on large subunit nuclear ribosomal DNA sequences. Mycologia 94, 1017–1031.
Catherinot E, Lanternier F, Bougnoux ME, Lecuit M et al. 2010 – *Pneumocystis jirovecii* pneumonia. Infectious Disease Clinics 24(1), 107–138.
Cavalier-Smith T. 1998 – A revised six-kingdom system of life. Biological Reviews 73(3), 203–266.
Cedeño-Sanchez M, Charria-Girón E, Lambert C, Luangsa-ard JJ et al. 2023a – Segregation of the genus *Parahypoxylon* (*Hypoxylaceae*, *Xylariales*) from *Hypoxylon* by a polyphasic taxonomic approach. MycoKeys 95, 131–62.
Cedeño-Sanchez M, Schiefelbein R, Stadler M, Voglmayr H et al. 2023b – Redisposition of apiosporous genera *Induratia* and *Muscodor* in the *Xylariales*, following the discovery of an authentic strain of *Induratia apiospora*. Botanical Studies 64(1), 1–7.

Cesati V de, Notaris G de. 1863 – Schema di classificazione degli sferiacei Italici aschigeri piu o meno appartenenti al genere Sphaeria nell'antico significato attribuitogli de Persoon. Comm. Soc. crittog. Ital.1 (fasc. 4), 205 (1863).
Chabé M, Aliouat-Denis CM, Delhaes L, Aliouat EM et al. 2011 – *Pneumocystis*: from a doubtful unique entity to a group of highly diversified fungal species. FEMS Yeast Research 11(1), 2–17.
Chabé M, Dei-Cas E, Creusy C, Fleurisse L et al. 2004 – Immunocompetent hosts as a reservoir of *Pneumocystis* organisms: histological and RT-PCR data demonstrate active replication. European Journal of Clinical Microbiology & Infectious Diseases 23, 89–97.
Chadefaud M. 1960 – Les Ve´ge´taux non Vasculaires (Cryptogamie). In: Emberger L (ed) Traite´ de Botanique Syste´matique (Chadefaud M. Masson, Paris, 1–1018.
Chagas C. 1909 – Nova tripanozomiazaea humana. Mem. Inst. Oswaldo Cruz 1, 159–218.
Chaiwan N, Lu YZ, Tibpromma S, Bhat DJ, Hyde KD et al. 2017 – *Neotubeufia* gen. nov. and *Tubeufia guangxiensis* sp. nov. (*Tubeufiaceae*) from freshwater habitats. Mycosphere 8(9), 1443–1456.
Chakraborty N, Tarafder E, Paul A, Paloi S et al. 2022 – *Trichoglossum benghalense* (*Geoglossales*, *Ascomycota*) from India: new to science. Phytotaxa 536(1), 072–082.
Chambers S, Cannon P, Coppins B, Simkin J. 2021 – *Vezdaeales*: *Vezdaeaceae*, including the genus *Vezdaea*. Revisions of British and Irish Lichens 10, 1–5.
Chambers SP, Gilbert OL, James PW, Aptroot A et al. 2009 – *Pertusaria* DC. In: The Lichens of Great Britain and Ireland (C. W. Smith, A. Aptroot, B. J. Coppins, A. Fletcher, O. L. Gilbert, P. W. James, P. A. Wolseley, eds). British Lichen Society, London, UK.
Chang F, Nurse P. 1996 – How fission yeast fission in the middle. Cell 84, 191–194.
Chang HS. 2001 – *Trichocladium* anamorph of *Ascotaiwania hsilio* and Monodictys-like anamorphic states of *Ascotaiwania lignicola*. Fungal Science 16, 35–38.
Chang JC, Hsiao G, Lin RK, Kuo YH et al. 2017a – Bioactive constituents from the termite nest-derived medicinal fungus *Xylaria nigripes*. Journal of Natural Products 80(1), 38–44.
Chang R, Duong TA, Taerum SJ, Wingfield MJ et al. 2017b – Ophiostomatoid fungi associated with conifer-infesting beetles and their phoretic mites in Yunnan, China. MycoKeys 28, 19–64.
Chang SW, Scheef E, Abler RAB, Thomson S et al. 2006 – Distribution of *Typhula* spp. and *Typhula ishikariensis* varieties in Wisconsin, Utah, Michigan, and Minnesota. Phytopathology 96, 926–933.
Chantawannakul J, Chatpattanasiri P, Wattayagorn V, Kongsema M et al. 2021 – Virtual screening for biomimetic anti-cancer peptides from *Cordyceps militaris* putative pepsinized peptidome and validation on colon cancer cell line. Molecules 26(19), 5767.
Chapla VM, Zeraik ML, Leptokarydis IH, Silva GH et al. 2014 – Antifungal compounds produced by *Colletotrichum gloeosporioides*, an endophytic fungus from *Michelia champaca*. Molecules 19, 19243–19252.
Chardón CE, Toro RA. 1934 – Mycological explorations of Venezuela. Monograph Universidad de Puerto Rico 2, 1–353.
Chardón CE. 1928 – Contribución al estudio de la flora micológica de Colombia. Boletín de la Real Sociedad Española de Historia Natural 28, 111–124.
Chardón CE. 1929 – New or interesting tropical *Dothideales* - II. Journal of the Department of Agriculture Porto Rico 13, 3–15.
Chardón CE. 1932 – New or interesting tropical *Dothideales* – III. Journal of the Department of Agriculture Porto Rico 16, 167–192.
Chardón CE. 1946 – Fungi Domingenses novi vel minus cogniti I. Farlowia 2, 455–473.
Charria-Girón E, Stchigel AM, Čmoková A, Kolařík M et al. 2023 – *Amesia hispanica* sp. nov., producer of the antifungal class of antibiotics dactylfungins. Journal of fungi 9(4), 463.
Charria-Girón E, Surup F, Marin-Felix Y. 2022 – Diversity of biologically active secondary metabolites in the ascomycete order *Sordariales*. Mycological Progress 21, 43.

Chatzidimopoulos M, Lioliopoulou F, Sotiropoulos T, Vellios E. 2020 – Efficient control of apple scab with targeted spray applications. Agronomy 10, 217.
Chaudhary VB, Aguilar-Trigueros CA, Mansour I, Rillig MC. 2022 – Fungal dispersal across spatial scales. Annual Review of Ecology, Evolution, and Systematics 53, 69–85.
Chaves-batista A, Silva-maia H. 1958 – Estudo iconográfico de alguns fungos *Valsaceae Xylariaceae*. Revista de Biologia (Lisbon) 19(3–4), 325–332.
Checa J, Barrasa JM, Martínez AT, Blanco MN et al. 1996 – *Bicornispora exophiala*, a new genus and species of the *Coryneliales* and its black yeast anamorph. Mycological Research 100(4), 500–504.
Checa J, Barrasa JM, Moreno G, Fort F et al. 1988 – The genus *Coniochaeta* (Sacc.) Cooke (*Coniochaetaceae*, *Ascomycotina*) in Spain. Cryptogamie, Mycologie 9, 1–34.
Checa J, Blanco MN, Moreno G, Alvarado P et al. 2014 – *Amplistroma erinaceum*, a new species and its anamorph from Panama. Mycological Progress 13, 277–283.
Checa J, Blanco MN, Moreno G, Manjón JL et al. 2012 – *Amplistroma longicollis*, a new species and its anamorph state described and sequenced from Europe. Mycological Progress 11, 647–653.
Checa J, Blanco MN, Moreno G. 2013 – Contributions to the family *Thyridiaceae*. New data on *Sphaeria mutabilis*. Mycotaxon 125, 149–164.
Checa J, Jaklitsch WM, Blanco MN, Moreno G et al. 2015 – Two new species of *Thyronectria* from mediteranean Europe, Additions to genus. Mycologia 107, 1314–1322.
Checa J, Shoemaker RA, Umaña L. 2007 – Some new hysteriaceous fungi from Costa Rica. Mycologia 99, 285–290.
Chechi A, Stahlecker J, Dowling ME, Schnabel G. 2019 – Diversity in species composition and fungicide resistance profiles in *Colletotrichum* isolates from apples. Pesticide Biochemistry and Physiology 158, 18–24.
Cheewangkoon R, Groenewald JZ, Summerell BA, Hyde KD et al. 2009 – *Myrtaceae*, a cache of fungal biodiversity. Persoonia-Molecular Phylogeny and Evolution of Fungi 23, 55–85.
Cheewangkoon R, Groenewald JZ, Verkley GJM, Hyde KD et al. 2010 – Re-evaluation of *Cryptosporiopsis eucalypti* and *cryptosporiopsis*-like species occurring on *Eucalyptus* leaves. Fungal Diversity 44, 89–105.
Chen AJ, Frisvad JC, Sun BD, Varga J et al. 2016a – *Aspergillus* section *Nidulantes* (formerly *Emericella*): Polyphasic taxonomy, chemistry and biology. Studies in Mycology 84, 1–118.
Chen ES. 2023 – Application of the fission yeast *Schizosaccharomyces pombe* in human nutrition. FEMS Yeast Research 23, p. foac064.
Chen HP, Li J, Zhao ZZ, Li X et al. 2020a – Diterpenes with bicyclo [2.2. 2] octane moieties from the fungicolous fungus *Xylaria longipes* HFG1018. Organic and Biomolecular Chemistry 18(13), 2410–2415.
Chen HP, Zhao ZZ, Cheng GG, Zhao K et al. 2020b – Immunosuppressive nor-isopimarane diterpenes from cultures of the fungicolous fungus *Xylaria longipes* HFG1018. Journal of Natural Products 83(2), 401–412.
Chen JL, Tzean SS. 2000 – *Conioscypha taiwaniana* sp. nov. and several new records of the genus from Taiwan. Botanical Bulletin of Academia Sinica 41, 315e322.
Chen JM, Hao OJ. 1998 – Microbial chromium (VI) reduction. Critical Reviews in Environmental Science and Technology 28, 219–251.
Chen KH, Miadlikowska J, Arnold AE, U'Ren JM et al. 2015a – Phylogenetic analyses of eurotiomycetous endophytes reveal their close affinities to *Chaetothyriales*, *Eurotiales*, and a new order – *Phaeomoniellales*. Molecular Phylogenetics and Evolution 85,117–130.
Chen KY, Chen ZC. 1996 – A new species of *Thermoascus* with a *Paecilomyces* anamorph and other thermophilic *Thermoascus* species from Taiwan. Mycotaxon 60, 225–240.
Chen L, Li E, Wu W, Wang G et al. 2022a – The secondary metabolites and biosynthetic diversity from *Aspergillus ochraceus*. Frontiers in Chemistry 10, 938626.

Chen MC, Wang GJ, Kuo YH, Chiang YR et al. 2019 – Isoprenyl phenolic ethers from the termite nest-derived medicinal fungus *Xylaria fimbriata*. Journal of Food and Drug Analysis 27(1), 111–117.
Chen MY, Yao ZX, Li YC, Wu HT et al. 2016b – Decolorizing synthetic dyes with fungi screened from a *Phyllostachys violascens* stand. Journal of Zhejiang A&F University 33(3), 418–426.
Chen Q, Bakhshi M, Balci Y, Broders KD et al. 2022b – Genera of phytopathogenic fungi: GOPHY 4. Studies in Mycology 101(1), 417–564.
Chen Q, Jiang JR, Zhang GZ, Cai L et al. 2015b – Resolving the *Phoma enigma*. Studies in Mycology 82, 137–217.
Chen R, Tang JW, Li XR, Liu M et al. 2018 – Secondary metabolites from the endophytic fungus *Xylaria* sp. hg1009. Natural Products and Bioprospecting 8, 121–9.
Chen S, Morgan DP, Hasey JK, Anderson K et al. 2014 – Phylogeny, morphology, distribution, and pathogenicity of *Botryosphaeriaceae* and *Diaporthaceae* from English walnut in California. Plant Disease 98, 636–652.
Chen WH, Liang JD, Ren XX, Zhao JH et al. 2021 – Cryptic diversity of Isaria-like species in Guizhou, China. Life 11(10), 1093.
Chen WH, Zeng GP, Luo Y, Liang ZQ et al. 2017a – Morphological traits and molecular analysis for *Geomyces fujianensis* sp. nov. from China. Mycosphere 8(1), 38–43.
Chen WT, Tu ME, Sun PL. 2016c – Superficial phaeohyphomycosis caused by *Aureobasidium melanogenum* mimicking tinea nigra in an immunocompetent patient and review of published reports. Mycopathologia 181, 555–560.
Chen XM, Tang X, Du TY, Lu YZ et al. 2024 – Two new species of *Rhodoveronaea* (*Rhamphoriales*, *Ascomycota*) from terrestrial habitats in China. Phytotaxa 638(1), 49–60.
Chen Y, Liu J, Kang S, Wei D et al. 2023a – A palisade-shaped membrane reservoir is required for rapid ring cell inflation in *Drechslerella dactyloides*. Nature Communications 14, 7376.
Chen Y, Su P, Hyde K, Maharachchikumbura S. 2023b – Phylogenomics and diversification of *Sordariomycetes*. Mycosphere 14(1), 414–451.
Chen Z, Chen Y, Huang H, Yang H et al. 2017b – Cytochalasin P1, a new cytochalasin from the marine-derived fungus *Xylaria* sp. SOF11. Zeitschrift für Naturforschung C. 72, 129–32.
Chenantais JE. 1919 – Études sur les Pyrenomycètes. Bull. Soc. Mycol. Fr. 35, 46–98.
Cheng X, Li W, Zhang T. 2014 – A new species of *Phaeoisaria* from intertidal marine sediment collected in Weihai, China. Mycotaxon 127, 17–24.
Chepkirui C, Stadler M. 2017 – The genus *Diaporthe*: a rich source of diverse and bioactive metabolites. Mycological Progress 16, 477–494.
Chesnokov SV, Konoreva LA. 2022 – Checklist of lichens of Shikotan Island (Southern Kuril Islands, Russian Far East). Novitates Systematicae Plantarum non Vascularium 56(2), 413–439.
Chethana KWT, Jayawardena RS, Chen YJ, Konta S et al. 2021a – Appressorial interactions with host and their evolution. Fungal Diversity 110(1), 75–107.
Chethana KWT, Jayawardena RS, Chen YJ, Konta S et al. 2021b – Diversity and function of appressoria. Pathogens 10(6), 746.
Chevallier FF. 1826 – Flore Générale des Environs de Paris 1, 1–674.
Chew H, Jungkind D, Mah D, Raber I et al. 2010 – Post-traumatic fungal keratitis caused by *Carpoligna* sp. Cornea 29, 449–552.
Chlebická M. 2014 – *Propolis rhodoleuca* (*Leotiomycetes*, inc. sed.) compared with *P. farinosa*, *P. occulta sp. nov.* and *P. strobilina*. Nova Hedwigia 98, 491–506.
Cho SE, Lee DH, Wingfield MJ, Marincowitz S. 2020 – *Ceratocystis quercicola* sp. nov. from *Quercus variabilis* in Korea, Mycobiology 48, 245–251.
Choe YH, Kim M, Lee YK. 2021– Distinct microbial communities in adjacent rock and soil substrates on a high arctic polar desert. Frontiers in Microbiology 11, 607396.

Choi GW, Um HJ, Kim M, Kim Y et al. 2010 – Isolation and characterization of ethanol-producing *Schizosaccharomyces pombe* CHFY0201. Journal of Microbiology and Biotechnology 20(4), 828–834.
Choi J, Lee Y, Chung HS, Koo JS et al. 2011 – Subcutaneous phaeohyphomycosis caused by *Phaeoacremonium* species in a kidney transplant patient: the first case in Korea. The Korean journal of laboratory medicine 31, 201–204.
Choisy M. 1949 Catalogue des lichens de la région lyonnaise. Bulletin Mensuel Linnéenne de Lyon 18, 317–152.
Chollet-Krugler M, Nguyen TTT, Sauvager A, Thüs H et al. 2019 – Mycosporine-like amino acids (MAAs) in time-series of lichen specimens from Natural History collections. Molecules 24(6), 1070.
Chomnunti P, Bhat D, Jones EG, Chukeatirote E et al. 2012 – *Trichomeriaceae*, a new sooty mould family of *Chaetothyriales*. Fungal Diversity 56, 63–76.
Chomnunti P, Hongsanan S, Aguirre-Hudson B, Tian Q et al. 2014 – The sooty moulds. Fungal Diversity 66, 1–36.
Chomnunti P, Schoch CL, Aguirre-Hudson B, Ko-Ko TW et al. 2011 – *Capnodiaceae*. Fungal Diversity 51, 103–134.
Chooi YH, Tang Y. 2012 – Navigating the fungal polyketide chemical space: from genes to molecules. The Journal of organic chemistry 77, 9933–9953.
Chrismas N, Tindall-Jones B, Jenkins H, Harley J et al. 2023 – Metatranscriptomics reveals diversity of symbiotic interaction and mechanisms of carbon exchange in the marine cyanolichen *Lichina pygmaea*. New Phytologist 41(5), 2243–2257.
Christita M, Auzane A, Overmyer K. 2023 – Witches' broom disease of birch. In F.O. Asiegbu and A. Kovalchuk (Eds.), Forest Microbiology, Vol. 3 (pp. 121-136) Academic Press.
Christita M, Auzane A, Wang K, Sipilä T et al. 2021 – A *Taphrina* strain infecting the model plant *Arabidopsis thaliana*. Preprint. bioRxiv.
Christita M, Sipilä TP, Auzane A, Overmyer K. 2022 – Distinct *Taphrina* strains from the phyllosphere of birch exhibiting a range of witches' broom disease symptoms. Environmental Microbiology 24(8), 3549–3564.
Chu H, Wang C, Li Z, Wang H et al. 2019 – The dark septate endophytes and ectomycorrhizal fungi effect on *Pinus tabulaeformis* Carr. seedling growth and their potential effects to pine wilt disease resistance. Forests 10, 140.
Chu Y, Alias SA, Rizman-idid M, Guo SY et al. 2015 – A molecular reappraisal of *Nimbospora* (*Halosphaeriaceae*, *Microascales*) and a new genus *Ebullia* for *N. octonae*. Mycoscience 56, 34–41.
Chuaseeharonnachai C, Somrithipol S, Suetrong S, Klaysuban A et al. 2017 – *Conioscypha nakagirii*, a new species from naturally submerged wood in Thailand based on morphological and molecular data. Mycoscience 58, 424–431.
Chuaseeharonnachai C, Suetrong S, Nuankaew S, Somrithipol S et al. 2020 – *Synnematotriadelphia* gen. nov. (*S. stilboidea* comb. nov. and *S. synnematofera* comb. nov.) and *Triadelphia hexaformispora* sp. nov. in the family *Triadelphiaceae*. Mycological Progress 19(2), 127−37.
Chun J, Hartung HP. 2010 – Mechanism of action of oral fingolimod (FTY720) in multiple sclerosis. Clinical Neuropharmacology 33(2), 91–101.
Chung D, Kim H, Choi HS. 2019 – Fungi in salterns. Journal of Microbiology 57, 717–724.
Ciferri R, Tomaselli R. 1953 – Specierum fungorum qui in lichenibus insunt descriptiones. Atti dell'Istituto Botanico della Università e Laboratorio Crittogamico di Pavia 10(2), 253–295.
Ciferri R. 1957 – *Trichocoma paradoxum* in Santo Domingo and the order *Onygenales*. Atti Ist. Bot. Univ. Pavia Ser 5 14 (1–3), 237–240.
Ciferri R. 1958 – Manuale di micologia medica. edn 2. Pavia, Cortina 1–178.
Cissé OH, Ma L, Dekker JP, Khil PP et al. 2021 – Genomic insights into the host specific adaptation of the *Pneumocystis* genus. Communications Biology 4, 305.

Clauzade G, Roux C. 1985 – Likenoj de Okcidenta Eŭropo. Ilustrita determinlibro. Bulletin de la Société Botanique de France. Centre-Ouest 7, 1– 829.
Clements FE, Shear CL. 1931 – Genera of fungi, edn 2. i–vii, 58 plates. H.W. Wilson Company, USA, New York 496.
Clemmensen KE, Finlay RD, Dahlberg A, Stenlid J et al. 2015 – Carbon sequestration is related to mycorrhizal fungal community shifts during long-term succession in boreal forests. New Phytologist 205, 1525–1536.
Clerc P. 2022 – Lichens (Ascomycètes lichénisés) nouveaux ou intéressants pour la Suisse et/ou le canton de Genève -3. Saussurea 51, 193–208.
Čmoková A, Kolařík M, Dobiáš R, Hoyer LL et al. 2020 – Resolving the taxonomy of emerging zoonotic pathogens in the *Trichophyton benhamiae* complex. Fungal Diversity 104(1), 333–387.
Cohen PA. 2002 – Halogenated anthraquinones from the rare southern Illinois lichen *Lasallia papulosa*. The Lichenologist 34(6), 521–525.
Coiffard C, Gomez B, Daviero-Gomez V, Dilcher DL. 2012 – Rise to dominance of angiosperm pioneers in European Cretaceous environments. Proc Natl Acad Sci USA 109, 20955–20959.
Contet-Audonneau N, Schmutz JL, Basile AM, Bièvre C et al. 1997 – A new agent of onychomycosis in the elderly: *Onychocola canadensis*. European journal of dermatology 7, 115–117.
Cooke MC. 1883 – Saccardo's Sylloge Fungorum. Grevillea 12(61), 34–35.
Cooke MC. 1885 – Synopsis pyrenomycetum. Grevillea 13, 61–72.
Cooke MC. 1891 – Australian fungi. Grevillea 20, 4–7.
Cooke MC. 1892 – Handbook of Australian fungi. London: Williams & Norgate.
Cooke RC, Rayner ADM. 1984 – Ecology of saprotrophic fungi. London; New York: Longman, 415.
Cookson IC. 1947 – Fossil fungi from Tertiary de- posits in the Southern Hemisphere. Proceedings of the Linnean Society of New South Wales 72, 207–214.
Copeland CA, Harper RW, Brazee NJ, Bowlick FJ. 2023 – A review of Dutch elm disease and new prospects for *Ulmus americana* in the urban environment. Arboricultural Journal 45, 3–29.
Coppins BJ, James PW, Hawksworth DL. 1992 – New species and combinations in the lichen flora of Great Britain and Ireland. The Lichenologist 24, 351–369.
Coppins BJ. 1987 – The genus *Ramonia* in the british isles. The Lichenologist 19, 409–417.
Coppins BJ. 2002 – Checklist of british and irish Lichens. British Lichen Society, London.
Coppins BJ. 2009 – *Pycnora* Hafellner. In: The Lichens of Great Britain and Ireland (C. W. Smith, A. Aptroot, B. J. Coppins, A. Fletcher, O. L. Gilbert, P. W. James, P. A. Wolseley, eds). British Lichen Society, London, UK.
Corda AC. 1838a – Icones Fungorum hucusque Cognitorum 2: i-viii, 1-43. J.G. Calve [Fridericum Ehrlich], Prague, Czechoslovakia.
Corda ACJ. 1831 – Die Pilze Deutschlands. In: Sturm J (ed) Deutschlands Flora in Abbildungen nach der Natur mit Beschreibungen, Sturm, Nurnberg 12, 33–64.
Corda ACJ. 1842a – Abbildungen der Pilze und Schwaemme. Icones Fungorum, Hucusque Cognitorum 5, 34.
Corda ACJ. 1842b – Icones fungorum hucusque cognitorum. Icones fungorum hucusque cognitorum 2. Elsevier.
Corda ACJ. 1854 – Icones fungorum hucusque cognitorum 6, 1–91.
Corda CI. 1838b – Icones Fungorum Hucusque Cognitorum II, 35.
Corlett M. 1986 – *Pyxidiophora lundqvistii* n. sp. (*Hypomycetales*, *Ascomycetes*). Canadian journal of botany 64(4), 805–807.
Correa Y, Cabanillas B, Jullian V, Álvarez D et al. 2019 – Identification and characterization of compounds from *Chrysosporium multifidum*, a fungus with moderate antimicrobial activity isolated from *Hermetia illucens* gut microbiota. PLoS ONE 14(12), e0218837.
Costa EO, Gandra CR, Pires MF, Couthino SD et al. 1993 – Survey of bovine mycotic mastitis in dairy herds in the State of São Paulo, Brazil. Mycopathologia 124, 13–17.

Courty PE, Pritsch K, Schloter M, Hartmann A et al. 2005 – Activity profiling of ectomycorrhiza communities in two forest soils using multiple enzymatic tests. New Phytologist 167, 309–319.
Cox J, Stone T, Ryan P, Burkle J et al. 2022 – Residential bacteria and fungi identified by high-throughput sequencing and childhood respiratory health. Environmental Research 204, 112377.
Cox RJ. 2007 – Polyketides, proteins and genes in fungi: programmed nano-machines begin to reveal their secrets. Organic & biomolecular chemistry 5, 2010–2026.
Crawford SD. 2015 – Lichens used in traditional medicine. In: Ranković, B. (eds) Lichen Secondary Metabolites. Springer, Cham.
Crittenden PD, Llimona X, Sancho LG. 2007 – Lichenized unicellular cyanobacteria fix nitrogen in the light. Botany 85(10), 1003–1006.
Crous PW, Begoude BAD, Boers J, Braun U et al. 2022a – New and interesting fungi. 5. Fungal Systematics and Evolution 10, 19–90.
Crous PW, Bishop-Hurley SL, Shivas RG, Cowan DA et al. 2022b – Fungal planet description sheets: 1436-1477. Persoonia 49, 261–350.
Crous PW, Boers J, Holdom D, Osieck ER et al. 2022c – Fungal planet description sheets: 1383-1435. Persoonia 48, 261–371.
Crous PW, Braun U, Groenewald JZ. 2007a – *Mycosphaerella* is polyphyletic. Studies in Mycology 58, 1–32.
Crous PW, Braun U, Hunter GC, Wingfield MJ et al. 2013a. Phylogenetic lineages in *Pseudocercospora*. Studies in Mycology 75, 37–114.
Crous PW, Braun U, McDonald BA, Lennox CL et al. 2021a – Redefining genera of cereal pathogens: *Oculimacula*, *Rhynchosporium* and *Spermospora*. Fungal systematics and evolution 7(1), 67–98.
Crous PW, Braun U, Schubert K, Groenewald JZ. 2007b – Delimiting *Cladosporium* from morphologically similar genera. Studies in Mycology 58(1), 33–56.
Crous PW, Braun U, Wingfield MJ, Wood AR et al. 2009a – Phylogeny and taxonomy of obscure genera of microfungi. Persoonia 22, 139–161.
Crous PW, Carris LM, Giraldo A, Groenewald JZ et al. 2015a – The genera of fungi - fixing the application of the type species of generic names – G2: *Allantophomopsis*, *Latorua*, *Macrodiplodiopsis*, *Macrohilum*, *Milospium*, *Protostegia*, *Pyricularia*, *Robillarda*, *Rotula*, *Septoriella*, *Torula*, and *Wojnowicia*. International Mycological Association Fungus 6, 163–198.
Crous PW, Costa MM, Kandemir H, Vermaas M et al. 2023 – Fungal planet description sheets: 1550–1613. Persoonia: Molecular Phylogeny and Evolution of Fungi 51, 280.
Crous PW, Cowan DA, Maggs-Kölling G, Yilmaz N et al. 2020a – Fungal planet description sheets: 1112–1181. Persoonia: Molecular Phylogeny and Evolution of Fungi 45, 251.
Crous PW, Cowan DA, Maggs-Kölling G, Yilmaz N et al. 2021b – Fungal planet description sheets: 1182–1283. Persoonia: Molecular Phylogeny and Evolution of Fungi 46, 313–528.
Crous PW, Gams W, Wingfield MJ, Van Wyk PS. 1996 – *Phaeoacremonium* gen. nov. associated with wilt and decline diseases of woody hosts and human infections. Mycologia 88, 786–796.
Crous PW, Gams W. 2000 – *Phaeomoniella chlamydospora* gen. et comb. nov., a causal organism of Petri grapevine decline and esca. Phytopathologia Mediterranea 39, 112–118.
Crous PW, Groenewald JZ, Lombard L, Wingfield MJ. 2012a – *Homortomyces* gen. nov., a new dothidealean pycnidial fungus from the Cradle of Humankind. IMA fungus 3(2), 109–115.
Crous PW, Groenewald JZ, Shivas RG, Edwards J et al. 2011a – Fungal planet description sheets: 69–91. Persoonia 26, 108–156.
Crous PW, Groenewald JZ, Summerell BA, Wingfield BD et al. 2009b – Co-occurring species of *Teratosphaeria* on *Eucalyptus*. Persoonia 22, 38–48.

Crous PW, Groenewald JZ, Wingfield MJ, Aptroot A. 2003 – The value of ascospore septation in separating *Mycosphaerella* from *Sphaerulina* in the *Dothideales*: a Saccardoan myth? Sydowia 55, 136–152.
Crous PW, Groenewald JZ. 2005 – Hosts, species and genotypes: opinions versus data. Australasian Plant Pathology 34, 463–470.
Crous PW, Groenewald JZ. 2017 – The Genera of Fungi – G 4: *Camarosporium* and *Dothiora*. IMA Fungus 8, 131–152.
Crous PW, Hernández-Restrepo M, Schumacher RK, Cowan DA et al. 2021c – New and interesting fungi. 4. Fungal Systematics and Evolution 7, 255–343.
Crous PW, Kendrick B, Alfenas AC. 1997 – New species of hyphomycetes associated with *Eucalyptus*. South African Journal of Botany 63, 286–290.
Crous PW, Lori CM, Giraldo A, Groenewald JZ et al. 2015b – The genera of fungi: fixing the application of the type species of generic names—G 2: *Allantophomopsis*, *Latorua*, *Macrodiplodiopsis*, *Macrohilum*, *Milospium*, *Protostegia*, *Pyricularia*, *Robillarda*, *Rotula*, *Septoriella*, *Torula*, and *Wojnowicia*. IMA Fungus 1, 163–198.
Crous PW, Luangsa-Ard J, Wingfield M, Carnegie A et al. 2018a – Fungal planet description sheets: 785–867. Persoonia: Molecular Phylogeny and Evolution of Fungi 41, 238–417.
Crous PW, Mohammed C, Glen M, Verkley GJ et al. 2007c – *Eucalyptus* microfungi known from culture. 3. *Eucasphaeria* and *Sympoventuria* genera nova, and new species of *Furcaspora*, *Harknessia*, *Heteroconium* and *Phacidiella*. Fungal Diversity 25, 19–36.
Crous PW, Osieck ER, Jurjevic Z, Boers J et al. 2021d – Fungal planet description sheets: 1294-1382. Persoonia 47, 178–374.
Crous PW, Quaedvlieg W, Hansen K, Hawksworth DL et al. 2014a – *Phacidium* and *Ceuthospora* (*Phacidiaceae*) are congeneric: taxonomic and nomenclatural implications. IMA Fungus 5, 173–193.
Crous PW, Rossman AY, Aime MC, Allen WC et al. 2021e – Names of phytopathogenic fungi: A Practical Guide'. Phytopathology 111, 1500–1508.
Crous PW, Schoch CL, Hyde KD, Wood AR et al. 2009c – Phylogenetic lineages in the *Capnodiales*. Studies in Mycology 64, 17–47.
Crous PW, Schubert K, Braun U, Hoog De GS et al. 2007d – Opportunistic, human-pathogenic species in the *Herpotrichiellaceae* are phenotypically similar to saprobic or phytopathogenic species in the *Venturiaceae*. Studies in Mycology 58, 185–217.
Crous PW, Schumacher RK, Akulov A, Thangavel R et al. 2019a – New and interesting fungi 2. Fungal Systematics and Evolution 3, 57–134.
Crous PW, Schumacher RK, Wingfield MJ, Lombard L et al. 2015c – Fungal systematics and evolution: FUSE 1. Sydowia 67, 81–118.
Crous PW, Schumacher RK, Wood AR, Groenewald JZ. 2019b – The genera of fungi – G5: *Arthrinium*, *Ceratosphaeria*, *Dimerosporiopsis*, *Hormodochis*, *Lecanostictopsis*, *Lembosina*, *Neomelanconium*, *Phragmotrichum*, *Pseudomelanconium*, *Rutola*, and *Trullula*. FUSE 5, 77–98.
Crous PW, Schumacher RK, Wood AR, Groenewald JZ. 2020b – The genera of fungi–G5: *Arthrinium*, *Ceratosphaeria*, *Dimerosporiopsis*, *Hormodochis*, *Lecanostictopsis*, *Lembosina*, *Neomelanconium*, *Phragmotrichum*, *Pseudomelanconium*, *Rutola*, and *Trullula*. Fungal Systematics and Evolution 5(1), 77–98.
Crous PW, Shivas RG, Quaedvlieg W, van der Bank M et al. 2014c – Fungal planet description sheets: 214–280. Persoonia 32, 184–306.
Crous PW, Summerell BA, Alfenas AC, Edwards J et al. 2012b – Genera of diaporthalean coelomycetes associated with leaf spots of tree hosts. Persoonia 28, 66–75.
Crous PW, Summerell BA, Carnegie AJ, Wingfield MJ et al. 2009d – Novel species of *Mycosphaerellaceae* and *Teratosphaeriaceae*. Persoonia: Molecular Phylogeny and Evolution of Fungi 23(1), 119–46.

Crous PW, Summerell BA, Carnegie AJ, Wingfield MJ. 2009e – Unravelling *Mycosphaerella*: do you believe in genera? Persoonia 23, 99–118.
Crous PW, Summerell BA, Shivas RG, Burgess TI et al. 2012c – Fungal Planet description sheets: 107–127. Persoonia 28, 138–182.
Crous PW, Summerell BA, Shivas RG, Romberg M et al. 2011b – Fungal Planet description sheets: 92-106. Persoonia 27, 130–162.
Crous PW, Summerell BA, Swart L, Denman S et al. 2011c – Fungal pathogens of *Proteaceae*. Persoonia: Molecular Phylogeny and Evolution of Fungi 27, 20–45.
Crous PW, Van der Linde EJ. 1993 – New and interesting fungi. 11. Eucalyptus leaf fungi. South African Journal of Botany 59, 300–304.
Crous PW, Verkley GJ, Groenewald JZ. 2006 – *Eucalyptus* microfungi known from culture. 1. *Cladoriella* and *Fulvoflamma* genera nova, with notes on some other poorly known taxa. Studies in Mycology 55(1), 53–63.
Crous PW, Verkley GJM, Groenewald JZ, Houbraken J (eds). 2019c – Fungal Biodiversity. Westerdijk Laboratory Manual Series 1, 1–425. Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands.
Crous PW, Verkley GJM. 2009 – *Xenocylindrosporium*. Persoonia 23, 200–201.
Crous PW, Wingfield MJ, Alfeans AC, Silveira SF. 1994 – *Cylindrocladium naviculatum* sp. nov., and two new vesiculate hyphomycete genera, *Falcocladium* and *Vesicladiella*. Mycotaxon 50, 441–458.
Crous PW, Wingfield MJ, Burgess TI, Carnegie AJ et al. 2017a – Fungal planet description sheets, 625–715. Persoonia 39, 270–467.
Crous PW, Wingfield MJ, Burgess TI, Hardy G et al. 2017b – Fungal planet description sheets: 558–624. Persoonia 38, 240–384.
Crous PW, Wingfield MJ, Burgess TI, Hardy GE et al. 2016a – Fungal planet description sheets: 469–557. Persoonia: Molecular Phylogeny and Evolution of Fungi 37, 218–403.
Crous PW, Wingfield MJ, Burgess TI, Hardy GESJ et al. 2018b – Fungal Planet description sheets: 716–784. Persoonia-Molecular Phylogeny and Evolution of Fungi 40, 240–393.
Crous PW, Wingfield MJ, Cheewangkoon R, Carnegie AJ et al. 2019d – Foliar pathogens of eucalypts. Studies In Mycology 94, 125–298.
Crous PW, Wingfield MJ, Chooi Y-H, Gilchrist CLM et al. 2020c – Fungal planet description sheets: 1042–1111. Persoonia 44, 301–459.
Crous PW, Wingfield MJ, Guarro J, Cheewangkoon R et al. 2013b – Fungal planet description sheets: 154-213. Persoonia 31, 188–296.
Crous PW, Wingfield MJ, Guarro J, Hernández-Restrepo M et al. 2015d – Fungal planet description sheets: 320–370. Persoonia 34, 167–266.
Crous PW, Wingfield MJ, Kendrick WB. 1995 – Foliicolous dematiaceous hyphomycetes from *Syzygium cordatum*. Canadian Journal of Botany 73, 224–234.
Crous PW, Wingfield MJ, Le Roux JJ, Richardson DM et al. 2015f – Fungal planet description sheets: 371–399. Persoonia 35, 264–327.
Crous PW, Wingfield MJ, Lombard L, Roets F et al. 2019e – Fungal planet description sheets: 951–1041. Persoonia: Molecular Phylogeny and Evolution of Fungi 43, 223–425.
Crous PW, Wingfield MJ, Richardson D, Leroux J et al. 2016b – Fungal planet description sheets: 400–468. Persoonia: Molecular Phylogeny and Evolution of Fungi 36, 316–458.
Crous PW, Wingfield MJ, Schumacher RK, Akulov A et al. 2020d – New and interesting fungi. 3. Fungal Systematics and Evolution 6, 157.
Crous PW, Wingfield MJ, Schumacher RK, Summerell BA et al. 2014b – Fungal planet description sheets: 281–319. Persoonia: Molecular Phylogeny and Evolution of Fungi 33(1), 212–289.
Crous PW, Wingfield MJ. 1994 – *Sporendocladia fumosa* and *Lauriomyces bellulus* sp. nov. from *Castanea cupules* in Switzerland. Sydowia 46, 193–203.
Crous PW. 1998 – *Mycosphaerella* spp. and their anamorphs associated with leaf spot diseases of *Eucalyptus*. Mycologia Memoir 21, 1–170. APS Press, MN, USA.

Crous PW. 2009 – Taxonomy and phylogeny of the genus *Mycosphaerella* and its anamorphs. Fungal Diversity 38, 1–24.
Crowther TW, Boddy L, Jones TH. 2012 – Functional and ecological consequences of saprotrophic fungus–grazer interactions. The ISME Journal 6, 1992–2001.
Cui X, Hao Z, Chen M, Song S, Zhang J, Li Y, Li J, Liu Y, Luo L. 2024 – Identification and pathogenicity of pestalotioid species on *Alpinia oxyphylla* in Hainan Province, China. Journal of Fungi 10, 371.
Culberson WL, Culberson CF. 1970 – A phylogenetic view of chemical evolution in the lichens. Bryologist 73, 1–31.
Cummings DJ, Belcour L, Grandchamp C. 1979 – Mitochondrial DNA from *Podospora anserina*. Molecular and General Genetics 171, 229–238.
Cuny D, Denayer FO, de Foucault B, Schumacker R et al. 2004 – Patterns of metal soil contamination and changes in terrestrial cryptogamic communities. Environmental Pollution 129(2), 289–97.
Currah RS. 1985 – Taxonomy of the *Onygenales*: *Arthrodermataceae*, *Gymnoascaceae*, *Myxotrichaceae* and *Onygenaceae*. Mycotaxon 24, 1–216.
Cushion MT, Keely SP, Stringer JR. 2004 – Molecular and phenotypic description of *Pneumocystis wakefieldiae* sp. nov., a new species in rats. Mycologia 96, 429–438.
Cushion MT, Keely SP, Stringer JR. 2005 – Validation of the name *Pneumocystis wakefieldiae.* Mycologia 97(1), 268.
Cushion MT, Keely SP. 2011 – *Pneumocystis* Delanoe & Delanoe (1912). In The Yeasts (pp. 709-717). Elsevier.
Cushion MT, Smulian AG, Slaven BE, Sesterhenn T et al. 2007 – Transcriptome of *Pneumocystis carinii* during fulminate infection: carbohydrate metabolism and the concept of a compatible parasite. PLoS ONE 2, e423.
Cushion MT. 2010 – Are members of the fungal genus *Pneumocystis* (a) commensals; (b) opportunists; (c) pathogens; or (d) all of the above? PLOS Pathogens 23, e1001009.
Czarnota P, Hernik E. 2014 – Some peltigericolous microlichens from Southern Poland. Acta Botanica Croatica 73, 159–170.
D'Agostino PM. 2023 – Highlights of biosynthetic enzymes and natural products from symbiotic cyanobacteria. Natural Product Reports 40, 1701–1717.
da Luz Morales M, Almeida LF, de Souza Ladeira Àzar RI, Guimarães VM et al. 2021 – First report on the enzymatic profile of *Kretzschmaria zonata*. 3 Biotech 11, 1–6.
da Silva Brandão M, Silva Abreu L, Geris R. 2019 – *Phialomyces macrosporus*: Chemical constituents, antimicrobial activity and complete NMR Assignments for the 7,7'-Biphyscion. Chemistry & Biodiversity 16(9), e1900353.
da Silva Cáceres ME, Aptroot A. 2016 – First inventory of lichens from the Brazilian Amazon in Amapá State. The Bryologist 119(3), 250–265.
da Silva Cáceres ME, Lücking R, Schumm F, Aptroot A. 2020 – A lichenized family yields another renegade lineage: *Papilionovela albothallina* is the first non-lichenized, saprobic member of *Graphidaceae* subfam. *Graphidoideae*. The Bryologist 123(2), 144–154.
Da Silva TH, Silva DA, de Oliveira FS, Schaefer CE et al. 2020 – Diversity, distribution, and ecology of viable fungi in permafrost and active layer of Maritime Antarctica. Extremophiles 24, 565–576.
Daengrot C, Rukachaisirikul V, Tansakul C, Thongpanchang T et al. 2015 – Eremophilane sesquiterpenes and diphenyl thioethers from the soil fungus *Penicillium copticola* PSU-RSPG138. Journal of Natural Products 78, 615–622.
Dahlkild Å, Källersjö M, Lohtander K, Tehler A. 2001 – Photobiont diversity in the *Physciaceae* (*Lecanorales*). The bryologist 104(4), 527–536.
Dai DQ, Phookamsak R, Wijayawardene NN, Li WJ et al. 2017 – Bambusicolous fungi. Fungal Diversity 82, 1–105.

Dai DQ, Tang LZ, Liu C, Wang HB et al. 2018 – Studies on *Parmulariaceae* I. A phylogeny based on available sequence data; introducing *Parmulariales* ord. nov., and *Hemigraphaceae*, *Melaspileellaceae* and *Stictographaceae* fam. nov. Phytotaxa 369, 63–79.
Dai DQ, Wijayawardene NN, Tang LZ, Tian Y et al. 2020 – Studies on *Parmulariaceae* II. re-examination of *Hysterostomella*, *Mintera*, *Rhipidocarpon* and *Viegasella*. Phytotaxa 458, 231–241.
Dai RQ, Lan JL, Chen WH, Li XM et al. 1989 – Research on *Paecilomyces hepiali* Chen et Dai, sp. nov. Acta Agriculturae Universitatis Pekinensis 15(2), 221–224.
Dal Grande F, Jamilloux V, Choisne N, Calchera A et al. 2022 – Transposable elements in the genome of the lichen-forming fungus *Umbilicaria pustulata* and their distribution in different climate zones along elevation. Biology 11(1), 24.
Dal Grande F, Meiser A, Greshake Tzovaras B, Otte J et al. 2018 – The draft genome of the lichen-forming fungus *Lasallia hispanica* (Frey) Sancho & A. Crespo. The Lichenologist 50(3), 329–340.
Daly DC, Millozza A. 2007 – "Lost" plant collections from the Amazon 1: the 1899 expedition of Dr. Luigi Buscalioni. Taxon 56, 185–199.
Damm U, Crous PW, Fourie PH. 2008a– A fissitunicate ascus mechanism in the *Calosphaeriaceae*, and novel species of Jattaea and *Calosphaeria* on *Prunus* wood. Persoonia 20, 39–52.
Damm U, Fourie PH, Crous PW. 2010 – *Coniochaeta* (*Lecythophora*), *Collophora* gen. nov. and *Phaeomoniella* species associated with wood necroses of Prunus trees. Persoonia 24, 60–80.
Damm U, Mostert L, Crous PW, Fourie PH. 2008b – Novel *Phaeoacremonium* species associated with necrotic wood of Prunus trees. Persoonia 20, 87–102.
Damm U, Sato T, Alizadeh A, Groenewald JZ et al. 2019 – The *Colletotrichum dracaenophilum*, *C. magnum* and *C. orchidearum* species complexes. Studies in mycology 92,1–46.
Danesi P, Corr`o M, Falcaro C, Carminato A et al. 2019 – Molecular detection of *Pneumocystis* in the lungs of cats. Medical Mycology 57, 813–824.
Danesi P, da Rold G, Rizzoli A, Hauffe HC et al. 2016 – Barcoding markers for *Pneumocystis* species in wildlife. Fungal Biology 120, 191–206.
Dang CK, Gessner MO, Chauvet E. 2007 – Influence of conidial traits and leaf structure on attachment success of aquatic hyphomycetes on leaf litter. Mycologia 99(1), 24–32.
Daranagama DA, Camporesi E, Tian Q, Liu X et al. 2015 – *Anthostomella* is polyphyletic comprising several genera in *Xylariaceae*. Fungal Diversity 73, 203–238.
Daranagama DA, Hyde KD, Sir EB, Thambugala KM et al. 2018 – Towards a natural classification and backbone tree for *Graphostromataceae*, *Hypoxylaceae*, *Lopadostomataceae* and *Xylariaceae*. Fungal Diversity 88(1), 1–165.
Daranagama DA, Tian Q, Liu XZ, Hyde KD. 2017 – Towards a natural classification of *Amplistromataceae*. Mycosphere 8, 1392–1402.
Darker GD. 1932 – The *Hypodermataceae* of conifers. Contrib Arnold Arboretum 1, 1−131.
Darker GD. 1963 – A new genus of *Phacidiaceae* on *Picea mariana.* Canadian Journal of Botany 41, 1389–1393.
Darker GD. 1967 – A revision of the genera of the *Hypodermataceae*. Canadian Journal of Botany 45, 1399−1444.
Darmostuk V, Etayo J, Rodriguez-Flakus P, Kukwa M et al. 2024 – A phylogenetic assessment of neglected habitats revealed a novel lineage in *Hypocreales*: a case of tropical lichen-inhabiting fungi. IMC12 Maastricht, Netherlands.
Darmostuk VV. 2021 – Lichenicolous fungi on *Verrucaria* s. lat. in Ukraine with the description of *Zwackhiomyces khodosovtsevii* sp. nov. and a key to the lichenicolous fungi on *Verrucaria* s. lat. Botanica Serbica 45(2), 293–301.
Dasgupta D, Baishkhiyar A, Chakraborty N. 2022 – A world review on the genus *Trichoglossum* (*Geoglossales*, *Ascomycota*). Kavaka 58(1), 33–39.
David JC, Hawksworth DL. 1991 – Validation of six family names of lichenized *Ascomycetes*. Systema Ascomycetum 10, 1318.

Davidson RW. 1942 – Some additional species of *Ceratostomella* in the United States. Mycologia 34(6), 650–662.
Davies JT, Barraclough TG, Chase MW, Soltis PS et al. 2004 – Darwin's abominable mystery: Insights from a supertree of the angiosperms. Proceedings of the National Academy of Sciences 101, 1904–1909.
Davis TS, Crippen TL, Hofstetter RW, Tomberlin JK. 2013 – Microbial volatile emissions as insect semiochemicals. Journal of chemical ecology 39, 840–59.
Davolos D, Pietrangeli B, Persiani AM, Maggi O. 2019 – *Victoriomyces antarcticus* gen. nov., sp. nov., a distinct evolutionary lineage of the *Cephalothecaceae* (*Ascomycota*) based on sequence-based phylogeny and morphology. International Journal of Systematic and Evolutionary Microbiology 69(4), 1099–1110.
Davydov EA, Blum OB, Kashevarov GP, Grakhov VP. 2019 – *Umbilicaria subpolyphylla* Oxner the correct name for *U. iberica* Sancho et *Krzewicka* and its bipolar distribution pattern. The Lichenologist 51(3), 205–220.
Davydov EA, Konoreva LA, Andreev MP, Zhdanov IS et al. 2012 – Additions to the lichen biota of Altai Mountains. IV. Turczaninowia 15(3), 23–36.
Davydov EA, Masson D. 2022 – *Umbilicaria meizospora* comb. nov. – a southwestern European endemic species of the subgenus *Papillophora*. The Lichenologist 54(1), 1–12.
Davydov EA, Peršoh D, Rambold G. 2010 – The systematic position of *Lasallia caroliniana* (Tuck.) Davydov, Peršoh & Rambold comb. nova and considerations on the generic concept of *Lasallia* (*Umbilicariaceae*, *Ascomycota*). Mycological Progress 9, 261–266.
Davydov EA, Peršoh D, Rambold G. 2017 – *Umbilicariaceae* (lichenized *Ascomycota*) – trait evolution and a new generic concept. Taxon 66(6): 1282–1303.
Davydov EA, Wei JC. 2009 – *Boreoplaca ultrafrigida* (*Umbilicariales*), the correct name for *Rhizoplacopsis weichingii*. Mycotaxon 108, 301–305.
Davydov EA, Yakovchenko LS, Urbanavichene I, Konoreva Let al. 2020. *Umbilicaria orientalis* – a new species of *Umbilicaria* subg. *Papillophora* with an East Asian distribution: morphological delimitation and molecular evidence. The Lichenologist 52(5), 353–364.
Davydov EA. 2007 – Approaches to a classification of the family *Umbilicariaceae* (lichenised *Ascomycota*) by anatomical and morphological characters. Turczaninowia 10 (3-4), 51–57.
Davydov EA. 2022 – *Umbilicaria platyrhiza* – a new Mediterranean endemic species of the subgenus *Papillophora* (*Umbilicariaceae*, lichenized *Ascomycota*). Phytotaxa 533 (2), 143–148.
Dayarathne MC, Jones EB, Maharachchikumbura SS, Devadatha B et al. 2020 – Morpho-molecular characterization of microfungi associated with marine based habitats. Mycosphere 11(1), 1–188.
Dayarathne MC, Jones EBG, Rämä T, Hagestad OC et al. 2025 – Towards an integrative morpho-molecular classification of the *Lulworthiomycetidae*. Mycosphere 16(1), 79–168.
Dayarathne MC, Maharachchikumbura SS, Jones EG, Dong W et al. 2019 – Phylogenetic revision of *Savoryellaceae* and evidence for its ranking as a subclass. Frontiers in Microbiology 10, 840.
Dayarathne MC, Maharachchikumbura SSN, Jones EBG, Goonasekara ID et al. 2017 – *Neophyllachora* gen nov. (*Phyllachorales*), three new species of *Phyllachora* from *Poaceae* and resurrection of *Polystigmataceae* (*Xylariales*). Mycosphere 8(10), 1598–1625.
De Almeida DAC, Gusmao LFP, Miller AN. 2014 – A new genus and three new species of Hysteriaceous *Ascomycetes* from the semiarid region of Brazil. Phytotaxa 176 (1), 298–308.
de Bary A. 1884 – Vergleichende Morphologie und Biologie der Pilze, Mycetozoen, und Bacterien. Engelmann, Leipzig.
De Beer ZW, Duong TA, Barnes I, Wingfield BD et al. 2014 – Redefining *Ceratocystis* and allied genera. Studies in Mycology 79, 187–219.
De Beer ZW, Duong TA, Wingfield MJ. 2016 – The divorce of *Sporothrix* and *Ophiostoma*: solution to a problematic relationship. Studies in mycology 83, 165–191.

De Beer ZW, Procter M, Wingfield MJ, Marincowitz S et al. 2022 – Generic boundaries in the *Ophiostomatales* reconsidered and revised. Studies in Mycology 101, 57–120.
De Beer ZW, Seifert KA, Wingfield MJ. 2013a – A nomenclator for ophiostomatoid genera and species in the *Ophiostomatales* and *Microascales*. CBS Biodiversity Series 12, 245–322.
De Beer ZW, Seifert KA, Wingfield MJ. 2013b – The ophiostomatoid fungi: their dual position in the *Sordariomycetes*. CBS Biodiversity Series 12, 1–9.
De Beer ZW, Wingfield MJ. 2013 – Emerging lineages in the *Ophiostomatales*. The ophiostomatoid fungi: expanding frontiers 21–46.
de Carvalho CR, Maia MQ, Sobral M, Pereira GMD et al. 2021 – Diversity and antimicrobial activity of culturable endophytic fungi associated with the neotropical ethnomedicinal plants *Copaifera langsdorffii* and *Copaifera pubiflora*. South African Journal of Botany 142, 305–315.
de Groot MD, Dumolein I, Hiller T, Sándor AD et al. 2020 – On the fly: tritrophic associations of bats, bat flies, and fungi. Journal of Fungi 6(4), 361.
De Gruyter J, Woudenberg JHC, Aveskamp AA, Verkley GJM et al. 2013 – Redisposition of *Phoma*-like anamorphs in *Pleosporales*. Studies in Mycology 75, 1–36.
De Hoog GD, Zalar P, Urzi C, De Leo F et al. 1999 – Relationships of dothideaceous black yeasts and meristematic fungi based on 5.8S and ITS2rDNA sequence comparison. Studies in Mycology 43, 31–37.
de Hoog GS, Ahmed SA, Danesi P, Guillot J et al. 2018 – Distribution of pathogens and outbreak fungi in the fungal kingdom. In: Seyedmousavi S, de Hoog GS, Guillot J, Verweij PE (eds) Emerging and epizootic fungal infections in animals. Springer International Publishing, New York.
De Hoog GS, Beguin H, Batenburg-Van de Vegte WH. 1997 – *Phaeotheca triangularis*, a new meristematic black yeast from a humidifier. Antonie van Leeuwenhoek 71, 289–295.
De Hoog GS, Gottlich E, Platas G, Genilloud O et al. 2005 – Evolution, taxonomy and ecology of the genus *Thelebolus* in Antarctica. Studies in Mycology 51, 33–76.
De Hoog GS, Guarro J, Gené J, Figueras MJ. 2011a – Atlas of clinical fungi. CD-ROM version 3.1. CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands.
De Hoog GS, Guarro J, Gené J, Figueras MJ. 2017 – Atlas of clinical fungi. Electronic version 4.1.4. Westerdijk Fungal Biodiversity Institute / Universitat Rovira i Virgili, Utrecht / Reus.
De Hoog GS, Guarro J, Gene´ J, Figueras MJ (Eds). 2000 – Atlas of Clinical Fungi, 2nd edn. Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands and Universitat Rovira i Virgili Reus, Spain
de Hoog GS, Vicente VA, Caligiorne R, Kantarcioglu S et al. 2003 – Species diversity and polymorphism in the *Exophiala spinifera* clade containing opportunistic black yeast-like fungi. Journal of Clinical Microbiology 41, 4767–4778.
de Hoog GS, Vicente VA, Najafzadeh M, Harrak M et al. 2011b – Waterborne *Exophiala* species causing disease in cold-blooded animals. Persoonia: Molecular Phylogeny and Evolution of Fungi 27, 46.
De Kesel A. 1995 – Relative importance of direct and indirect infection in the transmission of *Laboulbenia slackensis* (*Ascomycetes*, *Laboulbeniales*). Belgian Journal of Botany 128(2), 124–130.
De Lange PJ, Galloway DJ, Blanchon DJ, Knight A et al. 2012 – Conservation status of New Zealand lichens. New Zealand Journal of Botany 50(3), 303–363.
De Leo F, Marchetta A, Urzì C. 2022 – Black fungi on stone-built heritage: current knowledge and future outlook. Applied Sciences 12(8), 3969.
de los Angeles Herrera-Campos M, Huhndorf S, Lücking R. 2005 – The foliicolous lichen flora of Mexico IV: a new, foliicolous species of *Pyrenothrix* (*Chaetothyriales*: *Pyrenothrichaceae*). Mycologia 97, 356–361.

De Menezes GC, Godinho VM, Porto BA, Gonçalves VN et al. 2017 – *Antarctomyces pellizariae* sp. nov., a new, endemic, blue, snow resident psychrophilic ascomycete fungus from Antarctica. Extremophiles 21, 259–269.
De Notaris G. 1844 – Osservazione su alcuni generi e specie della Tribù de'Pirenomiceti Sferiacei. Giornale Botanico Italiano 1.1(2), 38–55.
De Notaris G. 1845 – *Abrothallus* novum lichenum genus. [ser. 2] Memorie della Reale Accademia delle Scienze di Torino 10, 351–355.
De Notaris G. 1846 – Frammenti lichenografici di un lavoro inedito. G Bot Ital 1, 174–224.
De Notaris G. 1867 – Nuove reclute per la pirenomicetologia italica. Commentario della Società Crittogamologica Italiana 2, 477–492.
De Silva NI, Phillips AJL, Liu JK, Lumyong S et al. 2019 – Phylogeny and morphology of *Lasiodiplodia* species associated with *Magnolia* forest plants. Scientific Reports 9, 14355.
De Silva NI, Tennakoon DS, Thambugala KM, Karunarathna SC et al. 2020 – Morphology and multigene phylogeny reveal a new species and a new record of *Rhytidhysteron* (*Dothideomycetes*, *Ascomycota*) from China. Asian Journal of Mycology 3, 295–306.
De Vries G. 1962 – *Cyphellophora laciniata* nov. gen., nov. sp. and *Dactylium Fusarioides* Fragoso et Ciferri. Mycopathologia et mycologia applicata 16, 47–54.
Dearness J, Foster WR. 1938 – *Coniosporium* disease of apples and crab-apples. Canadian Journal of Research 16(7), 274–276.
Debnath S, Chakraborty K, Datta BK, Das P et al. 2019 – *Trichoglossum tetrasporum*, newly recorded from India. Mycotaxonomy 134, 119–124.
Decock C, Rodriguez GD, Seifert K. 2005 – Taxonomy and phylogeny of *Synchaetomella lunatospora*, a new genus and species of synnematous fungi from Southeast Asia. Antonie van Leeuwenhoek 88, 231–240.
Degenkolb T, Vilcinskas A. 2016 – Metabolites from nematophagous fungi and nematicidal natural products from fungi as alternatives for biological control. Part II: metabolites from nematophagous basidiomycetes and non-nematophagous fungi. Applied Microbiology and Biotechnology 100, 3813–3824.
Dei-Cas E, Chabe M, Moukhlis R, Durand-Joly I et al. 2006 – *Pneumocystis oryctolagi* sp. nov., an uncultured fungus causing pneumonia in rabbits at weaning: review of current knowledge, and description of a new taxon on genotypic, phylogenetic and phenotypic bases. FEMS microbiology reviews 30(6), 853–871.
Dei-Cas E. 2000 – *Pneumocystis* infections: The iceberg? Medical Mycology 38 (S1), 23–32.
Deighton FC. 1969 – New genera and species and redispositions of some hyphomycetes, mainly African. Mycological Papers 117, 8–31.
Del Frari G, Cabral A, Nascimento T, Ferreira RB et al. 2019 – *Epicoccum layuense* a potential biological control agent of esca-associated fungi in grapevine. PLoS ONE 14, e0213273.
Del Prado R, Schmitt I, Kautz S, Palice Z et al. 2006 – Molecular data place *Trypetheliaceae* in *Dothideomycetes*. Mycological Research 110, 511–520.
Delanoë P, Delanoë M. 1912 – Sur les rapports des kystes de carinii du poumon des rats avec le *Trypanosoma lewisi*. C.R. Comptes rendus de l'Académie des Sciences (Paris) 155, 658–660.
Delaye L, Garcia-Guzman G, Heil M. 2013 – Endophytes versus biotrophic and necrotrophic pathogens are fungal lifestyles evolutionarily stable traits? Fungal Diversity 60, 125e135.
Delgado G, Koukol O, Miller AN, Piepenbring M. 2019 – *Septonema lohmanii* G. Delgado & O. Koukol, sp. nov., a new species in *Mytilinidiales* (*Dothideomycetes*) and the phylogenetic position of *S. fasciculare* (Corda) S. Hughes. Cryptogamie, Mycologie 40 (2), 3–21.
Delmail DD, Grube M, Parrot D, Cook-Moreau J et al. 2013 – Halotolerance in lichens: Symbiotic coalition against salt stress. In P. Ahmad, M. M. Azooz, and M. N. Prasad (Eds.), Ecophysiology and responses of plants under salt stress (115–148). New York, NY: Springer.
Demanche C, Berthelemy M, Petit T, Polack B et al. 2001 – Phylogeny of *Pneumocystis carinii* from 18 primate species confirms host specificity and suggests co-evolution. Journal of Clinical Microbiology 39, 2126–2133.

Demanche C. 2003 – Genetic variability and circulation of *Pneumocystis* in nonhuman primate's populations. Ph.D. Thesis Dissertation. Universitea de Paris XII.
Deng W, Zhang F, Fornacca D, Yang XY et al. 2023a – Those nematode-trapping fungi that are not everywhere: Hints towards soil microbial biogeography. Journal of Microbiology 61(5), 511–523.
Deng W, Zhang F, Li YP, Zhang X et al. 2023b – Uncovering the biogeographic pattern of the widespread nematode-trapping fungi *Arthrobotrys oligospora*: watershed is the key. Frontiers in Microbiology 14, 1152751.
Denison WC, Carroll GC. 1966 – The primitive *Ascomycete*: A new look at an old problem. Mycologia 58, 249–269.
Denman S, Crous PW, Taylor JE, Kang JC et al. 2000 – An overview of the taxonomic history of *Botryosphaeria*, and a re-evaluation of its anamorphs based on morphology and ITS rDNA phylogeny. Studies in Mycology 45, 129–140.
Dennis R. 1971 – New or Interesting British Microfungi. Kew Bulletin 25, 335–374.
Dennis RWG. 1968 – British *Ascomycetes*. J. Cramer, Lehre, Germany.
Dennis RWG. 1970 – Fungus flora of Venezuela and adjacent countries. Kew Bulletin Additional Series 3. Cramer, Lehre.
Dennis RWG. 1977 – British *Ascomycetes*. J. Cramer, Vaduz, Germany.
Dennis RWG. 1978 – British *Ascomycetes*. Cramer Vaduz 1–585.
Dennis RWG. 1982 – The name for the type species of *Propolomyces* Sherwood. Kew bulletin 36, 683–685.
Dennis RWG. 1986 – Fungi of the Hebrides. Royal Botanic Gardens, Kew 383.
Derouiche S, Deville M, Taylor M.L, Akbar H et al. 2009 – *Pneumocystis* diversity as a phylogeographic tool. Memórias do Instituto Oswaldo Cruz 104, 112–117.
Derviş S, Özer G. 2023 – Plant-associated *Neoscytalidium dimidiatum*—Taxonomy, host range, epidemiology, virulence, and management strategies: A comprehensive review. Journal of Fungi 9, 1048.
DesRochers P, Ouellette GB. 1994 – *Phaeotheca dimorphospora* sp. nov.: description et caractéristiques culturales. Canadian Journal of Botany 72, 808–817.
Dettman JR, Harbinski FM, Taylor JW. 2001 – Ascospore morphology is a poor predictor of the phylogenetic relationships of *Neurospora* and *Gelasinospora*. Fungal Genetics and Biology 34, 49–61.
Dhanasekaran V, Jeewon R, Hyde KD. 2006 – Molecular taxonomy, origins and evolution of freshwater *Ascomycetes*. Fungal Diversity 23, 351–390.
Dhillon B, Feau N, Aerts AL, Beauseigle S et al. 2015 – Horizontal gene transfer and gene dosage drives adaptation to wood colonization in a tree pathogen. Proceedings of the National Academy of Sciences 112, 3451–3456.
Dhillon B, Graham F, Laughinghouse HD, Chakrabarti S. 2024 – Assessment of endophytic fungal community in palm leaves and their biocontrol potential. PhytoFrontiers 4, 296–304.
Dianese J, Tessmann D, Furlanetto C. 1994 – Reinstating *Oswaldina icarahyensis* as the name of the anamorph of *Apiosphaeria guaranitica*. Fitopatologia Brasileira Suplemento 19, 273.
Dias DA, Urban S. 2009 – Chemical constituents of lichen, *Candelaria concolor*: a complete NMR and chemical degradative investigation. Natural Product Research 23(10), 925–939.
Díaz-Escandón D, Tagirdzhanova G, Vanderpool D, Allen CC et al. 2022 – Genome-level analyses resolve an ancient lineage of symbiotic *Ascomycetes*. Current Biology 32(23), 5209–5218.
Dickson J. 1793 – Fasciculus Tertius Plantarum Cryptogamicarum Britanniae. G. Nichol, London.
DiCosmo F, Nag Raj T, Kendrick W. 1984 – A revision of the *Phacidiaceae* and related anamorphs. Mycotaxon 21, 1–234.
DiCosmo F, Peredo H, Minter DW. 1983a – Prodromus for a revison of the *Phacidiaceae* and related anamorphs. Canadian Journal of Botany 61(1), 31–44.

DiCosmo F, Peredo H, Minter DW. 1983b – *Cyclaneusma* gen. nov., *Naemacyclus* and *Lasiostictis*, a nomenclatural problem resolved. European Journal of Forest Pathology 13, 206–212.
DiCosmo F, Raj TN, Kendrick B. 1983c – Prodromus for a revision of the *Phacidiaceae* and related anamorphs. Canadian Journal of Botany 61, 31–44.
Diederich P, Common RS, Braun U, Heuchert B et al. 2019 – Lichenicolous fungi from Florida growing on *Graphidales*. Plant and Fungal Systematics 64(2), 249–282.
Diederich P, Ertz D, Lawrey JD, Sikaroodi M et al. 2013 – Molecular data place the hyphomycetous lichenicolous genus *Sclerococcum* close to *Dactylospora* (*Eurotiomycetes*) and *S. parmeliae* in *Cladophialophora* (*Chaetothyriales*). Fungal Diversity 58, 61–72.
Diederich P, Etayo J. 2000 – A synopsis of the genera *Skyttea*, *Llimoniella* and *Rhymbocarpus* (lichenicolous *Ascomycota*, *Leotiales*). The Lichenologist 32(5), 423–485.
Diederich P, Lawrey JD, Ertz D. 2018 – The 2018 classification and checklist of lichenicolous fungi, with 2000 non-lichenized, obligately lichenicolous taxa. The Bryologist 121(3), 340–425.
Diederich P, Zhurbenko M, Etayo J. 2002 – The lichenicolous species of *Odontotrema* (syn. *Lethariicola*) (*Ascomycota*, *Ostropales*). The Lichenologist 34(6), 479–501
Diederich P. 2014 – *Aabaarnia* and *Normanogalla*, two new lichenicolous genera of *Ostropales*, *Ascomycota*. Bulletin de la Société des naturalistes luxembourgeois 115, 141.
Dighton J, White JF. 2017 – The fungal community: its organization and role in the ecosystem. CRC press.
Dilcher DL. 1965 – Epiphyllous fungi from Eocene deposits in western Tennessee, USA. Palaeontographica 116B, 1–54.
Dillenius JJ. 1719 – Cathalogus plantarum circa Gissam sponte nascentium. Cum appendice. Francofurti ad Moenum 480, 16.
Ding ST, Sun BN, Wu JY, Li XC. 2011 – Miocene *Smilax* leaves and associated epiphyllous fungi from Zhejiang, East China and their paleoecological implications. Review of Palaeobotany and Palynology 165, 209–223.
Dionne B, Neff L, Lee SA, Sutton DA et al. 2015 – Pulmonary fungal infection caused by *Neoscytalidium dimidiatum*. Journal of Clinical Microbiology 53(7), 2381–2384.
Dissanayake AJ, Chen YY, Cheewangkoon R, Liu JK. 2021a – Occurrence and morpho-molecular identification of *Botryosphaeriales* species from Guizhou Province, China. Journal of Fungi 7, 893.
Dissanayake AJ, Jayawardena RS, Boonmee S, Thambugala KM et al. 2014 – The status of family *Myriangiaceae* (*Dothideomycetes*). Phytotaxa 176, 219–237.
Dissanayake LS, Maharachchikumbura SS, Mortimer PE, Hyde KD et al. 2021b – *Acrocordiella yunnanensis* sp. nov. (*Requienellaceae*, *Xylariales*) from Yunnan, China. Phytotaxa 487(2), 103–113.
Ditengou FA, Müller A, Rosenkranz M, Felten J et al. 2015 – Volatile signaling by sesquiterpenes from ectomycorrhizal fungi reprogrammes root architecture. Nature Comm 6, 6279.
Döbbeler P. 1978 – Moosbewohnende Ascomyceten. I. Die Pyrenocarpen, den Gametophyten besiedelnden Arten. Mitt Bot Staatssamml Munch.
Döbbeler P. 1996 – *Potriphila navicularis* gen. et sp. nov. (*Ostropales*, *Ascomycetes*), ein bipolar verbreiteter Parasit von *Polytrichum alpinum*. Nova Hedwigia 62, 61–77.
Döbbeler P. 1999 – *Polytrichadelphus magellanicus* - a mycological Eldorado: five new *Ascomycetes* on a single collection from Tierra del Fuego. Haussknechtia 9, 79–96.
Dodge CW. 1973 – Lichen flora of the antarctic continent and adjacent islands. Phoenix, Canaan, New Hampshire.
Döğen A, Ilkit M, De Hoog GS. 2013 – Black yeast habitat choices and species spectrum on high altitude creosote-treated railway ties. Fungal biology 117, 692–696.
Doidge EM. 1942 – South african *Microthyriaceae*. Bothalia 4, 273–344.
Doilom M, Dissanayake AJ, Phillips AJL, Boonmee S et al. 2017 – Microfungi on *Tectona grandis* (teak) in Northern Thailand. Fungal Diversity 82, 107–182.

Doilom M, Hyde KD, Phookamsak R, Dai DQ et al. 2018 – Mycosphere Notes 225–274: types and other specimens of some genera of *Ascomycota*. Mycosphere 9(4), 647–754.
Dojani S, Lakatos M, Rascher U, Wanek W et al. 2007 – Nitrogen input by cyanobacterial biofilms of an inselberg into a tropical rainforest in French Guiana, Flora 202, 521–529.
Dombrowski A. 2022 – Systematics of the *Letrouitiaceae* (Lichen-forming *Ascomycota*): An overlooked tropical family [MS thesis]. Queen Mary, University of London 36–44.
Domizio P, Liu Y, Bisson LF, Barile D. 2017 – Cell wall polysaccharides released during the alcoholic fermentation by *Schizosaccharomyces pombe* and *S. japonicus*: Quantification and characterization. Food Microbiology 61, 136–149.
Dong JY, Zhao ZX, Cai L, Liu SQ et al. 2004 – Nematicidal effect of freshwater fungal cultures against the pine-wood nematode, *Bursaphelenchus xylophilus*. Fungal Diversity 15, 125–135.
Dong L, Xu J, Feng G, Li X et al. 2016 – Soil bacterial and fungal community dynamics in relation to Panax notoginseng death rate in a continuous cropping system. Scientific Reports 6, 31802.
Dong LQ, Zhang KQ. 2006 – Microbial control of plant-parasitic nematodes: A five-party interaction. Plant Soil 288, 31–45.
Dong W, Hyde KD, Jeewon R, Doilom M et al. 2021a – Towards a natural classification of *Annulatascaceae*-like taxa II: introducing five new genera and eighteen new species from freshwater. Mycosphere 12, 1–88.
Dong W, Hyde KD, Jeewon R, Liao CF et al. 2023 – Mycosphere notes 449–468: Saprobic and endophytic fungi in China, Thailand, and Uzbekistan. Mycosphere 14(1), 2208–2262.
Dong W, Jeewon R, Hyde KD, Yang EF et al. 2021b – Five novel taxa from freshwater habitats and new taxonomic insights of *Pleurotheciales* and *Savoryellomycetidae*. Journal of Fungi 7, 711.
Dong W, Wang B, Hyde KD, McKenzie EHC et al. 2020 – Freshwater *Dothideomycetes*. Fungal Diversity 105, 319–575.
Donk M. 1962. The generic names proposed for *Agaricaceae*. Beih. Nova Hedwigia 5, 1–320.
Döring H, Lumbsch HT. 1998 – Ascoma ontogeny: is this character set of any use in the systematics of the lichenized *Ascomycetes*? The Lichenologist 30(4–5), 489–500.
Dos Santos MDM, Fonseca MEN, Boiteux LS, Câmara PEAS et al. 2016 – ITS phylogeny and taxonomy of *Phyllachora* species on native *Myrtaceae* from the Brazilian Cerrado. Mycologia 108, 1141–1164.
Doveri F, Coué B. 2006 – First record of *Pyxidiophora badiorostris* from France. Documents Mycologigues XXXIV 133, 33–41.
Doveri F, Pecchia S, Vergara M, Sarrocco S et al. 2012 – A comparative study of *Neogymnomyces virgineus*, a new keratinolytic species from dung, and its relationships with the *Onygenales*. Fungal Diversity 52, 13–34.
Doveri F. 2016 – Description of *Chaetomium aureum*, *Corynascus sepedonium* and *Coniochaeta hansenii* newly recorded from Italy and a key to coprophilous *Chaetomiaceae* and *Coniochaetaceae*. *Ascomycete*. Org 8(1), 7–24.
Dowle E, Morgan-Richards M, Trewick S. 2013 – Molecular evolution and the latitudinal biodiversity gradient. Heredity 110, 501–510.
Dowling ME, Hu MJ, Brewer MT, Yang X. 2020 – Fungicide resistance in *Colletotrichum* species: an increasing problem for plant disease management. Journal of Fungi 6(2), 93.
Drees M, Wickes BL, Gupta M, Hadley S. 2007 – *Lecythophora mutabilis* prosthetic valve endocarditis in a diabetic patient. Medical Mycology 45(5), 46367.
Dreyfuss M, H€arri E, Hofmann H, Kobel H et al. 1976 – Cyclosporin A and C: new metabolites from *Trichoderma polysporum* (Link ex Pers.) Rifai. European Journal of Applied Microbiology and Biotechnology 3, 125–133.
Du BX, Yan DF, Sun BN, Li XC et al. 2012 – *Cunninghamia praelanceolata* sp. nov. with associated epiphyllous fungi from the upper Miocene of eastern Zhejiang, S.E. China and their palaeoecological implications. Review of Palaeobotany and Palynology 182, 32–43.

Du HZ, Yang J, Liu NG, Cheewangkoon R et al. 2022 – Morpho-phylogenetic evidence reveals new species of *Fuscosporellaceae* and *Savoryellaceae* from freshwater habitats in Guizhou province, China. Journal of Fungi 8, 1138.
Dua M, Singh A, Sethunathan N, Johri AK. 2012 – Biotechnology and bioremediation: successes and limitations. Applied Microbiology and Biotechnology 96(2), 313–334.
Duan JX, Wu WP, Liu XZ. 2007 – *Dinemasporium* (*Coelomycetes*). Fungal Diversity 26, 205–218.
Duarte LL, de Macedo DM, Barreto RW. 2021 – Cryptic but ubiquitous: *Claviradulomyceae* fam. nov. with five novel species of the lenticel fungus *Claviradulomyces* from Brazil. Cryptogamie, Mycologie 42(7), 121–135.
Duby JE. 1861 – Mémoire sur la tribu des Hystérinées de la famille des Hypoxylées (*Pyrénomycètes*). Mémoires de la Société de Physique et Histoire Naturelle de Genève 16 (1), 15–70.
Dudka IO, Heluta VP, Tykhonenko YY, Andrianova TV, Hayova VP, Prydiuk MP, Dzhagan VV, Isikov VP. 2004 – [Fungi of the Crimean Peninsula] (Translated from Russian). M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, 452.
Dufour E, Boulay J, Rincheval V, Sainsard-Chanet A. 2000 – A causal link between respiration and senescence in *Podospora anserina*. Proceedings of the National Academy of Sciences 97(8), 4138–4143.
Dugan FM, Braun U, Groenewald JZ, Crous PW. 2008 – Morphological plasticity in *Cladosporium sphaerospermum*. Persoonia 21, 9–16.
Dukik K, de Hoog GS, Stielow JB, Freeke J et al. 2020 – Molecular and phenotypic characterization of *Nannizzia* (*Arthrodermataceae*). Mycopathologia 185(1), 9–35.
Dumortier BC. 1829 – Analyse des familles des plantes. J. Casteman Ainé, Tournay.
Dunlap JC, Borkovich KA, Henn MR, Turner GE et al. 2007 – Enabling a community to dissect an organism: Overview of the *Neurospora* functional genomics project, Advances in Genetics 57, 49–96.
Durall DM, Todd AW, Trappe JM. 1994 – Decomposition of 14C – labelled substrates by ectomycorrhizal fungi in association with Douglas fir. New Phytologist 127, 725– 729.
Durand EJ. 1922 – The Genus *Catinella*. Bulletin of the Torrey Botanical Club 49(1), 15–21.
Durand-Joly I, Wakefield AE, Palmer RJ, Denis CM et al. 2000 – Ultrastructural and molecular characterization of *Pneumocystis carinii* isolated from a rhesus monkey (*Macaca mulatta*). Medical Mycology 38, 61–72.
Ebabhi AM, Adekunle AA. 2016 – Potential of some agro-wastes in bioethanol production using two indigenous yeast strains; *Candida tropicalis* and *Schizosaccharomyces pombe*. Nigerian Journal of Mycology 8, 8–22.
Ebead GA, Overy DP, Berrué F, Kerr RG. 2012 – *Westerdykella reniformis* sp. nov., producing the antibiotic metabolites melinacidin Iv and chetracin B. IMA fungus 3, 189–201.
Ebersohn C, Eicker A. 1992 – *Trichodelitschia microspora*, a new coprophilous species from South Africa. South African Journal of Botany 58(3), 145–146.
Eckblad FE. 1968 – The genera of the operculate *Discomycetes*. A re-evaluation of their taxonomy, phylogeny and nomenclature. Nytt Magasin for Botanikk 15, 1–191.
Edathodu J, Al-Abdely HM, AlThawadi S, Wickes BL et al. 2013 – Invasive fungal infection due to *Triadelphia pulvinata* in a patient with acute myeloid leukemia. Journal of Clinical Microbiology 51, 3426–3429.
Edlind TD, Bartlett MS, Weinberg GA, Prah GN et al. 1992 – The beta-tubulin gene from rat and human isolates of *Pneumocystis carinii*. Molecular Microbiology 6, 3365–3373.
Edman JC, Kovacs JA, Masur H, Santi DV et al. 1988 – Ribosomal RNA sequence shows *Pneumocystis carinii* to be a member of the fungi. Nature 334(6182), 519–522.
Edwards A, Leech T, Senior I. 2020 – A gall-inducing infection of *Lepista* spp. in Norfolk by *Mycosymbioces* mycenophila-first record for Britain. Field Mycology 21(4), 119–123.
Edwards J, Pascoe I. 2004 – Occurrence of *Phaeomoniella chlamydospora* and *Phaeoacremonium aleophilum* associated with Petri disease and esca in Australian grapevines. Australasian Plant Pathology 33, 273–279.

Egidi E, de Hoog GS, Isola D, Onofri S et al. 2014 – Phylogeny and taxonomy of meristematic rock-inhabiting black fungi in the *Dothideomycetes* based on multi-locus phylogenies. Fungal Diversity 65, 127–65.
Eijk GW van, Roeymans HJ. 1982 – Distribution of carotenoids and sterols in relation to the taxonomy of *Taphrina* and *Protomyces*. Antonie van Leeuwenhoek Journal of Microbiology 48(3), 257–264.
Ekanayaka AH, Ariyawansa HA, Hyde KD, Jones EB et al. 2017a – *Discomycetes*: the apothecial representatives of the phylum *Ascomycota*. Fungal Diversity 87, 237–298.
Ekanayaka AH, Dissanayake AJ, Jayasiri SC, To-anun C et al. 2016 – *Aplosporella thailandica*; a novel species revealing the sexual-asexual connection in *Aplosporellaceae* (*Botryosphaeriales*). Mycosphere 7, 440–447.
Ekanayaka AH, Hyde KD, Gentekaki E, McKenzie EH et al. 2019a – Preliminary classification of *Leotiomycetes*. Mycosphere 10(1), 310–489.
Ekanayaka AH, Hyde KD, Jones EBG, Zhao Q et al. 2019b – New and known discolichens from Asia and eastern Europe. Asian Journal of Mycology 2, 48–86.
Ekanayaka AH, Hyde KD, Jones EG, Zhao Q et al. 2017b – A new species of *Trichoglossum* (*Geoglossales*, *Ascomycota*) from Thailand. Phytotaxa 316(2), 161–170.
Ekanayaka AH, Hyde KD, Jones EG, Zhao QI. 2018 – Taxonomy and phylogeny of operculate *Discomycetes*: *Pezizomycetes*. Fungal Diversity 90, 161–243.
Ekman S, Andersen HL, Wedin M. 2008 – The limitations of ancestral state reconstruction and the evolution of the ascus in the *Lecanorales* (lichenized *Ascomycota*). Systematic Biology 57(1), 141–156.
Ekman S. 1993 – A taxonomic study of *Ropalospora chlorantha*, and a comparison between *Ropalospora* and *Fuscidea*. The Bryologist 96(4), 582–591.
El-Elimat T, Raja HA, Figueroa M, Al-Sharie AH et al. 2021 – Freshwater fungi as a source of chemical diversity: A review. Journal of Natural Products 84(3), 898–916.
Elenkin AA, Savicz VP. 1910 – Enumeratio lichenum in Sibiria orientali a cl. I. Sczegolev anno 1903 lectorum // Travaux du Musée Botanique de l'Académie Impériale des Sciences de St.-Pétersbourg. Livr. 8, 26–49.
Elenkin AA. 1911a – Flora lishajnikov Srednej Rossii. Part 3–4. Juriev.
Elenkin AA. 1911b – Lichenes Florae Rossiae Mediae. Partes 3 et 4, 361–682.
El-Garawani IM, Elkhateeb WA, Zaghlol GM, Almeer RS et al. 2019 – *Candelariella vitellina* extract triggers *in vitro* and in vivo cell death through induction of apoptosis: A novel anticancer agent. Food and Chemical Toxicology 127, 110–119.
Elix J. 2009 – *Physciaceae*. In Flora of Australia. Lichens 5, 57 CSIRO Publishing.
Elix JA, Corush J, Lumbsch HT. 2009 – Triterpene chemosyndromes and subtle morphological characters characterise lineages in the *Physcia aipolia* group in Australia (*Ascomycota*). Systematics and Biodiversity 7(4), 479–487.
Elix JA, Stocker-Wörgötter E. 2008 – Biochemistry and secondary metabolites. 104–133 in: Nash, T.H., III (ed.), Lichen biology, 2nd ed. Cambridge, U.K.: Cambridge University Press.
Elix JA. 2014 – A Catalogue of Standardized Chromatographic Data and Biosynthetic Relationships for Lichen Substances. Published by the author, Canberra.
Ellis JB, Everhart BM. 1892 – The north american *Pyrenomycetes*. Published by the authors, Newfield, New Jersey 793.
Ellis JB, Everhart BM. 1895 – New species of fungi from various localities. Proceedings of the Academy of Natural Sciences of Philadelphia 413–441.
Ellis JP. 1976a – British *Microthyrium* species and similar fungi. Transactions of the British Mycological Society 67, 381–394.
Ellis JP. 1977 – The genera *Trichothyrina* and *Actinopeltis* in Britain. Transactions of the British Mycological Society 68, 145–155.
Ellis M. 1959 – *Clasterosporium* and some allied dematiaceae-phragmosporae. II. Mycological Papers 72, 1–75.

Ellis MB. 1963 – Dematiaceous *Hyphomycetes*. V. Mycological Papers 93, 1–33.
Ellis MB. 1971a – Dematiaceous *Hyphomycetes*. Commonwealth Mycological Institute, Kew, U.K., 608.
Ellis MB. 1971b – Dematiaceous *Hyphomycetes*. CMI Kew, England.
Ellis MB. 1976b – More Dematiaceous *Hyphomycetes*. Commonwealth Mycological Institute, Kew 507.
Emanuel DA, Lawton BR, Wenzel FJ. 1962 – Maple-bark disease: pneumonitis due to *Coniosporium corticale*. New England Journal of Medicine 266(7), 333–337.
Enespa, Chandra P. 2019 – Fungal community for novel secondary metabolites. Recent Advancement in White Biotechnology Through Fungi: Volume 2: Perspective for Value-Added Products and Environments 249–283.
Engler HGA, Prantl KAE. 1897 – Die Natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten 1(1), 1–513.
Eriksson B. 1974 – On *Ascomycetes* on *Diapensiales* and *Ericales* in Fennoscandia. 2. *Pyrenomycetes*. Svensk Botanisk Tidskrift 68, 192–234.
Eriksson OE, Baral HO, Currah RS, Hansen K et al. 2003a – Notes on *ascomycete* systematics. Nos 3580–3623. Myconet 9, 91–103.
Eriksson OE, Baral HO, Currah RS, Hansen K et al. 2003b – Outline of *Ascomycota*–2003. Myconet 9, 1–89.
Eriksson OE, Baral HO, Currah RS, Hansen K et al. 2004 – Outline of *Ascomycota*–2004. Myconet 10, 1–99.
Eriksson OE, Baral HO, Currah RS, Hansen K et al. 2006 – Outline of *Ascomycota*–2006.
Eriksson OE, Hawksworth DL. 1986a – An alphabetical list of the generic names of *Ascomycetes.* Systema Ascomycetum 5, 3–111.
Eriksson OE, Hawksworth DL. 1986b – Notes on *Ascomycete* systematics. Nos. 1–224. Syst Ascomycetum 5, 113–174.
Eriksson OE, Hawksworth DL. 1986c – Outline of *Ascomycetes*. Systema Ascomycetum 5, 185–324.
Eriksson OE, Hawksworth DL. 1988 – Notes on *Ascomycete* systematics – Nos 552–732. Systema Ascomycetum 7(1), 59–101.
Eriksson OE, Hawksworth DL. 1990 – Outline of the *Ascomycetes* –1989. Systema Ascomycetum 8, 119–318.
Eriksson OE, Hawksworth DL. 1991a − Notes on *Ascomycetes* systematics. Nos 1128–1251. Systema Ascomycetum 10(1), 27−67.
Eriksson OE, Hawksworth DL. 1991b – Outline of the *Ascomycetes* –1990. Systema Ascomycetum 8, 39–271.
Eriksson OE, Hawksworth DL. 1993a – Notes on *ascomycete* systematics – Nos 1418–1529. Systema Ascomycetum 11, 163–194.
Eriksson OE, Hawksworth DL. 1993b – Outline of the *Ascomycetes* –1993. Systema Ascomycetum 12, 51–257.
Eriksson OE, Hawksworth DL. 1995 – Notes on *Ascomycete* systematics – Nos 1885–2023. Systema Ascomycetum 14, 41–77.
Eriksson OE, Hawksworth DL. 1998 – Outline of the *Ascomycetes*-1998. Systema Ascomycetum 16, 83–296.
Eriksson OE, Strand A. 1995 – Relationships of the genera *Nephroma*, *Peltigera* and *Solorina* (*Peltigerales*, *Ascomycota*) inferred from 18S rDNA sequences. Systema Ascomycetum 14, 33–39.
Eriksson OE, Winka K. 1997 – Supraordinal taxa of *Ascomycota*. Myconet 1(1), 1–16.
Eriksson OE, Yue JZ. 1989 – An amended description and disposition of the genus *Thyridium*. Systema Ascomycetum 8, 9–16.
Eriksson OE. 1981 – The families of bitunicate *Ascomycetes*. Nordic Journal of Botany 1(6), 800.
Eriksson OE. 1982 – Outline of the *Ascomycetes*. Mycotaxon 15, 203–248.

Eriksson OE. 1986 – *Lahmia* Körber (= *Parkerella* A. Funk) a misinterpreted genus with isolated position. Mycotaxon 27, 347–360.
Eriksson OE. 1993 – Molecular evidence for the evolutionary hiatus between *Saccharomyces cerevisiae* and *Schizosaccharomyces pombe*. Systema Ascomycetum 11, 119–162.
Eriksson OE. 1994a – *Pneumocystis carinii*, a parasite in lungs of mammals, referred to a new family and order (*Pneumocystidaceae*, *Pneumocystidales*, *Ascomycota*). Systema Ascomycetum 13(2), 165–180.
Eriksson OE. 1994b – Problems in the classification of fissitunicate Ascomycetes. In: Hawksworth DL (ed) *Ascomycete* systematics. Problems and perspectives in the nineties. NATO ASI, vol 269. Plenum Press, New York and London, 341–345.
Eriksson OE. 1999 – Outline of *Ascomycota*. Myconet 3, 1–88.
Eriksson OE. 2001 – Outline of *Ascomycota*. Myconet 6, 1–27.
Eriksson OE. 2005 – Outline of *Ascomycota*. Myconet 11, 1–113.
Eriksson OE. 2006 – Outline of *Ascomycota*. Myconet 12, 1–82.
Eriksson OE. 2014 – Checklist of the non-lichenized *Ascomycetes* of Sweden. Acta Univ Upsal Symb Bot Upsal 36(2), 7–499.
Errampalli D, Saunders JM, Holley JD. 2001 – Emergence of silver scurf (*Helminthosporium solani*) as an economically important disease of potato. Plant Pathology 50, 141–153.
Ertz D, Diederich P, Lawrey JD, Berger F et al. 2015 – Phylogenetic insights resolve *Dacampiaceae* (*Pleosporales*) as polyphyletic: *Didymocyrtis* (*Pleosporales*, *Phaeosphaeriaceae*) with *Phoma*-like anamorphs resurrected and segregated from *Polycoccum* (*Trypetheliales*, *Polycoccaceae* fam. nov.). Fungal Diversity 74, 53–89.
Ertz D, Guzow-Krzemińska B, Thor G, Łubek A et al. 2018a – Photobiont switching causes changes in the reproduction strategy and phenotypic dimorphism in the *Arthoniomycetes*. Scientific Reports 8, 4952.
Ertz D, Heuchert B, Braun U, Freebury CE et al. 2016 – Contribution to the phylogeny and taxonomy of the genus *Taeniolella*, with a focus on lichenicolous taxa. Fungal Biology 120, 1416–1447.
Ertz D, Lawrey JD, Common RS, Diederich P. 2014 – Molecular data resolve a new order of *Arthoniomycetes* sister to the primarily lichenized *Arthoniales* and composed of black yeasts, lichenicolous and rock-inhabiting species. Fungal Diversity 66, 113–137.
Ertz D, Lawrey JD, Sikaroodi MMGP, Fischer E et al. 2008 – A new lineage of lichenized *Basidiomycetes* inferred from a two-gene phylogeny: the *Lepidostromataceae* with three species from the tropics. American Journal of Botany 95, 1548–1556.
Ertz D, Miadlikowska J, Lutzoni F, Dessein S et al. 2009 – Towards a new classification of the *Arthoniales* (*Ascomycota*) based on a three-gene phylogeny focussing on the genus *Opegrapha*. Mycological Research 113(1), 141–152.
Ertz D, Sanderson N, Lebouvier M. 2021 – *Thelopsis* challenges the generic circumscription in the *Gyalectaceae* and brings new insights to the taxonomy of *Ramonia*. The Lichenologist 53(1), 45–61.
Ertz D, Sanderson N, Łubek A, Kukwa M. 2018b – Two new species of *Arthoniaceae* from old-growth European forests, *Arthonia thoriana* and *Inoderma sorediatum*, and a new genus for *Schismatomma niveum*. The Lichenologist 50, 161–172.
Ertz D, Tehler A. 2011 – The phylogeny of *Arthoniales* (*Pezizomycotina*) inferred from nucLSU and RPB2 sequences. Fungal Diversity 49, 47–71.
Ertz D, Tønsberg T. 2021– A new species of *Sagiolechia* (*Sagiolechiaceae*) from Norway, with lirelliform ascomata and 1-septate ascospores. Graphis Scripta 33(1), 1–11. Oslo. ISSN 2002–4495.
Eschweiler FG. 1824 – Systema lichenum, genera exhibens rite distincta, pluribus novis adaucta: commentatio. Schrag.
Eschweiler FG. 1833 – Lichenes. In Flora Brasiliensis (C. F. P. von Martius, ed.), 51–293. Stuttgart and Tübingen: J. G. Cotta.

Eshet Y, Rampino MR, Visscher H. 1995 – Fungal event and palynological record of ecological crisis and recovery across the Permian-Triassic boundary. Geology 23, 967–970.
Espagne E, Lespinet O, Malagnac F, Da Silva C et al. 2008 – The genome sequence of the model ascomycete fungus *Podospora anserina*. Genome Biology 9, R77.
Espoz C, Guzman G, Castilla JC. 1995 – The lichen *Thelidium litorale* on shells of intertidal limpets: A case of lichen-mediated cryptic mimicry. Marine Ecology Progress Series 119, 191–197.
Essakhi S, Mugnai L, Crous P, Groenewald J et al. 2008 – Molecular and phenotypic characterisation of novel *Phaeoacremonium* species isolated from esca diseased grapevines. Persoonia 21, 119–134.
Esumi Y, Suzuki Y, Ichikawa T, Ikeda Y et al. 2003 – SNF-4794; New enzyme inhibitors produced by *Chaetomella* sp. The Journal of Antibiotics 56(2), 169–172.
Etayo J, Diederich P. 2001 – *Gyalideopsis floridae*, sp. nov. a new lichenicolous lichen from Florida (*Gomphillaceae*, *Ascomycetes*). Bryologist 104, 130–133.
Etayo J, Mayrhofer H. 2003 – *Thelenella melanospora* (*Thelenellaceae*, lichenized *Ascomycetes*), a new species from the Mediterranean region. Nova Hedwigia 77(1-2), 109114.
Etayo J, Palice Z, Spribille T. 2009 – *Candelariella boleana*, a new epiphytic species from southern and central Europe (*Candelariaceae*, *Ascomycota*). Nova Hedwigia 89(3–4), 545–552.
Etayo J, Sancho LG, Gómez-Bolea A, Søchting U et al. 2021 – Catalogue of lichens (and some related fungi) of Navarino Island, Cape Horn Biosphere Reserve, Chile. Anales Instituto de la Patagonia 49, 1–110.
Evans HC, Johnston PR, Park D, Barreto RW et al. 2010 – *Claviradulomyces*, a new genus of *Odontotremataceae* from West African rainforest. Fungal Biology 114(1), 41–48.
Evidente A, Sparapano L, Andolf A, Bruno G. 2000 – Two naphthalenone pentakides from liquid cultures of *Phaeoacremonium aleophilum*, a fungus associated with esca of grapevine. Phytopathologia Mediterranea 39, 162–168.
Eyupoglu C, Eyupoglu S, Merdan N. 2022 – Investigation of dyeing properties of mohair fiber dyed with natural dyes obtained from *Candelariella reflexa*. Journal of Natural Fibers 19, 12829–12848.
f Kirk DL. 1981 – *Lichenothelia*, a new genus for the *Microthelia aterrima* group. The Lichenologist 13, 141–153.
Faisal M, Elsayed E, Fitzgerald SD, Silva V et al. 2007 – Outbreaks of phaeohyphomycosis in the chinook salmon (*Oncorhynchus tshawyscha*) caused by *Phoma herbarum*. Mycopathologia 163, 41–48.
Fallah PM, CraneJL, Shearer CA. 1999 – Freshwater *Ascomycetes*: two new species of *Ascotaiwania* from North America. Canadian Journal of Botany 77(1), 87–92.
Fallah PM, Shearer CA. 1998 – Freshwater *Ascomycetes*: *Phomatospora* spp. from lakes in Wisconsin. Mycologia 90(2), 323–329.
Fan Q, Wang YB, Tang DX, Wang Y et al. 2020a – Species Diversity of *Cordyceps sinensis* in Yeyahu Forest Park, Kunming. Journal of edible fungi 27(2), 101–108.
Fan Q. 2020 – Preliminary study on the classification and phylogenesis of general *Cordyceps* in Kunming. Yunnan University.
Fan XL, Barreto RW, Groenewald JZ, Bezerra JDP et al. 2017 – Phylogeny and taxonomy of the scab and spot anthracnose fungus *Elsinoë* (*Myriangiales*, *Dothideomycetes*). Studies in Mycology 87, 1–41.
Fan XL, Bezerra JDP, Tian CM, Crous PW. 2018 – Families and genera of diaporthalean fungi associated with canker and dieback of tree hosts. Persoonia 40, 119–134.
Fan XL, Bezerra JDP, Tian CM, Crous PW. 2020b – *Cytospora* (*Diaporthales*) in China. Persoonia 45, 1–45.
Fan XL, Tian CM, Yang Q, Liang YM et al. 2014 – *Cytospora* from *Salix* in northern China. Mycotaxon 129, 303–315.
Fan Y, Du M, Zhang W, Deng W et al. 2024 – The genomes of nematodetrapping fungi provide insights into the origin and diversification of fungal carnivorism. bioRxiv 2024-03.

Fan Y, Zhang W, Chen Y, Xiang M et al. 2021 – DdaSTE12 is involved in trap formation, ring inflation, conidiation, and vegetative growth in the nematode-trapping fungus *Drechslerella dactyloides*. Applied Microbiology and Biotechnology 105, 7379–7393.

Fantes PA, Hoffman CS. 2016 – A brief history of *Schizosaccharomyces pombe* research: a perspective over the past 70 years. Genetics 203(2), 621–629.

Farr D, Rossman A. 2016 – Fungal databases, systematic mycology and microbiology laboratory, ARS, USDA. Retrieved March 19, 2018, from http://nt.ars-grin.gov/ fungaldatabases/.

Farr DF, Bills GF, Chamuris GP, Rossman AY. 1989 – Fungi on plants and plant products in the United States, 1st edn. American Phytopathological Society, USA.

Favero-Longo SE, Castelli D, Fubini B, Piervittori R. 2009 – Lichens on asbestos-cement roofs: bioweathering and biocovering effects. Journal of Hazardous Materials 162(2–3), 1300–1308.

Favero-Longo SE, Castelli D, Salvadori O, Belluso E et al. 2005 – Pedogenetic action of the lichens *Lecidea atrobrunnea*, *Rhizocarpon geographicum* gr. and *Sporastatia testudinea* on serpentinized ultramafic rocks in an alpine environment. International Biodeterioration & Biodegradation 56(1), 17–27.

Favero-Longo SE, Siniscalco C, Piervittori R. 2006 – Plant and lichen colonization in a asbestos mine: spontaneous bioattenuation limits air dispersion of fibres. Plant Biosystems 140(2), 190–205.

Favero-Longo SE, Tabasso ML, Brigadeci F, Capua MC et al. 2022 – A first assessment of the biocidal efficacy of plant essential oils against lichens on stone cultural heritage, and the importance of evaluating suitable application protocols. Journal of Cultural Heritage 55, 68–77.

Fedosova AG, Popov ES, Lizoň P, Kučera V. 2018 – Towards an understanding of the genus *Glutinoglossum* with emphasis on the *Glutinoglossum glutinosum* species complex (*Geoglossaceae*, *Ascomycota*). Persoonia: Molecular Phylogeny and Evolution of Fungi 41(1), 18–38.

Fee AL. 1824 – Essai sur les cryptogames des ´ecorces exotiques officinales I. Didot, Paris.

Fée ALA. 1831 – Monographie du genre *Trypethelium*. Annales des Sciences Naturales, Botanique 23, 410–459.

Feltgen J 1903 – Vorstudien zu einer Pilzflora des Grossherzogthums Luxemburg. Nachtråge III. J. Beffort, Luxemburg.

Feng JW, Liu WT, Chen JJ, Zhang CL. 2021 – Biogeography and ecology of *Magnaporthales*: a case study. Frontiers in Microbiology 12, 654380.

Fennell DI. 1973 – *Pectomycetes*; *Eurotiales*. In: The Fungi, an advance treatise. (Ainsworth GC, Sparrow FK, Sussman AS, eds) Volume 4, Academic press, London 45–68.

Feofilovaa EP, Kuznetsovab LS, Sergeevaa YaE, Galaninaa LA. 2009 – Species composition of food-spoiling mycelial fungi. Microbiology, Vol. 78, No. 1, 112–116.

Fernandes RF, Ferreira GR, Spielmann AA, Edwards HG et al. 2015 – FT-Raman spectroscopy of the *Candelaria* and *Pyxine* lichen species: A new molecular structural study. Journal of Molecular Structure 1102, 57–62.

Fernández FA, Huhndorf SM. 2005 – New species of *Chaetosphaeria*, *Melanopsammella* and *Tainosphaeria* gen. nov. from the Americas. Fungal Diversity 18, 15–57.

Fernández FA, Lutzoni FM, Huhndorf SM. 1999 – Teleomorph-anamorph connections: the new pyrenomycetous genus *Carpoligna* and its *Pleurothecium* anamorph. Mycologia 91, 251–262.

Fernández-Brime S, Gaya E, Llimona X, Wedin M et al. 2020 – *Rhagadodidymellopsis endocarpi* gen. et sp. nov. and *Arthopyrenia symbiotica* (*Dothideomyceta*), two lichenicolous fungi growing on *Endocarpon* species. Plant and Fungal Systematics 65(1), 176–184.

Fernandez-Brime S, Llimona X, Navarro-Rosines P. 2010 – *Lichenostigma rupicolae* (*Lichenotheliaceae*), a new lichenicolous species growing on *Pertusaria rupicola*. The Lichenologist 42(3), 241–247.

Fernández-Martínez MA, Pérez-Ortega S, Pointing SB, Allan Green TG et al. 2017 – Microbial succession dynamics along glacier forefield chronosequences in Tierra del Fuego (Chile). Polar Biology 40, 1939–1957.
Fernández-Toirán LM, Águeda B. 2007 – Fruitbodies of *Cenococcum geophilum*. Mycotaxon 100, 109–114.
Ferreira BW, Barreto RW. 2019 – Debunking *Acroconidiella*. Mycological Progress 18(11), 1303–1315.
Ferrer A, Miller AN, Sarmiento C, Shearer CA. 2012 – Three new genera representing novel lineages of *Sordariomycetidae* (*Sordariomycetes*, *Ascomycota*) from tropical freshwater habitats in Costa Rica. Mycologia 104(4), 865–879.
Ferrer A, Miller AN, Shearer CA. 2011 – *Minutisphaera* and *Natipusilla*: two new genera of freshwater *Dothideomycetes*. Mycologia 103, 411–423.
Filson RB. 1975 – Studies in Antarctic lichens V: Lichenes Antarctici Exsiccati, Fascicle I, with additional notes on the taxonomy of each species. Muelleria 3, 146–158.
Fink B. 1935 – The lichen flora of the United States. Completed for Publication by Joyce Hedrick. University of Michigan Press, Ann Arbor.
Fintelmann RE. 2011 – Recurrent *Lecythophora mutabilis keratitis* and *Endophthalmitis* after deep anterior lamellar keratoplasty. Archives of Ophthalmology 129(1), 106.
Firmino AL, Pereira OL. 2021 – A simple method for the cultivation of the "unculturable" asterinaceous fungi (*Asterinales*/*Dothideomycetes*). Journal of Microbiological Methods 187, 106272.
Fischer E. 1897 – *Plectacineae*. In: Die natürlichen Pflanzenfamilien. (Engler A, Prantl K, eds). Volume I, Engelmann, Leipzig.
Fischer JM, Keely SP, Stringer JR. 2006 – Evolutionary rate of ribosomal DNA in *Pneumocystis* species is normal despite the extraordinarily low copy-number of rDNA genes. Journal of Eukaryotic Microbiology 53, S156–S158.
Fischer M, Lu H. 2015 – Climate change effects on the biodiversity of fungi. Fungal Diversity 71(1), 169–189.
Fisher MC, Koenig GL, White TJ, Taylor JW. 2002 – Molecular and phenotypic description of *Coccidioides posadasii* sp. *nov*., previously recognized as the non-California population of *Coccidioides immitis*. Mycologia 94, 73–84.
Fishman JA. 2020 – *Pneumocystis jiroveci*. In Seminars in Respiratory and Critical Care Medicine (Vol. 41, No. 01, pp. 141-157). Thieme Medical Publishers.
Fitzpatrick HM. 1920 – Monograph of the *Coryneliaceae*. Mycologia 12(4), 206–237.
Fitzpatrick HM. 1942 – Revisionary studies in the *Coryneliaceae*. Mycologia 34, 464–488.
Fitzpatrick RE. 1934 – The life history and parasitism of *Taphrina deformans*. Scientific Agriculture 14(6), 305–326.
Flakus A, Etayo J, Miadlikowska J, Lutzoni F et al. 2019 – Biodiversity assessment of *Ascomycetes* inhabiting *Lobariella* lichens in Andean cloud forests led to one new family, three new genera and 13 new species of lichenicolous fungi. Plant and Fungal Systematics 64(2), 283–344.
Flakus A, Kukwa M. 2012 – New species of lichenicolous fungi from Bolivia. The Lichenologist 44(4), 469–477.
Flakus A, Kukwa M. 2014 – The first squamulose *Thelocarpon* species *Thelocarpaceae*, *Ascomycota* discovered in the biological soil crusts in the Bolivian Andes. Phytotaxa 175(5), 281–286.
Flakus A. 2009 – *Aspidothelium lueckingii*: a new lichenized fungus from Bolivia. Nova Hedwigia 88(1-2), 139–143.
Flessa F, Peršoh D, Rambold G. 2012 – Annuality of Central European deciduous tree leaves delimit community development of epifoliar pigmented fungi. Fungal Ecology 5, 554–561.
Flewelling AJ, Ellsworth KT, Sanford J, Forward E et al. 2013 – Macroalgal endophytes from the Atlantic Coast of Canada: a potential source of antibiotic natural products? Microorganisms 1, 175–187.

Follmann G, Werner B. 2003 – Lichenicolous fungi occurring on *Roccellaceae* (*Arthoniales*). I. New species from South America. Journal of the Hattori Botanical Laboratory 94, 261–292.
Follmann G. 2001 – An integrated key to, and a critical survey of, the South American representatives of the lichen family *Roccellaceae* (*Arthoniales*). Journal of the Hattori Botanical Laboratory 90, 251–267.
Fonseca Á, Inácio J. 2011 – *Lalaria* R.T. Moore emend. Á. Fonseca (2004). In C.P. Kurtzman, J.W. Fell and T. Boekhout (Eds.) The Yeasts, a Taxonomic Study, Amsterdam: Elsevier. (Fifth Edition) 2, 1291–129.
Fonseca A, Rodrigues MG. 2011 – *Taphrina* Fries (1832). In C.P. Kurtzman, J.W. Fell and T. Boekhout (Eds.) The Yeasts, a Taxonomic Study (Fifth Edition), Vol. 2 (pp. 823-858) Amsterdam: Elsevier.
Forcelini BB, Lee S, Oliveira M, Peres NA. 2018 – Development of high-throughput SNP genotyping assays for rapid detection of strawberry *Colletotrichum* species and the G143A mutation. Phytopathology 108, 1501–1508.
Fornacca D, Deng W, Yang Y, Zhang F et al. 2024 – Linking watershed formation with the phylogenetic distribution of a soil microscopic fungus in Yunnan Province, China. BMC Microbiology 24, 305.
Fouda AH, Hassan SED, Eid AM, Ewais EE et al. 2019 – Biocontrol of tomato gray mold disease and enhance plant growth using endophytic fungi. Applied Microbiology and Biotechnology 103(2), 985–996.
Fournier J, Lechat C. 2010 – *Phomatospora luteotingens* sp. nov., a new aquatic species of *Phomatospora* from France and Spain. Mycosphere 1, 39–43.
Franco ME, Wisecaver JH, Arnold AE, Ju YM et al. 2022 − Ecological generalism drives hyperdiversity of secondary metabolite gene clusters in xylarialean endophytes. New Phytologist 233(3), 1317−30.
Friebes G, Jaklitsch WM, García S, Voglmayr H. 2016 – *Lopadostoma taeniosporum* revisited and a new species of *Coniochaeta*. Sydowia 68, 87–97.
Frenkel JK. 1976 – *Pneumocystis jiroveci* sp. from man: morphology, physiology, and immunology in relation to pathology. National Cancer Institute Monographs 43, 13–30.
Frey E. 1931 – Weitere Beiträge zur Kenntnis der Umbilicariaceen. Hedwigia 71, 94–119.
Frey E. 1933 – *Cladoniaceae* (unter Ausschluß d. Gatt. Cladonia) *Umbilicariaceae* – Dr. L. Rabenhorst's Kryptogamenflora von Deutschland, Österreich und der Schweiz. Vol. 9. Leipzig.
Frey E. 1936 – Vorarbeiten zu einer Monographie der Umbilicariaceen. Ber. Schweiz. Bot. Ges. 45, 198–230.
Frey E. 1949 – Neue Beitrage zu einer Monographie des Genus Umbilicaria. (Hoffm.) Nyl. // Berichte der Schweizerischen Botanischen Gesellschaft 59, 427–470.
Fries E. 1817 – Lichenum dianome nova. Lund.
Fries E. 1825 – Systema orbis vegetabilis. Lund.
Fries E. 1828 – Elenchus fungorum. II. Greifswald. 154 p.
Fries EM. 1815 – Observationes mycologicae. Gerh. Bonnier, Copenhagen 1, 1–230.
Fries EM. 1818 – Observationes mycologicae. Gerh. Bonnier, Copenhagen 2, 1–376.
Fries EM. 1821–1832 – Systema mycologicum: sistens fungorum ordines, genera et species, huc usque cognitas, quas ad normam methodi naturalis determinavit. – Lundæ: Officina Berlingiana; Greifswald (vol. 3).
Fries EM. 1823 – Systema mycologicum, Sweden. Lund 2, 275–620.
Fries EM. 1825 – Systema orbis vegetabilis. Primas lineas novæ constructionis periclitatur Elias Fries. Pars I. Plantæ homonemeæ. – Lundæ: Typographia Academica 374.
Fries EM. 1835 – Corpus florarum provincialium Sueciæ. I. Floram Scanicam. –Upsaliæ: Typis Palmblad, Sebell et C 394.
Fries EM. 1836–1838 – Epicrisis systematis mycologici, seu synopsis Hymenomycetum. – Upsaliae: Typographia Academica 610.

Fries EM. 1849a – Summa vegetabilium Scandinaviae, seu enumeratio systematica et critica plantarum quum cotyledonearum, tum nemearum inter mare occidentale et album, inter 2003 Eidoram et Nordkap, hactenus lectarum, indicata simul distributione geographica. Sectio posterior. – Uppsaliae: Typograph. Academici 259–572.
Fries EM. 1849b – Summa vegetabilium Scandinaviae. Sectio posterior 2, 259–572.
Fries TM. 1860 – Lichenes Arctoi Europae Groenlandiaeque hactenus cogniti 1–298.
Fries TM. 1861 – Genera Heterolichenum Europaea recognita. Upsaliae.
Fries TM. 1871 – Lichenographia Scandinavica sive dispositio lichenum in Dania, Suecia, Norvegia, Fennia, Lapponia Rossica hactus collectorum. Vol. I Archilichenes discocarpos continens. Pars I. Upsaliae.
Fries TM. 1874 – Lichenographia Scandinavica sive dispositio lichenum in Dania, Suecia, Norvegia, Fennia, Lapponia Rossica hactus collectorum. Vol. I Archilichenes discocarpos continens. Pars II. Upsaliae.
Frisch A, Ohmura Y, Ertz D, Thor G. 2015 – *Inoderma* and related genera in *Arthoniaceae* with elevated white pruinose pycnidia or sporodochia. The Lichenologist 47, 233–256.
Frisch A, Thor G, Ertz D, Grube M. 2014 – The Arthonialean challenge: Restructuring *Arthoniaceae*. Taxon 63, 727–744.
Frisvad JC, Hubka V, Ezekiel CN, Hong SB et al. 2019 – Taxonomy of *Aspergillus* section Flavi and their production of aflatoxins, ochratoxins and other mycotoxins. Studies in Mycology 93, 1–63.
Frisvad JC, Thrane U, Filtenborg O. 1998 – Role and use of secondary metabolites in fungal taxonomy. In: Frisvad JC, Bridge PD, Arora DK (eds) Chemical fungal taxonomy. Marcel Dekker, New York 289–319.
Fröberg L. 1989 – The Calcicolous Lichens on the Great Alvar of Öland, Sweden. Doctoral Thesis, Institutionen för Sys-tematisk Botanik, Lund.
Fryar SC, Booth W, Davies J, Hodgkiss IJ, Hyde KD. 2004 – Distribution of fungi on wood in the Tutong River, Brunei. Fungal Diversity 17, 17–38
Fryar SC, Catcheside DEA. 2023 – *Neospadicoides australiensis* (*Xenospadicoidaceae*), a new freshwater fungus from South Australia. Australian Journal of Taxonomy 25, 1–6.
Fryar SC, Hyde KD. 2004 – New species and genera of ascomycetes from fresh and brackish water in Brunei: *Ayria appendiculata* and *Sungaiicola bactrodesmiella* gen. et spp. nov., *Fluviatispora boothii*, *Torrentispora crassiparietis* and *T. fusiformis* spp. nov. Cryptogamie, Mycologie 25, 245–260.
Fryday A, Cannon P, Coppins B, Aptroot A et al. 2024 – *Lecideales*, including *Amygdalaria*, *Bellemerea*, *Bryobilimbia*, *Cecidonia*, *Clauzadea*, *Farnoldia*, *Immersaria*, *Koerberiella*, *Lecidea*, *Lecidoma*, *Porpidia*, *Porpidinia* and *Romjularia* (*Lecideaeae*) and *Lopadium* (*Lopadiaceae*). Revisions of Britishand Irish Lichens 40, 1–51.
Fryday AM, Common RS. 2001 – A new species of *Schaereria* (lichenized fungi) from the Falkland Islands. The Bryologist 104(1), 109–114.
Fryday AM, Coppins BJ. 2004 – A reassessment of the genera *Chromatochlamys* and *Thelenella*, and a new species of *Strigula* from the British Isles. The Lichenologist 36, 8995.
Fryday AM, Hertel H. 2014 – A contribution to the family *Lecideaceae s. lat.* (*Lecanoromycetidae* inc. sed., lichenized *Ascomycota*) in the southern subpolar region; including eight new species and some revised generic circumscriptions. The Lichenologist 46, 389–412.
Fryday AM. 2008 – The genus *Fuscidea* (*Fuscideaceae*, lichenized *Ascomycota*) in North America. The Lichenologist 40(4), 295–328.
Fuckel KW. 1869 − Symbolae mycologicae: Beiträge zur Kenntniss der rheinischen Pilze. J. Niedner.
Fuckel KWGL. 1871 – Symbolae mycologicae: Beiträge zur Kenntniss der rheinischen Pilze. Nachtrag 1. Jahrbücher Nassauischen Vereins Naturkunde 25–26, 287–346.
Fuckel L. 1867 – Fungi Rhenani Exsiccati Cent. XIX-XXI. 19-21, 1801–2100.
Fuckel L. 1869 – Symbolae mycologicae: Beiträge zur Kenntniss der rheinischen Pilze. Symbolae mycologicae: Beiträge zur Kenntniss der rheinischen Pilze. Elsevier.

Fuckel L. 1870 – Symbolae mycologicae. Beiträge zur Kenntniss der Rheinischen Pilze. Jahrbücher des Nassauischen Vereins für Naturkunde 23–24, 1–459.
Fuckel L. 1872 – Symbolae mycologicae. Beiträge zur Kenntniss der Rheinischen Pilze. Erster Nachtrag. Jahrbücher des Nassauischen Vereins für Naturkunde 25–26, 287–346.
Fujimoto H, Fujimaki T, Okuyama E, Yamazaki M. 1999 – Immunomodulatory constituents from an ascomycete, *Microascus tardifaciens*. Chemical and Pharmaceutical Bulletin 47, 1426–1432.
Fujita T, Inoue K, Yamamoto S, Ikumoto T et al. 1994 – Fungal metabolites. Part 11. A potent immunosuppressive activity found in *Isaria sinclairii* metabolite. The Journal of antibiotics 47(2), 208–215.
Fukasawa Y, Takashi O, Takeda H. 2010 – Beech log decomposition by wood-Inhabiting fungi in a cool temperate forest floor: a quantitative analysis focused on the decay activity of a dominant basidiomycete *Omphalotus guepiniformis*. Ecological Research 25, 959–966.
Funk A, Zalasky H. 1975 – *Rhytidiella baranyanyi* n. sp., associated with cork bark of Aspen. Canadian Journal of Botany 53, 752–755.
Funk A. 1963 – Studies in the genus *Caliciopsis*. Canadian Journal of Botany 41, 503–543.
Funk A. 1975 – Stem cankers of young Douglas-firs associated with larval feeding galleries of *Laspeyresia pseudotsugae* (*Lepidoptera*: *Olethreutidae*). Forest Pathology 5, 143–146.
Funk A. 1976 – *Parkerella*, a new genus of *Coronophorales*. Canadian Journal of Botany 54, 868–871
Funk A. 1979 – New species of *Gelatinosporium* on western conifers. Canadian Journal of Botany 57(7), 765–767.
Funk A. 1985 – Foliar fungi of western trees. Pacific Forest Re- search Centre, Victoria, B.C.
Furtado SEJ, Jones EBG. 1980 – The colonization of selected naturally durable timbers by marine fungi and borers. Bulletin de liaison de Comite International Permanent pour les Recherche sur la Preservation des Materiaux en Milieu Marin 8, 63–93
Gaber SE, Hashem AH, El-Sayyad GS, Attia MS. 2023 – Antifungal activity of mycosynthesized bimetallic ZnO-CuO nanoparticles against fungal plant pathogen *Fusarium oxysporum*. Biomass Conversion and Biorefinery 13(11), 1–15.
Gagarina LV, Chesnokov SV, Konoreva LA, Stepanchikova IS et al. 2020 – Lichens of the former manors in the Smolensk Region of Russia. Novitates Systematicae Plantarum non Vascularium 54(1), 93–116.
Gajbhiye M, Sathe S, Shinde V, Kapadnis B. 2016 – Morphological and molecular characterization of pomegranate fruit rot pathogen, *Chaetomella raphigera*, and its virulence factors. Indian journal of microbiology 56, 99–102.
Galán R, Checa J, Blanco MN, Platas G et al. 2015 – Taxonomic position of the genus *Bicornispora* and the appearance of a new species *Bicornispora seditiosa*. Mycologia 107, 793–807.
Galarneau ER, Lawrence DP, Travadon R, Baumgartner K. 2019 – Drought exacerbates botryosphaeria dieback symptoms in grapevines and confounds host-based molecular markers of infection by *Neofusicoccum parvum*. Plant Disease 103, 1738–1745.
Galloway DJ, Guzmán G. 1988 – A new species of *Phlyctis* from Chile. The Lichenologist 20(4), 393–397.
Galloway DJ. 1985 – Flora of New Zealand lichens. P.D. Hasselberg, Government Printer, Wellington.
Galloway DJ. 1988 – Studies in *Pseudocyphellaria* (lichens) I. The New Zealand species. Bulletin of the British Museum (Natural History), Botany 17, 1–267.
Galloway DJ. 1991 – Chemical evolution in the order *Peltigerales*: triterpenoids. Symbiosis 11, 327–344.
Galun M, Reichert I. 1960 – A study of lichens of the Negev. The Bulletin of the Research Council of Israel 9(3), 127–148.
Gamble WR, Gloer JB. 1983 – Polytolypin, a new antifungal triterpenoid from the coprophilous fungus *Polytolypa hystricis*. Journal of Natural Products 58(12), 1984–1986.

Gams V. 1996 – *Phaeoacremonium* gen. novo associated with wilt and decline diseases of woody hosts and human infections.
Gams W, Arnold G. 2007 – The hyphomycete genus *Pleurocatena*, anamorphs of *Pyxidiophora*. Nova Hedwigia 84(3/4), 381–393.
Gams W, Boekhout T. 1985 – Pigment localization in dematiaceous hyphomycetes and the segregation of *Pseudogliomastix* gen. nov. from *Acremonium*. Proceedings: Plant Sciences 94, 273–280.
Gams W, Holubová-Jechová V. 1976 – *Chloridium* and some other dematiaceous *hyphomycetes* growing on decaying wood. Studies in Mycology 13, 1–99.
Gams W, McGinnis MR. 1983a – *Lecythophora hoffmannii* (J.F.H. Beyma). Mycologia 75, 985.
Gams W, McGinnis MR. 1983b – *Phialemonium*, a new anamorph genus intermediate between *Phialophora* and *Acremonium*. Mycologia 75, 977–987.
Gams W, von Arx JA. 1980 – Validation of *Symbiotaphrina* (imperfetc yeasts). Persoonia-Molecular Phylogeny and Evolution of Fungi 10(4), 542–543.
Gams W. 2000 – *Phialophora* and some similar morphologically little-differentiated anamorphs of divergent *Ascomycetes*. Studies in Mycology 45, 187–199.
Gamundí IJ, Spinedi HA. 1985 – *Phaneromyces* Speg. & Hariot, a discomycetous genus of critical taxonomic position. In Sydowia: Annales mycologici.
Gangadevi V, Muthumary J. 2009 – A novel endophytic taxol-producing fungus *Chaetomella raphigera* isolated from a medicinal plant, Terminalia arjuna. Applied biochemistry and biotechnology 158, 675–684.
Gao Y, Frank M, Teusch N, Woschko D et al. 2024 – Aplospojaveedins A–C, unusual sulfur-containing alkaloids produced by the endophytic fungus *Aplosporella javeedii* using OSMAC strategy. Frontiers in Microbiology 15, 1458622.
García D, Stchigel AM, Cano J, Calduch M et al. 2006 – Molecular phylogeny of *Coniochaetales*. Mycological Research 110(11), 1271–1289.
García D, Stchigel AM, Cano J, Guarro J et al. 2004 – A synopsis and re-circumscription of *Neurospora* (syn. *Gelasinospora*) based on ultrastructural and 28S rDNA sequence data. Mycological Research 108, 1119–1142.
Gargas A, DePriest PT, Grube M, Tehler A. 1995 – Multiple origins of lichen symbiosis in fungi suggested by SSU rDNA phylogeny. Science 268, 1492–1495.
Gargas A, Taylor JW. 1995 – Phylogeny of *Discomycetes* and early radiations of the apothecial *Ascomycotina* inferred from SSU rDNA sequence data. Experimental Mycology 19, 7–15.
Garrido-Benavent I, de los Ríos A, Núñez-Zapata J, Ortiz-Álvarez R et al. 2023 – Ocean crossers: A tale of disjunctions and speciation in the dwarf-fruticose *Lichina* (lichenized *Ascomycota*). Molecular Phylogenetics and Evolution 185, 107829.
Garrido-Benavent I. 2015 – Contribución al conocimiento del género *Sarea* Fr. (*Ascomycota*, *Incertae sedis*) en la Península Ibérica. Sociedad Micológica Errotari 12, 42–51.
Gäumann E. 1964 – Die Pilze: Grundzüge ihrer Entwicklungsgeschichte und Morphologie, 2nd edition. Birkhäuser, Basel, Stuttgart.
Gäumann EA, Dodge CW. 1928 – Comparative Morphology of Fungi. New York: McGraw-Hill Book Company Inc.
Gaumann EA. 1928 – Comparative Morphology of Fungi. McGraw-Hill Book Company, Inc., New York and London, England.
Gäumann EA. 1949 – Die Pilze, Grundzüge ihrer Entwicklungsgeschichte und Morphologie. Birkhäuser. Basel.
Gaya E, Fernández-Brime S, Vargas R, Lachlan RF et al. 2015 – The adaptive radiation of lichen-forming *Teloschistaceae* is associated with sunscreening pigments and a bark-to-rock substrate shift. Proceedings of the National Academy of Sciences 112(37), 11600–11605.
Gaya E, Högnabba F, Holguin Á, Molnar K et al. 2012 – Implementing a cumulative supermatrix approach for a comprehensive phylogenetic study of the *Teloschistales* (*Pezizomycotina*, *Ascomycota*). Molecular Phylogenetics and Evolution 63(2), 374–387.

Gazis R, Kuo A, Riley R, LaButti K et al. 2016 – The genome of *Xylona heveae* provides a window into fungal endophytism. Fungal Biology 120(1), 26–42.
Gazis R, Miadlikowska J, Lutzoni F, Arnold AE et al. 2012 – Culture-based study of endophytes associated with rubber trees in Peru reveals a new class of *Pezizomycotina*, *Xylonomycetes*. Molecular Phylogenetics and Evolution 65(1), 294–304.
Ge ZW, Yang ZL, Pfister DH, Carbone M et al. 2014 – Multigene molecular phylogeny and biogeographic diversification of the earth tongue fungi in the genera *Cudonia* and *Spathularia* (*Rhytismatales*, *Ascomycota*). PLoS ONE 9, e103457.
Geiser DM, Gueidan C, Miadlikowska J, Lutzoni F et al. 2006 – *Eurotiomycetes*: *Eurotiomycetidae* and *Chaetothyriomycetidae*. Mycologia 98(6), 1053–1064.
Geiser DM, LoBuglio KF, Gueidan C. 2015 – 5 *Pezizomycotina*: *Eurotiomycetes*. Systematics and evolution: Part B 121–141.
Geiser DM, LoBuglio KL. 2001 – The monophyletic *Plectomycetes*: *Ascosphaerales*, *Onygenales*, *Eurotiales*. In: McLaughlin DJ, McLaughlin EG, Lemke PA (eds) The mycota: systematics and evolution, vol. VIIA. Springer, Berlin.
Geldenhuys CJ. 1993 – Reproductive biology and population structures of *Podocarpus falcatus* and *P. latifolius* in southern Cape forests. Botanical Journal of the Linnean Society 112, 59–74.
Gené J, Hernández-Restrepo M, Castañeda-Ruiz RF, Mena-Portales J et al. 2017 – Phylogeny of saprobic microfungi from Southern Europe.
Gernandt DS, Platt JL, Stone JK, Spatafora JW et al. 2001 – Phylogenetics of *Helotiales* and *Rhytismatales* based on partial small subunit nuclear ribosomal DNA sequences. Mycologia 93, 915–933.
Geyer M. 1985 – Hochdruck-Flüssigkeits-Chromatographie (HPLC) von Flechten-Sekundärstoffen. Mechtild Geyer, Essen.
Gibas C, Sigler L, Summerbell R, Currah R. 2002a – Phylogeny of the genus *Arachnomyces* and its anamorphs and the establishment of *Arachnomycetales*, a new eurotiomycete order in the *Ascomycota*. Studies in Mycology 47(47), 131–139.
Gibas CFC, Sigler L, Summerbell RC, Hofstader SLR et al. 2002b – *Arachnomyces kanei* (anamorph *Onychocola kanei*) sp. nov., from human nails. Medical Mycology 40, 573–580.
Gigliotti F, Limper AH, Wright T. 2014 – *Pneumocystis*. Cold spring harbor perspectives in medicine 4(12).
Gilbert OL, Coppins BJ. 2009 – *Sporastatia* Massal. In: The Lichens of Great Britain and Ireland (C. W. Smith, A. Aptroot, B. J. Coppins, A. Fletcher, O. L. Gilbert, P. W. James, P. A. Wolseley, eds). British Lichen Society, London, UK.
Gilbert OL. 2004 – The phenology of *Sarcosagium campestre* observed over three years. The Lichenologist 36(2), 159–161.
Gilenstam, G. 1969 – Studies in the lichen genus *Conotrema*. Arkiv för Botanik, ser 2, 7 (2), 149–179.
Giménez-Abián M, Bernabé M, Leal A, Jiménez-Barbero J et al. 2007 – Structure of a galactomannan isolated from the cell wall of the fungus *Lineolata rhizophorae*. Carbohydrate Research 342(17), 2599–2603.
Ginns JH. 1986 – Compendium of plant disease and decay fungi in Canada 1960-1980. Research Branch, Agriculture Canada 1813, 416.
Giraldo A, Crous PW, Schumacher RK, Cheewangkoon R et al. 2017 − The genera of fungi—G3: *Aleurocystis*, *Blastacervulus*, *Clypeophysalospora*, *Licrostroma*, *Neohendersonia* and *Spumatoria*. Mycological Progress 16, 325−48.
Giraldo A, Gené J, Sutton DA, Madrid H et al. 2014a – Phylogenetic circumscription of *Arthrographis* (*Eremomycetaceae*, *Dothideomycetes*). Persoonia: Molecular Phylogeny and Evolution of Fungi 32, 102–114.
Giraldo A, Sutton DA, Samerpitak K, de Hoog G et al. 2014b – Occurrence of *Ochroconis* and *Verruconis* species in clinical specimens from the United States. Journal of Clinical Microbiology 52, 4189–4201.

Glawe DA. 1985 – The pleomorphic asexual state of *Valsaria insitiva* in artificial culture. Mycologia 77, 62–71.
Glocker EO, Hennigs A, Nabavi M, Schäffer AA et al. 2009 – A homozygous CARD9 mutation in a family with susceptibility to fungal infections. New England Journal of Medicine 361, 1727–1735.
Goh TK, Ho WH, Hyde KD, Whitton SR et al. 1998a – New records and species of *Canalisporium* (*Hyphomycetes*), with a revision of the genus. Canadian Journal of Botany 76, 142–152.
Goh TK, Hyde KD, Tsui KM. 1998b – The hyphomycete genus *Acrogenospora*, with two new species and two new combinations. Mycological Research 102, 1309–1315.
Goh TK, Hyde KD. 1996 – *Spadicoides cordanoides* sp. nov., a new dematiaceous hyphomycete from submerged wood in Australia, with a taxonomic review of the genus. Mycologia 88, 1022–1031.
Goh TK, Hyde KD. 1998 – A new hyphomycete genus, *Conioscyphopsis*, from wood submerged in a freshwater stream and a review of *Conioscypha*. Mycological Research 102, 305–312.
Goh TK, Kuo CH. 2018 – A new species of Helicoön from Taiwan. Phytotaxa 346, 141.
Goh TK, Kuo CH. 2021 – Reflections on *Canalisporium*, with descriptions of new species and records from Taiwan. Mycological progress 20, 647–680.
Goh TK, Ou JH, Kuo CH. 2021 – *Phaeonawawia*, a novel chaetosphaeriaceous anamorph from submerged wood in Malaysia. Mycological Progress 20, 227–245.
Gold HS. 1959 – Distribution of some lignicolous *Ascomycetes* and Fungi Imperfecti in an estuary. Journal of the Elisha Mitchell Scientific Society 75, 25–28.
Goldie SJ, Freedberg KA. 1999 – Diagnosis and treatment of *Pneumocystis carinii* pneumonia: Economic issues and cost-effectiveness. In Seminars in respiratory and critical care medicine (Vol. 20, No. 03, pp. 213-220). Copyright© 1999 by Thieme Medical Publishers, Inc.
Goldmann L, Weir A, Rossi W. 2013 – Molecular analysis reveals two new dimorphic species of *Hesperomyces* (*Ascomycota*, *Laboulbeniomycetes*) parasitic on the ladybird *Coleomegilla maculata* (*Coleoptera*, *Coccinellidae*). Fungal Biology 117, 807–813.
Goldmann L, Weir A. 2012 – Position specificity in *Chitonomyces* (*Ascomycota*, *Laboulbeniomycetes*) on *Laccophilus* (*Coleoptera*, *Dytiscidae*): a molecular approach resolves a century-old debate. Mycologia 104(5), 1143–1158.
Goldmann L, Weir A. 2018 – Molecular phylogeny of the *Laboulbeniomycetes* (*Ascomycota*). Fungal Biology 122(2–3), 87–100.
Golonka AM, Vilgalys R. 2013 – Nectar inhabiting yeasts in Virginian populations of *Silene latifolia* (*Caryophyllaceae*) and coflowering species. American Midland Naturalist Golubkova NS. 1988 – Lishajniki semejstva Acarosporaceae Zahlbr. v SSSR, Nauka, Leningrad.
Golubkova NS. 1973 – Species lichenum pro flora URSS novae. Novitates Systematicae Plantarum non Vascularium 10, 200–206.
Golubkova NS. 1982 – Genus *Sporastatia* Massal. in URSS. Novitates Systematicae Plantarum non Vascularium 19, 131–143.
Gomdola D, Bhunjun CS, Hyde KD, Jeewon R et al. 2023 – Ten important forest fungal pathogens: a review on their emergence and biology. Mycosphere 13(1), 612–671.
Gonthier P, Nicolotti G, Linzer R, Guglielmo F et al. 2007 – Invasion of European pine stands by a North American forest pathogen and its hybridization with a native interfertile taxon. Molecular ecology 16, 1389–400.
Gonzalez F, Martin S. 1996 – Contribución al conocimiento de cinco géneros de la familia *Nitschkiaceae* (*Hymenoascomycetes*: *Sordariales*). Acta Botánica Mexicana 36, 43–52.
González MC, Chavarría A. 2005 – Some freshwater ascomycetes from Mexico. Mycotaxon 91, 315–322.
Goodwin SB, Dunkle LD, Zismann VL. 2001 – Phylogenetic analysis of *Cercospora* and *Mycosphaerella* based on the internal transcribed spacer region of ribosomal DNA. Phytopathology 91, 648–658.
Goos R. 1985 – A review of the anamorph genus *Helicomyces*. Mycologia 77, 606–618.

Goos R. 1986 – A review of the anamorph genus *Helicoma*. Mycologia 78, 744–761.
Goos R. 1989 – On the anamorph genera *Helicosporium* and *Drepanospora*. Mycologia 81, 356–374.
Goos RD, Andersons JH. 1974 – The *Meliolaceae* of Hawaii. Sydowia 26, 73–80.
Gottwald TR. 1995 – Spatio-temporal analysis and isopath dynamics of citrus scab in nursery plots. Phytopathology 85, 1082–1092.
Gou H, Wei H, Duan R, Chen T et al. 2022 – Spatial distribution of modern pollen and fungal spores and their ecological indication in Qinghai Lake on northeastern Tibetan Plateau, China. Ecological Indicators 144, 109474.
Graddon W. 1984 – Some new discomycete species: 6. Transactions of the British Mycological Society 83, 377–382.
Gramaje D, Agustí-Brisach C, Pérez-Sierra A, Moralejo E et al. 2012 – Fungal trunk pathogens associated with wood decay of almond trees on *Mallorca* (Spain). Persoonia: Molecular Phylogeny and Evolution of Fungi 28, 1–13.
Gramaje D, Armengol J, Mohammadi H, Banihashemi Z et al. 2009 – Novel *Phaeoacremonium* species associated with Petri disease and esca of grapevine in Iran and Spain. Mycologia 101, 920–929.
Gramaje D, Mostert L, Groenewald JZ, Crous PW. 2015 – *Phaeoacremonium*: from esca disease to phaeohyphomycosis. Fungal Biology 119, 759–783.
Grasso S, Panebianco C, La Ferla R. 1990 – Lignicolous marine fungi in the straits of Messina, Italy. Hyrobiologia 206, 149–154.
Gray SF. 1821 – A natural arrangement of British plants: according to their relations to each other as pointed out by Jussieu, De Candolle, Brown, &c. London: Baldwin, Cradock, and Joy.
Green AT, Schlensog M, Sancho LG, Winkler BJ et al. 2002 – The photobiont determines the pattern of photosynthetic activity within a single lichen thallus containing cyanobacterial and green algal sectors (photosymbiodeme). Oecologia 130 (2), 191–198.
Gregersen IK, Hegseth MN, Hestmark G, Kongsbak RH et al. 2006 – The relationship between thallus mass, surface area and apothecium production in *Umbilicaria rigida*. - Nova Hedwigia 82(1-2), 115–121.
Greif MD, Currah RS. 2003 – A functional interpretation of the role of the reticuloperidium in whole-ascoma dispersal by arthropods. Mycological Research 107, 77–81.
Greif MD, Gibas CFC, Tsuneda A, Currah RS. 2007 – Ascoma development and phylogeny of an apothecioid *Dothideomycete*, *Catinella olivacea*. American Journal of Botany 94(11), 1890–1899.
Greif MD, Tsuneda A, Currah RS. 2004 – The peridial development and dehiscence mechanism of *Cryptendoxyla hypophloia*, a cleistothecial ascomycete isolated from the bodies of arthropods. International Journal of Plant Sciences 165(6), 957–964.
Grey ABJ, Cadelis MM, Diao Y, Park D et al. 2021 – Screening of fungi for antimycobacterial activity using a medium-throughput bioluminescence-based assay. Frontiers in Microbiology 12, 739995.
Groenewald M, Hittinger CT, Bensch K, Opulente DA et al. 2023 – A genome-informed higher rank classification of the biotechnologically important fungal subphylum *Saccharomycotina*. Studies in Mycology 105(1), 1–22.
Groenewald M, Kang JC, Crous PW, Gams W. 2001 – ITS and beta-tubulin phylogeny of *Phaeoacremonium*, *Phaeomoniella* spp. Mycological Research 105, 651–657.
Groenhart P. 1938 – Einige *Cryptotheciaceae* van Java. Natuurk. Tijdschr. Ned. Indie 98, 304–310.
Grove JF, Pople M. 1981 – The insecticidal activity of some fungal dihydroisocoumarins. Mycopathologia 76, 65–67.
Grove WB. 1885 – New or noteworthy fungi. Part II. Journal of Botany, British and Foreign 23, 161–168.
Groves JW. 1954 – The genus *Durandiella*. Canadian Journal of Botany 32(1), 116–144.

Grube M, Baloch E, Lumbsch HT. 2004 – The phylogeny of *Porinaceae* (*Ostropomycetidae*) suggests a neotenic origin of perithecia in *Lecanoromycetes*. Mycological Research 108(10), 1111–1118.
Grube M, Hafellner J. 1990 – Studien an flechtenbewohnenden Pilzen der Sammelgattung *Didymella* (*Ascomycetes*, *Dothideales*). Nova Hedwigia 51(3–4), 283–360.
Grube M, Poelt J. 1993 – Beiträge zur Kenntnis der Flechtenflora des Himalaya X. *Sporastatia* testudinea, ihre Variabilität, ihre Ökologie und ihre Parasiten in Hochasien. Fragmenta Floristica et Geobotanica Supplementum 2, 113–122.
Grube M, Ryan BD. 2002 – *Collemopsidium*. In: Nash TH, Ryan BD, Gries C, Bungartz F (eds) Lichen flora of the Greater Sonoran Desert Region. Lichens Unlimited, Tempe 1162–1164.
Grube M. 1998 – Classification and phylogeny in the *Arthoniales* (lichenized *Ascomycetes*). Bryologist 101, 377–391.
Grube M. 1999 – Epifluorescence studies of the ascus in *Verrucariales* (lichenized *Ascomycotina*). Nova Hedwigia 68, 241–249.
Grube M. 2001 – *Sporostigma*, a new calicioid genus in *Arthoniales*. The Lichenologist 33, 387–391.
Grube M. 2005 – *Frigidopyrenia*–A new genus for a peculiar subarctic lichen, with notes on similar taxa. Phyton 45(2), 305–318.
Gryzenhout M, Myburg H, Hodges CS, Wingfield BD et al. 2006a – *Microthia*, *Holocryphia* and *Ursicollum*, three new genera on *Eucalyptus* and *Coccoloba* for fungi previously known as *Cryphonectria*. Studies in Mycology 55, 35–52.
Gryzenhout M, Myburg H, Rodas CA, Wingfield BD et al. 2006b – *Aurapex penicillata* gen. sp. nov. from native *Miconia theaezans* and *Tibouchina* spp. in Colombia. Mycologia 98(1), 105–115.
Gu HL, Lin YR, Peng F, Li Q et al. 2015 – *Marthamyces chinensis* sp. nov. on *Fissistigma* from China. Mycotaxon 130, 815–820.
Guarro J, Nucci M, Akiti T, Gené J et al. 1999 – *Phialemonium* fungemia, two documented nosocomial cases. Journal of Clinical Microbiology 37, 2493–2497.
Guarro J, Vieira LA, De Freitas D, Gené J et al. 2000 – *Phaeoisaria clematidis* as a Cause of Keratomycosis. Journal of Clinical Microbiology 38, 2434–2437.
Guatimosim E, Firmino AL, Bezerra JL, Pereira OL et al. 2015a – Towards a phylogenetic reappraisal of *Parmulariaceae* and *Asterinaceae* (*Dothideomycetes*). Persoonia: Molecular Phylogeny and Evolution of Fungi 35(1), 230–41.
Guatimosim E, Pinto HJ, Pereira OL, Fuga CA et al. 2015b – Pathogenic mycobiota of the weeds *Bidens pilosa* and *Bidens subalternans*. Tropical Plant Pathology 40, 298–317.
Guatimosim E, Schwartsburd PB, Barreto RW, Crous PW. 2016 – Novel fungi from an ancient niche: Cercosporoid and related sexual morphs on ferns. Persoonia 37, 106–141.
Gubler WD, Thind TS, Feliciano AJ, Eskalen A. 2020 – Pathogenicity of *Phaeoacremonium aleophilum* and *Phaeomoniella chlamydospora* on grape berries in California. Phytopathologia Mediterranea 43, 70–74.
Guegan H, Cailleaux M, Le Gall F, Robert-Gangneux F et al. 2021 – Chromoblastomycosis due to a never-before-seen dematiaceous fungus in a kidney transplant patient. Microorganisms 9(10), 2139.
Gueidan C, Aptroot A, Cáceres MES. 2016 – Molecular phylogeny of the tropical family *Pyrenulaceae*: contribution from dried specimens and FTA card samples. Mycological Progress 15(7), 1–21.
Gueidan C, Aptroot A, da Silva Cáceres ME, Badali H et al. 2014a – A reappraisal of orders and families within the subclass *Chaetothyriomycetidae* (*Eurotiomycetes*, *Ascomycota*). Mycological Progress 13, 1027–1039.
Gueidan C, Hill DJ, Miadlikowska J, Lutzoni F. 2015 – *Pezizomycotina*: *Lecanoromycetes*. Systematics and Evolution: Part B 89–120.
Gueidan C, Roux C, Lutzoni F. 2007 – Using a multigene phylogenetic analysis to assess generic delineation and character evolution in *Verrucariaceae* (*Verrucariales*, *Ascomycota*). Mycological Research 111(10), 1145–1168.

Gueidan C, Ruibal C, De Hoog G, Schneider H. 2011 – Rock-inhabiting fungi originated during periods of dry climate in the late Devonian and middle Triassic. Fungal Biology 115, 987–996.

Gueidan C, Villaseñor CR, De Hoog GS, Gorbushina AA et al. 2008 – A rock-inhabiting ancestor for mutualistic and pathogen-rich fungal lineages. Studies in Mycology 61(1), 111–119.

Gueidan CT, Do V, Lu NT. 2014b – Phylogeny and taxonomy of *Staurothele* (*Verrucariaceae*, lichenized *ascomycetes*) from the karst of northern Vietnam. The Lichenologist 46(4), 515–533.

Guevara-Suarez M, García D, Cano-Lira JF, Guarro J et al. 2020 – Species diversity in *Penicillium* and *Talaromyces* from herbivore dung, and the proposal of two new genera of *Penicillium*-like fungi in *Aspergillaceae*. Fungal Systematics and Evolution 5(1), 39–76.

Guillot J, Chevalier V, Queney G, Berthelemy M et al. 1999 – Acquisition and biodiversity of *Pneumocystis carinii* in a colony of wild rabbits (*Oryctolagus cuniculus*). Journal of Eukaryotic Microbiology 46, S100–S101.

Guillot J, Demanche C, Hugot JP, Berthelemy M et al. 2001 – Parallel phylogenies of *Pneumocystis* species and their mammalian hosts. Journal of Eukaryotic Microbiology 47, S113–S115.

Guo C, Wu P, Xue J, Li H et al. 2018 − Xylaropyrones B and C, new γ-pyrones from the endophytic fungus *Xylaria* sp. SC1440. Natural Product Research 32, 1525–31.

Guo CJ, Wu P, Xue JH, Li HX et al. 2019 − Xylarodons A and B, new hexaketides from the endophytic fungus *Xylaria* sp. SC1440. Journal of Asian Natural Products Research 21, 343–50.

Guo MJ, Zhuo L, Wang SJ, Sui XN et al. 2024 − Hyperdiverse *Rhytismatales* on twigs of *Rhododendron* spp. Mycosphere 15(1), 764−880.

Gupta AK, Gregurek-Novak T, Konnikov N, Lynde CW et al. 2001 – Itraconazole and terbinafine treatment of some nondermatophyte molds causing onychomycosis of the toes and a review of the literature. Journal of cutaneous medicine and surgery 5(3), 206–210.

Gupta AK, Jain HC, Lynde CW, Watteel GN et al. 1997 – Prevalence and epidemiology of unsuspected onychomycosis in patients visiting dermatologists' ofces in Ontario, Canada--a multicenter survey of 2001 patients. International journal of Dermatology 36, 783–787.

Gupta D, Chatterjee S, Datta S. 2019 – Potential of *Cladosporium cladosporioides* for heavy metal bioremediation. Environmental Science and Pollution Research 26(21), 21202–21215.

Gurgel RS, Pereira DIM, Martins B, Falco LS et al. 2024 – Global phenolic composition and antioxidant capacity of extracts from the endophytic fungi *Cophinforma mamane* with potential use in food systems: The effects of time, temperature, and solvent on the extraction process. Applied Sciences 14, 8784.

Guterres DC, Dos Santos MD, Silva RA, Souza ES et al. 2020 – *Cladosterigma*: an enigmatic fungus, previously considered a basidiomycete, now revealed as an ascomycete member of the *Gomphillaceae*. Mycologia 112(4), 829–46.

Guterres DC, Dos Santos MDM, Furlanetto C, Pinho DB et al. 2022 – Filling a gap in the taxonomy of phyllachoroid fungi: Proposition of *Neopolystigma*, gen. nov., and the new family *Neopolystigmataceae*. Mycologia 114, 900–913.

Guterres DC, Galvão-Elias S, dos Santos MDM, Pereira de Souza BC et al. 2019 – Phylogenetic relationships of *Phaeochorella parinarii* and recognition of a new family, *Phaeochorellaceae* (*Diaporthales*). Mycologia 111 (4), 660–675.

Guterres DC, Galvão-Elias S, Pereira de Souza BC, Batista-Pinho D et al. 2018 – Taxonomy, phylogeny, and divergence time estimation for *Apiosphaeria guaranitica*, a Neotropical parasite on bignoniaceous hosts, Mycologia 110 (3), 526–545.

Gutierrez AC, Ordoqui E, Leclerque A, López Lastra C. 2020 – A new species of *Herpomyces* (*Laboulbeniomycetes*: *Herpomycetales*) on *Periplaneta fuliginosa* (*Blattodea*: *Blattidae*) from Argentina. Mycologia 112(6), 1184–1191.

Gutierrez RMP, Gonzalez AMN, Ramirez AM. 2012 – Compounds derived from endophytes: A review of phytochemistry and pharmacology. Current Medicinal Chemistry 19: (18), 2992 – 3030.
Guzmán-Guillermo J, Barrera Bernal C, Llarena-Hernández RC. 2021 – The lichenized fungi of the genus *Glyphis* in Veracruz, Mexico. Acta botánica Mexicana 128.
Gyelnik V. 1934 – Lichenes argentinenses a professore C.C. Hosseus collecti. Feddes Repert. Spec. Nov. Regni veg. 33, 304.
Gyelnik V. 1937 – Lichenotheca 9, no. 164.
Habib K, Chiva S, Firdous Q, Nadeem S et al. 2023 – A new species of *Clavascidium* (*Verrucariales*, Lichenized *Ascomycota*) from Pakistan and Spain, with remarks on the photosymbiont. Plant Systematics and Evolution 309(3), 17.
Habibi A, Banihashemi Z, Mostowfizadeh-Ghalamfarsa R. 2015 – Phylogenetic analysis of *Polystigma* and its relationship to *Phyllachorales*. Phytopathologia Mediterranea 54, 45–54.
Haeberli W, King L, Flotron A. 1979 – Surface movement and lichen-cover studies at the active rock glacier near the Grubengletscher, Wallis, Swiss Alps. Arctic and Alpine Research 11, 421–441.
Haeckel E. 1894 – Systematische Phylogenie. Entwurf eines Natürlichen Systems der Organismen auf Grund ihrer Stammesgeschichte. Theil1, Systematische Phylogenie der Protisten und Pflanzen. (Berlin: G. Reimer) 1–400.
Haelewaters D, Blackwell M, Pfister DH. 2021a – *Laboulbeniomycetes*: intimate fungal associates of arthropods. Annual Review of Entomology 66, 257–276.
Haelewaters D, Boer P, Báthori F, Rádai Z et al. 2019a – Studies of *Laboulbeniales* on *Myrmica* ants (IV): host-related diversity and thallus distribution patterns of *Rickia wasmannii*. Parasite 26–29.
Haelewaters D, De Kesel A, Gorczak M, Bao K et al. 2019b – *Laboulbeniales* (*Ascomycota*) of the Boston Harbor Islands II: species parasitizing *Carabidae*, and the *Laboulbenia flagellata* species complex. Northeastern Naturalist 25(Special Issue 9), 110–149.
Haelewaters D, De Kesel A, Pfister DH. 2018 – Integrative taxonomy reveals hidden species within a common fungal parasite of ladybirds. Scientific Reports 8(1), 15966.
Haelewaters D, Dima B, Abdel-Hafiz BII, Abdel-Wahab MA et al. 2020a – Fungal systematics and evolution: FUSE 6. Sydowia 72, 231–356.
Haelewaters D, Gorczak M, Kaishian P, De Kesel A et al. 2021b – *Laboulbeniomycetes*, enigmatic fungi with a turbulent taxonomic history. In: Zaragoza Ó, Casadevall A, editors. Encyclopedia of mycology. Vol. 1. Oxford: Elsevier 263–283.
Haelewaters D, Gorczak M, Pfliegler WP, Tartally A et al. 2015 – Bringing *Laboulbeniales* into the 21st century: enhanced techniques for extraction and PCR amplification of DNA from minute ectoparasitic fungi. IMA Fungus 6, 363–372.
Haelewaters D, Hiller T, Kemp EA, van Wielink PS et al. 2020b – Mortality of native and invasive ladybirds co-infected by ectoparasitic and entomopathogenic fungi. PeerJ 8, e10110.
Haelewaters D, Lubbers M, De Kesel A. 2022a – The haustorium as a driving force for speciation in thallus-forming *Laboulbeniomycetes*. IMA Fungus 13, 1.
Haelewaters D, Matthews TJ, Wayman JP, Cazabonne J et al. 2024 – Biological knowledge shortfalls impede conservation efforts in poorly studied taxa–A case study of *Laboulbeniomycetes*. Journal of Biogeography 51, 29–39.
Haelewaters D, Park D, Johnston PR. 2021c – Multilocus phylogenetic analysis reveals that *Cyttariales* is a synonym of *Helotiales*. Mycological Progress 20(10), 1323–1330.
Haelewaters D, Pfister DH. 2019 – Morphological species of *Gloeandromyces* (*Ascomycota*, *Laboulbeniales*) evaluated using single-locus species delimitation methods. Fungal Systematics and Evolution 3(1), 19–34.
Haelewaters D, Pfliegler WP, Gorczak M, Pfister DH. 2019c – Birth of an order: comprehensive molecular phylogenetic study excludes *Herpomyces* (Fungi, *Laboulbeniomycetes*) from *Laboulbeniales*. Molecular Phylogenetics and Evolution 133, 286–301.

Haelewaters D, Stallman JK, Henkel TW, Aime MC. 2022b – Molecular phylogenetic analyses and micromorphology reveal placement of the enigmatic tropical discomycete *Polydiscidium* in *Sclerococcum* (*Sclerococcales*, *Eurotiomycetes*). Mycologia 114(3), 626–641.
Haelewaters D. 2018 – Studies of the *Laboulbeniomycetes*: Diversity, evolution, and patterns of speciation (Doctoral dissertation, Harvard University).
Hafellner J, Egan RS. 1981 – Studies on the genus *Speerschneidera*. The Lichenologist 13(1), 11–26.
Hafellner J, Mayrhofer H, Poelt J. 1979 – Die Gattungen der Flechtenfamilie *Physciaceae.* Herzogia 5, 39–79.
Hafellner J, Obermayer W, Tretiach M. 2014 – *Miriquidica invadens*, an obligate youth parasite on *Sporastatia*, with remarks and a key to species of the *M. griseoatra* group. The Lichenologist 46, 303–331.
Hafellner J, Poelt J. 1976 – Die Gattung *Karschia*—Bindeglied zwischen bitunicaten Ascomyceten und lecanoralen Flechtenpilzen?/The Genus *Karschia*—Link Between Bitunicate *Ascomycetes* and *Lecanorales*?. Plant Systematics and Evolution 243–254.
Hafellner J, Poelt J. 1979 – Die Arten der Gattung Caloplaca mit pluriloculären Sporen (*Meroplacis*, *Triophthalmidium*, *Xanthocarpia*). J. Hattori Bot. Lab. 46, 1–41.
Hafellner J, Türk R. 2001 – Die lichenisierten Pilze Österreichs - eine Checkliste der bisher nachgewiesenen Arten mit verbreitungsangaben. Stapfia 76, 1–167.
Hafellner J. 1979 – *Karschia*. Revision einer Sammelgattung an der grenze von lichenisierten und nichtlichenisierten Ascomyceten. Beihefte Nova Hedwigia 62, 1–248.
Hafellner J. 1982 – Studien über lichenicole Pilze und Flechten II. *Lichenostigma maureri* gen. et spec. nov., ein in den Ostalpen häufiger lichenicoler Pilz (*Ascomycetes, Arthoniales)*. Herzogia 6, 299–308.
Hafellner J. 1984 – Studien in Richtung einer naturlicheren Gliederung der Sammelfamilien *Lecanoraceae* und *Lecideaceae*. Beiheft zur Nova Hedwigia 79, 241–371.
Hafellner J. 1988 – Principles of classification and main taxonomic groups. In CRC handbook of lichenology. Galun, M., ed.: 41–52. Boca Raton, Florida: CRC Press.
Hafellner J. 1993 – *Acarospora* und *Pleopsidium* – zwei lichenisierte Ascomycetengattungen (*Lecanorales*) mit zahlreichen Konvergenzen. Nova Hedwigia 56, 281–305.
Hafellner J. 1994 – Problems in *Lecanorales* systematics. In: Hawksworth DL (ed.), Ascomycete Systematics: Problems and perspectives in the Nineties. Plenum Press: New York and London. 315–320.
Hafellner J. 1995 – Towards a better circumscription of the *Acarosporaceae* (lichenized *Ascomycotina*, *Lecanorales*). Cryptogamic Botany 5, 99–104.
Hafellner J. 2019 – A reinvestigation of *Microthelia umbilicariae* results in a contribution to the species diversity in *Endococcus*. Institut für Biologie, Bereich Pflanzenwissenschaften der Karl-Franzens-Universität Graz.
Hagestad OC, Hou L, Andersen JH, Hansen EH et al. 2021 – Genomic characterization of three marine fungi, including *Emericellopsis atlantica* sp. nov. with signatures of a generalist lifestyle and marine biomass degradation. IMA Fungus 12(1), 21.
Haituk S, Withee P, Sangta J, Senwanna C et al. 2022 – Production of non-volatile metabolites from sooty molds and their bio-functionalities. Processes 10(2), 329.
Hakulinen R. 1954 – Dir Flechtengattung *Candelariella* Mull. Argoviensis, mit besonderer Berucksichtigung ihres Auftretens und ihrer Verbreitung in Fennoskandien. Ann. Bot. Soc. Zool. Bot. Fenn. 'Vanamo'27(3), 1–127.
Halbwachs H, Bässler C. 2020 – No bull: Dung-dwelling mushrooms show reproductive trait syndromes different from their noncoprophilous allies. Mycological Progress 19(8), 817–824.
Halda J. 2003 – A taxonomic study of the calcicolous endolithic species of the genus *Verrucaria* (*Ascomycotina*, *Verrucariales*) with the lid-like and radiately opening involucrellum. Rychnov nad Knežnou: Muzeum a galerie Orlických ˇ hor 10, 1–148.

Halici MG, Kahraman Yiğit M, Bölükbaşi E, Güllü M. 2023 – New record and new species of lichenized fungal genus *Candelariella* Müll. Arg. in Antarctica. Polish Polar Research 44(1), 69–83.
Halıcı MG, Kocakaya M, Aksoy A. 2009 – *Lichenostigma anatolicum* sp. nov. (*Ascomycota*, *Lichenotheliaceae*) on a brown *Acarospora* from central Turkey. Mycotaxon 108(1), 67–72.
Halleen F, Crous PW, Petrini O. 2003 – Fungi associated with healthy grapevine cuttings in nurseries, with special reference to pathogens involved in the decline of young vines. Australasian Plant Pathology 32, 47–52.
Halleen F, Groenewald M. 2005 – Grapevine diagnostic observations with special reference to trunk diseases. In The 15th Biennial Australasian Plant Pathology Society Conference Handbook 26–29.
Halleen F, Mostert L, Crous PW. 2007 – Pathogenicity testing of lesser-known vascular fungi of grapevines. Australasian Plant Pathology 36, 277–285.
Halleen F, Schroers HJ, Groenewald JZ, Rego C et al. 2006 – *Neonectria liriodendri* sp. nov., the main causal agent of black foot disease of grapevines. Studies in Mycology 55, 227–234.
Hamayun M, Afzal Khan S, Khan A, Afzal M et al. 2012 – Endophytic *Cephalotheca sulfurea* AGH07 reprograms soybean to higher growth. Journal of Plant Interactions 7, 301–306.
Hambleton S, Tsuneda A, Currah RS. 2003 – Comparative morphology and phylogenetic placement of two microsclerotial black fungi from Sphagnum. Mycologia 95(5), 959–975.
Hammerschmidt L, Aly AH, Abdel-Aziz M, Müller WEG et al. 2015 – Cytotoxic acyl amides from the soil fungus *Gymnascella dankaliensis*. Bioorganic & Medicinal Chemistry 23(4), 712–719.
Han JG, Hosoya T, Sung GH, Shin HD. 2014 – Phylogenetic reassessment of (*Hyaloscyphaceae sensu lato Helotiales*, *Leotiomycete*s) based on multigene analyses. Fungal Biology 118, 150–167.
Han WB, Zhai YJ, Gao Y, Zhou HY et al. 2019 − Cytochalasins and an abietane-type diterpenoid with allelopathic activities from the endophytic fungus *Xylaria* species. Journal of Agricultural and Food chemistry 67(13), 3643−50.
Hanlin RT. 1990 – *Acerviclypeatus*, a new genus for the anamorph of *Ophiodothella vaccinii*. Mycotaxon 37, 379–384.
Hansen K, Pfister DH. 2006 – Systematics of the *Pezizomycetes*-the operculate *Discomycetes*. Mycologia 98, 1029–1040.
Hansford CG. 1946 – The foliicolous *Ascomycetes* their parasites and associated fungi especially as illustrated by Uganda specimens. Mycological Papers 15, 1–240.
Hansford CG. 1961 – The *Meliolaceae* a monograph. Sydowia Beih 2, 1–806.
Harada H. 2015 – *Thelocarpon epibolum Ascomycota*, *Thelocarpaceae* newly found in Japan. Lichenology 13(2), 53–57.
Haridas S, Albert R, Binder M, Bloem J et al. 2020 – 101 *Dothideomycetes* genomes: a test case for predicting lifestyles and emergence of pathogens. Studies in Mycology 96, 141–153.
Harman GE, Doni F, Khadka RB, Uphoff N. 2021 – Endophytic strains of *Trichoderma* increase plants' photosynthetic capability. Journal of Applied Microbiology 130(2), 529–546.
Harms K, Milic A, Stchigel AM, Stadler M et al. 2021 – Three new derivatives of zopfinol from *Pseudorhypophila mangenotii* gen. et comb. nov. Journal of Fungi 7(3), 181.
Harnpicharnchai P, Champreda V, Sornlake W, Eurwilaichitr L. 2009 – A thermotolerant β-glucosidase isolated from an endophytic fungi, *Periconia* sp., with a possible use for biomass conversion to sugars. Protein Expr Purif 67, 61–69.
Harrington AH, del Olmo-Ruiz M, U'Ren JM, Garcia K et al. 2019 – *Coniochaeta endophytica* sp. nov., a foliar endophyte associated with healthy photosynthetic tissue of *Platycladus orientalis* (*Cupressaceae*). Plant and Fungal Systematics 64, 65–79.
Harrington AH, Sarmiento C, Zalamea PC, Dalling JW et al. 2022 – *Acrogenospora terricola* sp. nov., a fungal species associated with seeds of pioneer trees in the soil seed bank of a lowland forest in Panama. International Journal of Systematic and Evolutionary Microbiology 72(10), 5558.

Harrington FA, Pfister DH, Potter D, Donoghue MJ. 1999 – Phylogenetic studies within the *Pezizales*. I. 18S rRNA sequence data and classification. Mycologia 91, 41–50.
Harrington TC. 2005 – Ecology and evolution of mycophagous bark beetles and their fungal partners. In: Vega FE, Blackwell M (eds) Insect-fungal associations: ecology and evolution. Oxford University Press, New York, 1–22
Harris RC, Buck WR. 1978 – Lichens of the Mackinae Straits Region. II. *Candelariella* Müll. Arg. Michigan Botanist 17, 155–161.
Harris RC. 1984 – The family *Trypetheliaceae* (*Loculoascomycetes*: lichenized *Melanommatales*) in Amazonian Brazil. Acta Amazonica (Suppl.) 14(1/2), 55–80.
Harris RC. 1990 – Some Florida lichens. Publ. by the Author, Bronx
Harris RC. 1991 – A revision of *Polymeridium*(Muell.Arg.) R. C. Harris (*Trypetheliaceae*). Bol. Mus. Paraense "Emílio Goeldi", N.S., Bot. 7, 619–644.
Harris RC. 1995 – More Florida Lichens including the 10 c Tour of the Pyrenolichens. - New York, privately published.
Harris RC. 1998 – A preliminary revision of *Pseudopyrenula* Müll.Arg. (lichenized *Ascomycetes*, *Trypetheliaceae*) with a redisposition of the names previously assigned to the genus. in: Glenn, M.G., Harris, R.C., Dirig, R. & Cole, M.S. (eds.), Lichenographia Thomsoniana: North American lichenology. Ithaca: Mycotaxon 133–148.
Harris RC. 2006 – A preliminary glance at *Maronea* (*Fuscideaceae*) in North America. - Opuscula Philolichenum 3, 65–68.
Harris, RC. 1989 – A sketch of the family *Pyrenulaceae* (*Melanommatales*) in eastern North America. Memoirs of the New York Botanical Garden 49, 74–107.
Hartwell LH, Culotti J, Pringle JR, Reid BJ. 1974 – Genetic control of the cell division cycle in yeast: V. Genetic analysis of cdc mutants. Genetics 77(4), 405–426.
Harvey JBJ. 2004 – Phylogenetic studies of the marine brown algae *Cystoseira* and *Halidrys* including coevolution with the associated fungal endophyte *Haloguignardia irritans*. University of California, Santa Cruz.
Hasenhüttl G, Poelt J. 1978 – Über die Brutkorner bei der Flechtengattung Umbilicaria. Berichte der Deutschen Botanischen Geselschaft 91, 275–296.
Hashemi H, Mohammadi H. 2016 – Identification and characterization of fungi associated with internal wood lesions and decline disease of willow and poplar trees in Iran. Forest Pathology 46, 341–352.
Hashimoto A, Masumoto H, Endoh R, Degawa Y et al. 2021 – Revision of *Xylonaceae* (*Xylonales*, *Xylonomycetes*) to include *Sarea* and *Tromera*. Mycoscience 62(1), 47–63.
Hashimoto A, Matsumura M, Hirayama K, Tanaka K. 2017 – Revision of *Lophiotremataceae Pleosporales*, *Dothideomycetes*: *Aquasubmersaceae*, *Cryptocoryneaceae*, and *Hermatomycetaceae* fam. nov. Persoonia 39, 51–73.
Hassan O, Chang T. 2019 – Phylogenetic and morphological reassessment of *Mycosphaerella nawae*, the causal agent of circular leaf spot in persimmon. Plant Disease 103, 200–213.
Hatai K, Fujimaki Y, Egusa S. 1986 – A visceral mycosis in ayu fry, *Plecoglossus altivelis* Temmink & Schlegel, caused by a species of *Phoma*. Journal of Fish Diseases 9, 111–116.
Haughland DL, Hood A, Thauvette D, Toni SA et al. 2022 – Getting to know our biomonitor neighbours: urban lichens and allied fungi of Edmonton, Alberta, Canada. Opuscula Philolichenum 21, 33–181.
Hausner G, Eyjólfsdóttir GG, Reid J, Klassen GR. 1992 – Two additional species of the genus *Togninia*. Canadian Journal of Botany 70(4), 724–734.
Hawkes M, Rennie R, Sand C, Vaudry W. 2005 – *Aureobasidium pullulans* infection: fungemia in an infant and a review of human cases. Diagnostic Microbiology and Infectious Disease 51(3), 209–213.
Hawksworth D, Webster J. 1977 – Studies on *Mycorhynchus* in Britain. Transactions of the British Mycological Society 68(3), 329–340.

Hawksworth DL, Aguirre-Hudson B, Ainsworth M. 2014 – *Sphinctrina tigillaris*, an overlooked species of *Chaenothecopsis* growing on *Perenniopora meridionalis*, a polypore new to UK. The Lichenologist 46, 729 –735.
Hawksworth DL, Dyko BJ. 1979 – *Lichenodiplis* and *Vouauxiomyces*: Two genera of lichenicolous *Coleomycetes*. The Lichenologist 11, 51–61.
Hawksworth DL, Eriksson OE. 1986 – The names of accepted orders of *Ascomycetes*. Systematics and Applied Microbiology 5, 175–184.
Hawksworth DL, Hafellner J. 1986 – *Phaeosporobolus usneae*, a new and widespread lichenicolous deuteromycete. Nova Hedwigia 43(3–4), 525–530.
Hawksworth DL, James PW, Coppins BJ. 1980 – Checklist of British lichen-forming, lichenicolous and allied fungi. The Lichenologist 12, 1–115.
Hawksworth DL, Kirk PM, Sutton BC, Pegler DM. 1995 – Ainsworth & Bisby's dictionary of the fungi. 8th edition. CABI, Wallingford.
Hawksworth DL, Kirk PM, Sutton BC, Pegler DN. 1983a – Ainsworth & Bisby's dictionary of the fungi. Commonwealth Mycological Institute, Kew.
Hawksworth DL, Rossman AY. 1997 – Where are all the undescribed fungi? Phytopathology 87(9), 888–891.
Hawksworth DL, Santesson R, Tibell L 2011 – *Racoleus*, a new genus of sterile filamentous lichen-forming fungi from the tropics, with observations on the nomenclature and typification of *Cystocoleus* and *Racodium*. IMA Fungus 2, 71–79.
Hawksworth DL, Sherwood MA. 1981 – A reassessment of three wide- spread resinicolous *discomycetes*. Canadian Journal of Botany 59, 357–372.
Hawksworth DL, Sherwood MA. 1982 – Two new families in the *Ascomycotina*. Mycotaxon 16, 262–264.
Hawksworth DL, Sutton BC, Ainsworth GC. 1983b – Ainsworth & Bisby's Dictionary of the Fungi. 7th Edn. CMI, 1–455.
Hawksworth DL. 1975 – A revision of lichenicolous fungi accepted by Keissler in *Coniothecium*. Transactions of the British Mycological Society 65, 219–238.
Hawksworth DL. 1978 – A new species of *Coniochaeta* with an interesting conidial state. Norwegian Journal of Botany 25, 15–18.
Hawksworth DL. 1979 – The lichenicolous hyphomycetes. Bulletin of the British Museum of Natural History, Botanical Series 6, 183–300.
Hawksworth DL. 1980a – Notes on some fungi occurring on *Peltigera*, with a key to accepted species. Transactions of the British Mycological Society 74, 363–386.
Hawksworth DL. 1980b – Two little-known members of the *Mycocaliciaceae* on polypores. Transactions of the British Mycological Society 74(43), 650–651.
Hawksworth DL. 1985 – *Kirschsteiniothelia*, a new genus for the *Microthelia incrustans* group (*Dothideales*). Botanical Journal of the Linnean Society 91, 181–202.
Hawksworth DL. 1988 – The variety of fungal-algal symbioses, their evolutionary significance, and the nature of lichens. Botanical journal of the Linnean Society 96, 3–20.
Hawksworth DL. 1994 – Ascomycete Systematics. Progress and Perspectives in the Nineties. Plenum Press, New York.
Hawksworth DL. 1995 – Biodiversity: measurement and estimation, vol 345. Springer, Dordrecht.
Hawksworth DL. 2011 – A new dawn for the naming of fungi: impacts of decisions made in Melbourne in July 2011 on the future publication and regulation of fungal names. IMA Fungus 2, 155–162.
Hay R, Denning DW, Bonifaz A, Queiroz-Telles F et al. 2019 – The diagnosis of fungal neglected tropical diseases (fungal NTDs) and the role of investigation and laboratory tests: an expert consensus report. Tropical Medicine and Infectious Disease 4, 122.
Hayakawa Y, Adachi H, Kim JW, Shin-ya K et al. 1998 – Adenopeptin, a new apoptosis inducer in transformed cells from *Chrysosporium* sp. Tetrahedron 54(52), 15871–15878.

Hayles J, Nurse P. 2018 – Introduction to fission yeast as a model system. Cold Spring Harbor Protocols (5), pp.pdb-top079749.
He ZQ, Tan JL, Li N, Zhang HX, Chen YH et al. 2019 – Sesquiterpenyl epoxy-cyclohexenoids and their signaling functions in nematode-trapping fungus *Arthrobotrys oligospora*. Journal of Agricultural and Food Chemistry 67(47), 13061–13072.
Healy RA, Smith ME, Bonito GM, Pfister DH et al. 2013 – High diversity and widespread occurrence of mitotic spore mats in ectomycorrhizal *Pezizales*. Molecular Ecology 22(6), 1717−1732.
Heath IB, Ashton ML, Kaminskyj SGW. 1987 – Mitosis as a phylogenetic marker among the yeasts - review and observations on novel mitotic systems in freeze substituted cells of the *Taprhinales*. In G.S. de Hoog, M.Th. Smith and A.C.M. Weijman (Eds.), The Expanding Realm of Yeast-like Fungi. Studies in Mycology 30, 279–297.
Heiðmarsson S. 2003 – Molecular study of *Dermatocarpon miniatum* (*Verrucariales*) and allied taxa. Mycological Progress 107, 459– 468.
Heikkila H, Stubb S. 1995 – The prevalence of onychomycosis in Finland. British Journal of Dermatology 133, 699–703.
Hein SM, Gloer JB, Koster B, Malloch D et al. 1998 − a new antifungal metabolite from the coprophilous fungus *Ascodesmis sphaerospora*. Journal of Natural Products 61(12), 1566−1567.
Helaly SE, Thongbai B, Stadler M. 2018 − Diversity of biologically active secondary metabolites from endophytic and saprotrophic fungi of the ascomycete order *Xylariales*. Natural Product Reports 35(9), 992−1014.
Held BW, Blanchette RA. 2017 – Deception Island, Antarctica, harbors a diverse assemblage of wood decay fungi. Fungal Biology 121(2), 145–157.
Helms G, Friedl T, Rambold G. 2003 – Phylogenetic relationships of the *Physciaceae* inferred from rDNA sequence data and selected phenotypic characters. Mycologia 95(6), 1078–1099.
Helston RM, Box JA, Tang W, Baumann P. 2010 – *Schizosaccharomyces cryophilus* sp. nov., a new species of fission yeast. FEMS yeast research 10(6), 779–786.
Henk DA, Weir A, Blackwell M. 2003 – *Laboulbeniopsis termitarius*, an ectoparasite of termites newly recognized as a member of the *Laboulbeniomycetes*. Mycologia 95(4), 561–564.
Hensen N, Bonometti L, Westerberg I, Brännström IO et al. 2023 – Genome-scale phylogeny and comparative genomics of the fungal order *Sordariales*. Molecular Phylogenetics and Evolution 189, 107938.
Henssen A, Büdel B, Titze A. 1987 – *Euopsis* and *Harpidium*, genera of the *Lichinaceae* (Lichenes) with rostrate asci. Botanica Acta, Berichte der Deutschen Botanischen Gesellschaft 101, 49–55.
Henssen A, Büdel B. 1986 – No.115. *Lichinales* Henssen and Büdel ordo nov. In Notes on ascomycete systematics, nos. 1–224, In: Eriksson OE, Hawksworth DL (Eds). Systema Ascomycetum 5, 138.
Henssen A, Jahns HM. 1974 – Lichenes. Eine Einführung in die Flechtenkunde. Georg Thieme Verlag, Stuttgart.
Henssen A, Keuck G, Renner B, Vobis G. 1981 – The lecanoralean centrum. In: D.R. Reynolds (ed) Ascomycete Systematics: The Luttrellian Concept, 138–234. New York, NY: Springer New York.
Henssen A. 1963a – Eine Revision der Flechtenfamilien *Lichinaceae* und *Ephebaceae*. Symbolae Botanicae Upsalienses 18, 1–123.
Henssen A. 1963b – Study of the genus *Koerberia*. Canadian Journal of Botany 41(9), 1347–1357.
Henssen A. 1970 – Die Apothecienentwicklung bei *Umbilicaria* Hoffm. emend. Frey. Vorträge aus dem Gesamtgebiet der Botanik, N. F. [Deutsche Botanische Gesellschaft] 4, 103–126.
Henssen A. 1976 – Studies in the developmental morphology of lichenized *Ascomycetes*. In: Brown DH, Hawksworth DL, Bailey RH (eds) Lichenology: progress and problems. Academic, London 107–138.

Henssen A. 1980 – Problematik der Gattungsbegrenzung bei den Lichinaceen. Berichte der Deutschen Botanischen Gesellschaft 92, 483–506.
Henssen A. 1987 – *Lichenothelia*, a genus of microfungi on rocks. In: Peveling E (ed) Progress and problems in lichenology in the eight- ies. Bibliotheca Lichenologica No.25. J. Cramer, Berlin-Stuttgart 257–293.
Henssen A. 1994 – Contribution to the morphology and species delimitation in *Heppia sensu stricto* (lichenized *Ascomycotina*). Acta Botanica Fennica 150, 57–73.
Henssen A. 1995 – The new lichen family *Gloeoheppiaceae* and its genera *Gloeoheppia*, *Pseudopeltula* and *Gudelia* (*Lichinales*). The Lichenologist 27, 261–290.
Heo YM, Kim K, Ryu SM, Kwon SL et al. 2018 – Diversity and ecology of marine algicolous *Arthrinium* species as a source of bioactive natural products. Marine Drugs 16, 508.
Hernãndez-Restrepo M, Bezerra JD, Tan YP, Wiederhold N et al. 2019 - Re-evaluation of *Mycoleptodiscus* species and morphologically similar fungi. Persoonia: Molecular Phylogeny and Evolution of Fungi 42(1), 205–27.
Hernández-Restrepo M, Decock CA, Costa MM, Crous PW. 2022 – Phylogeny and taxonomy of *Circinotrichum*, *Gyrothrix*, *Vermiculariopsiella* and other setose *hyphomycetes*. Persoonia - Molecular Phylogeny and Evolution of Fungi 49(1), 99–135.
Hernandez-Restrepo M, Gené J, Castañeda-Ruiz RF, Mena-Portales J et al. 2017 – Phylogeny of saprobic microfungi from Southern Europe. Studies in Mycology 86(1), 53–97.
Hernández-Restrepo M, Gené J, Castañeda-Ruiz RF, Mena-Portales J et al. 2015 – Emendation of the genus *Bactrodesmiastrum* (*Sordariomycetes*) and description of *Bactrodesmiastrum monilioides* sp. nov. from plant debris in Spain. Mycological Progress 14, 1–7.
Hernández-Restrepo M, Gené J, Mena-Portales J, Cano J et al. 2014 – New species of *Cordana* and epitypification of the genus. Mycologia 106, 723–734.
Hernández-Restrepo M, Giraldo A, van Doorn A, Wingfield MJ et al. 2020 – The genera of fungi–G6: *Arthrographis*, *Kramasamuha*, *Melnikomyces*, *Thysanorea*, and *Verruconis*. Fungal Systematics and Evolution 6(1), 1–24.
Hernandez-Restrepo M, Groenewald JZ, Elliott ML, Canning G et al. 2016 – Take-all or nothing. Studies in Mycology 83(1), 19–48.
Herre AWCT. 1910 – The lichen flora of the Santa Cruz Peninsula, California. Proceedings of the Washington Academy of Sciences 12, 27–269.
Hertel H, Rambold G. 1988 – *Lecidea mosigii* (Koerb.) Anzi – eine Art der Gattung *Orphniospora* Koerb. (*Fuscideaceae*, *Teloschistales*). Mitteilungen der Botanischen Staatssammlung München 27, 111–123.
Hertel H, Zürn L. 1986 – *Schaereria fabispora* (*Ascomycetes* lichenisati) – eine neue Art aus Norwegen. Mitteilungen der Botanischen Staatssammlung München 22, 477–483.
Hertel H. 1987 – Progress and problems in taxonomy of Antarctic saxicolous lecideoid lichens. Bibliotheca Lichenologica 25, 219–242.
Hertel H. 2007 – Notes on and records of Southern Hemisphere lecideoid lichens. Bibliotheca Lichenologica 95, 267–296.
Hessenauer P, Fijarczyk A, Martin H, Prunier J et al. 2020 – Hybridization and introgression drive genome evolution of Dutch elm disease pathogens. Nature Ecology & Evolution 4, 626–38.
Hestmark G, Miądlikowska J, Kauff F, Fraker E et al. 2011 – Single origin and subsequent diversification of central Andean endemic Umbilicaria species. Mycologia 103, 45–56.
Hestmark G. 1990 – *Thalloconidia* in the genus *Umbilicaria*. Nordic Journal of Botany 9, 547–574.
Hestmark G. 1992 – Sex, size, competition and escape - strategies of reproduction and dispersal in *Lasallia pustulata* (*Umbilicariaceae*, *Ascomycetes*). Oecologia 92, 305–312.
Heuchert B, Braun U, Diederich P, Ertz D. 2018 – Taxonomic monograph of the genus *Taeniolella s. lat*. (*Ascomycota*). Fungal Systematics and Evolution 2, 69–261.
Heuchert B, Braun U, Schubert K. 2005 – Morphotaxonomic revision of fungicolous *Cladosporium* species (*Hyphomycetes*). Schlechtendalia 13, 1–78.

Heuchert B, Zhurbenko MP, Braun U. 2014 – Reassessment of the lichenicolous hyphomycete genus *Talpapellis*. Herzogia 27(1), 83–92.
Hibbett D. 2016 – The invisible dimension of fungal diversity. Science 351, 1150–1151.
Hibbett DS, Binder M, Bischoff J, Blackwell M et al. 2007 – A higher-level phylogenetic classification of the Fungi. Mycological Research 111, 509–547.
Hibbett DS, Blackwell M, James TY, Spatafora JW et al. 2018 – Phylogenetic taxon definitions for fungi, dikarya, *Ascomycota* and *Basidiomycota*. IMA Fungus 9, 291–298.
Higginbotham SJ, Arnold AE, Ibañez A, Spadafora C et al. 2013 – Bioactivity of fungal endophytes as a function of endophyte taxonomy and the taxonomy and distribution of their host plants. PLoS ONE 8(9), e73192.
Hillmann J, Grummann V. 1957 – Kryptogamenflora der Mark Brandenburg und angrenzender Gebiete. Band VIII: Flechten. Gebrüder Borntraeger, Berlin-Nikolassee 898.
Hino I, Katumoto K. 1965 – Notes on bambusicolous fungi (1). Journal of Japanese Botany 40, 81–89.
Hirabayashi K, Iwata S, Ito M, Shigeta S et al. 1989 – Inhibitory effect of a lichen polysaccharide sulfate, GE-3-S, on replication of human immunodeficiency virus (HIV) *in vitro*. Chemical and Pharmaceutical Bulletin 37, 2410–2412.
Hirata A, Tanaka K. 1982 – Nuclear behavior during conjugation and meiosis in the fission yeast *Schizosaccharomyces pombe*. The Journal of General and Applied Microbiology 28(3), 263–274.
Hironaga M, Nakano K, Yokoyama I, Kitajima J. 1989 – *Phialophora repens*, an emerging agent of subcutaneous phaeohyphomycosis in humans. Journal of Clinical Microbiology 27, 394–399.
Hirooka Y, Tanney JB, Nguyen HDT, Seifert KA. 2016 – Xerotolerant fungi in house dust: taxonomy of *Spiromastix*, *Pseudospiromastix* and *Sigleria* gen. nov. in *Spiromastigaceae* (*Onygenales*, *Eurotiomycetes*). Mycologia 108(1), 135–156.
Hjeljord L, Tronsmo A, Harman GE, Kubicek CP. 1998 – *Trichoderma* and *Gliocladium.* Biological control: an overview. In: *Trichoderma* and *Gliocladium*: Enzymes, biological control and commercial applications. Harman GE, Kubice CP.(Eds) 2, 131–151.
Ho RHT, Bernard PJ, McClellan KA. 1991 – *Phialophora mutabilis keratomycosis*. American Journal of Ophthalmology 112 (6): 72829.
Ho WH, Hyde KD, Hodgkiss IJ. 2001 – Fungal communities on submerged wood from streams in Brunei, Hong Kong, and Malaysia. Mycological Research 105, 1492–1501.
Ho WWH, Tsui CKM, Hodgkiss IJ, Hyde KD. 1999 – *Aquaticola*, a new genus of *Annulatascaceae* from freshwater habitats. Fungal Diversity 3, 87–97.
Hocking AD. 2006 – Food spoilage microorganisms. (In Blackburn, C. de W ed.) *Aspergillus* and related teleomorphs. Woodhead Publishing Ltd., Cambridge, UK 451–487.
Hodkinson BP, Lendemer JC. 2011 – The orders of *Ostropomycetidae* (*Lecanoromycetes*, *Ascomycota*): recognition of *Sarrameanales* and *Trapeliales* with a request to retain *Pertusariales* over *Agyriales*. Phytologia 93(3), 407–412.
Hodkinson BP, Lendemer JC. 2013 – Next-generation sequencing reveals sterile crustose lichen phylogeny. Mycosphere 4, 1028–1039.
Hodkinson BP. 2012 – An evolving phylogenetically based taxonomy of lichens and allied fungi. Opuscula Philolichenum 11, 4–10.
Hoffman CS, Wood V, Fantes P.A. 2015 – An ancient yeast for young geneticists: a primer on the *Schizosaccharomyces pombe* model system. Genetics 201(2), 403–423.
Hoffmann GF. 1789 – Descriptio et adumbratio plantarum e classe cryptogamica Linnaei, quae Lichenes dicuntur, vol. 1. Lipsiae. 105 pp.
Hoffmann GF. 1794 – Descriptio et Adumbratio plantarum e classe cryptogamica, 2: Lipsiae [Leipzig].
Hoffmann M, Van Landuyt W. 1997 – Lichenized *Caliciales* with stalked apothecia in Flanders (northern Belgium): Rare or poorly known? Belgian Journal of Botany 130, 25–37.

Hoffmann N, Hafellner J. 2000 – Eine Revision der lichenicolen Arten der Sammelgattungen Guignardia und *Physalospora*. Bibliotheca Lichenologica 77, 1–190.
Hofmann TA, Kirschner R, Piepenbring M. 2010 – Phylogenetic relationships and new records of *Asterinaceae* (*Dothideomycetes*) from Panama. Fungal Diversity 43, 39–53.
Hofstetter RW, Cronin JT, Klepzig KD, Moser JC et al. 2006 – Antagonisms, mutualisms and commensalisms affect outbreak dynamics of the southern pine beetle. Oecologia 147, 679–91.
Hofstetter RW, Moser JC. 2014 – Fungi associated with bark beetles in western North America: taxonomy, ecology, and management. Insecta Mundi 1–66.
Hofstetter V, Miadlikowska J, Kauff F, Lutzoni F. 2007 – Phylogenetic comparison of protein-coding versus ribosomal RNA-coding sequence data: a case study of the *Lecanoromycetes* (*Ascomycota*). Molecular Phylogenetics and Evolution 44(1), 412–426.
Höhnel F von. 1904 – Mycologische Fragmente. Annales Mycologici 2, 38e60.
Höhnel F von. 1910 – Fragmente zur Mykologie (XI. Mitteilung, Nr. 527 bis 573). Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Math.-naturw. Klasse Abt. I. 119(6), 617–679.
Höhnel F von. 1910 – Fragmente zur Mykologie (XI. Mitteilung, Nr. 527 bis 573). Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Math.-naturw. Klasse Abt. I. 119(6), 617–679.
Höhnel F. 1917a – Mycologische Fragmente 174. Uber *Sphaeria uliginosa* Fr. Und die Cephalothecaceen. Annales Mycolologici 15, 360–363.
Höhnel F. 1917b – System der *Phacidiales* v. H. Berichte der Deutschen Botanischen Gesellschaft 34, 416–422.
Höhnel F. Von. 1905 – Mykologische Fragmente CVI-CXVII. Annales Mycologici. 3(6), 548–560.
Höhnel Fr Von. 1917c − Mycologische Fragmente. Annales Mycologici 15(5), 293–383.
Höhnel FXR von. 1909 – Fragmente zur Mykologie (VI. Mitteilung, Nr. 182 bis 288). Sitzungsberichte der Kaiserliche Akademie der Wissenschaften in Wien. Mathematisch-naturwissenschaftliche. K1asse (Abt. 1) 118, 275–452.
Holec J. 2005 – Distribution and ecology of *Camarops tubulina* (*Ascomycetes*, *Boliniaceae*) in the Czech Republic and remarks on its European distribution. Czech Mycolgy 57, 97.
Holger THÜS, Nascimbene J. 2008 – Contributions toward a new taxonomy of central European freshwater species of the lichen genus *Thelidium* (*Verrucariales*, *Ascomycota*). The Lichenologist 40(6), 499–521.
Holien H, Triebel D. 1996 – *Spirographa vinosa*, a new odontotremoid fungus on *Ochrolechia* and *Pertusaria*. The Lichenologist 28, 307–313
Holland LA, Trouillas FP, Nouri MT, Lawrence DP et al. 2020 – Fungal pathogens associated with canker diseases of almond in California. Plant Disease 105, 346–360.
Holliday P. 1980 – Fungal diseases of tropical crops. Cambridge University Press, Cambridge, UK.
Holm K, Holm L. 1977 – Nordic junipericolous *Ascomycetes*. Symbolae Botanicae Upsalienses 21, 1–70.
Holm L. 1975 – Nomeclatural notes on *Pyrenomycetes*. Taxon 24, 475–488.
Holtan-Hartwig J, Timdal E. 1987 – Notes on some parasitic *Rhizocarpon* species. The Lichenologist 19(3), 335–338.
Holubová-Jechová V. 1982 – Lignicolous *Hyphomycetes* from Czechoslovakia 6. *Spadicoides* and *Diplococcium*. Folia Geobotanica et Phytotaxonomica 17, 295–327.
Holubová-Jechová V. 1984 – *Bactrodesmiastrum*, a new genus of lignicolous *Hyphomycetes*. Folia Geobotanica et Phytotaxonomica 19, 103–106.
Honegger R. 1978 – The ascus apex in lichenized fungi I. The *Lecanora*-, *Peltigera*- and *Teloschistes*-types. The Lichenologist 10, 47–67.
Honegger R. 1985 – The hyphomycetous anamorph of *Coniocybe furfuracea*. The Lichenologist 17, 273–279.
Hongsanan S, Bahkali AH, Chomnunti P, Liu JK et al. 2016a– *Discopycnothyrium palmae* gen. & sp. nov. (*Asterinaceae*). Mycotaxon 131, 859–869.

Hongsanan S, Hyde KD, Phookamsak R, Wanasinghe DN et al. 2020a − Refined families of *Dothideomycetes*: Orders and families *incertae* sedis in *Dothideomycetes*. Fungal Diversity 105, 17–318.
Hongsanan S, Hyde KD, Phookamsak R, Wanasinghe DN et al. 2020b – Refined families of *Dothideomycetes*: *Dothideomycetidae* and *pleosporomycetidae*. Mycosphere 11(1), 1553–2107.
Hongsanan S, Hyde KD. 2017 − Phylogenetic placement of *Micropeltidaceae*. Mycosphere 8, 1930 –1942.
Hongsanan S, Li YM, Liu JK, Hofmann T et al. 2014 – Revision of genera in *Asterinales*. Fungal Diversity 68, 1–68.
Hongsanan S, Maharachchikumbura SS, Hyde KD, Samarakoon MC et al. 2017a – An updated phylogeny of *Sordariomycetes* based on phylogenetic and molecular clock evidence. Fungal Diversity 84, 25–41.
Hongsanan S, Norphanphoun C, Senanayake IC, Jayawardena RS et al. 2023 – Annotated notes on *Diaporthe* species. Mycosphere 14(1), 918–1189.
Hongsanan S, Sánchez-Ramirez S, Crous PW, Ariyawansa HA et al. 2016b – The evolution of fungal epiphytes. Mycsphere 7, 1690–1712.
Hongsanan S, Tian Q, Bahkali AH, Yang JB et al. 2015a – *Zeloasperisporiales* ord. nov., and two new species of *Zeloasperisporium*. Cryptogamie, Mycologie 36, 301–317.
Hongsanan S, Tian Q, Peršoh D, Zeng XY et al. 2015b – *Meliolales*. Fungal Diversity 74, 1 91–141.
Hongsanan S, Zeng YJ, Hyde KD, Xie N. 2018 – Familial status of *Lophiotremataceae* and its related families in *Pleosporales*. Phytotaxa 383, 093–102.
Hongsanan S, Zhao RL, Hyde KD. 2017b – A new species of *Chaetothyrina* on branches of mango, and introducing *Phaeothecoidiellaceae* fam. nov. Mycosphere 8, 137–146.
Hoog GS de. 1977 – *Rhinocladiella* and allied genera. Studies in Mycology 15, 1–140.
Horie Y, Udagawa S, Cannon P. 1986 – Four new Japanese species of the *Ceratostomataceae* (*Ascomycetes*). Mycotaxon 25(1), 229–245.
Hosagoudar VB, Abraham TK, Pushpangadan P. 1997a – The *Meliolineae* a supplement. The Director TBG and RI, Pal ode, Thiruvananthapuram 20.
Hosagoudar VB, Krishnan PN, Abraham TK. 1997b – Biochemical changes in the sandal tree infected with *Asterina congesta* Cooke. New Botanist 24, 27–32.
Hosagoudar VB, Riju MC. 2013 – Foliicolous fungi of Silent Valley National Park, Kerala, India. Journal of Threatened Taxa 5, 3701–3788.
Hosagoudar VB. 2003 – *Armatellaceae,* a new family segregated from the *Meliolaceae*. Sydowia 55, 162–167.
Hosoe T, Gloer JB, Raja H, Shearer CA. 2010 – Radicinol analogs from the freshwater aquatic fungus *Xylomyces chlamydosporus*. Mycotoxins 60, 1–6.
Hosoe T, Iizuka T, Komai S, Wakana D et al. 2005 – 4-Benzyl-3-phenyl-5H-furan-2-one, a vasodilator isolated from *Malbranchea filamentosa* IFM 41300. Phytochemistry 66(23), 2776–2779.
Hosoe T, Okada H, Itabashi T, Nozawa K et al. 2000 – A new pentanorlanostane derivative, cladosporide A, as a characteristic antifungal agent against *Aspergillus fumigatus*, isolated from *Cladosporium* sp. Chemical and Pharmaceutical Bulletin 48, 1422–1426.
Hosoe T, Okamoto S, Nozawa K, Kawai KI et al. 2001 – New pentanorlanostane derivatives, cladosporide B–D, as characteristic antifungal agents against *Aspergillus fumigatus*, isolated from *Cladosporium* sp. The Journal of Antibiotics 54, 747–750.
Hou CL, Piepenbring M. 2005 – Known and two new species of *Rhytisma* (*Rhytismatales*, *Ascomycota*) from China. Mycopathologia 159, 299–306.
Hou CL. 2004 – *Rhytismatales* (*Ascomycota*) in China-morphology, ecology, and systematics. PhD Dissertation, J.W. Goethe-Universität Frankfurt, Frankfurt am Main 1–272.
Hou JX. 2016 – Mitochondrial genome sequencing and comparative mitochondrial genomics study of *Cordyceps sinensis*. Shanxi University.

Houbraken J, de Vries RP, Samson RA. 2014 – Modern Taxonomy of Biotechnologically Important *Aspergillus* and *Penicillium* Species in (Ed. Sariaslani S and Gadd GM) Advances in Applied Microbiology. Academic Press 86, 199–249.
Houbraken J, Frisvad JC, Seifert KA et al. 2012a – New penicillin-producing *Penicillium* species and an overview of section *Chrysogena*. Persoonia 29, 78–100.
Houbraken J, Kocsubé S, Visagie CM, Yilmaz N et al. 2020 – Classification of *Aspergillus*, *Penicillium*, *Talaromyces* and related genera (*Eurotiales*): An overview of families, genera, subgenera, sections, series and species. Studies in Mycology 95, 5–169.
Houbraken J, Samson RA. 2011 – Phylogeny of *Penicillium* and the segregation of *Trichocomaceae* into three families. Studies in Mycology 15, 70(1), 1–51.
Houbraken J, Samson RA. 2017 – Current taxonomy and identification of foodborne fungi. Current Opinion in Food Science 17, 84–88.
Houbraken J, Spierenburg H, Frisvad JC. 2012b – *Rasamsonia*, a new genus comprising thermotolerant and thermophilic *Talaromyces* and *Geosmithia* species. Antonie van Leeuwenhoek 101, 403–421.
Hsiao Y, Cheng MJ, Chang HS, Wu MD et al. 2016 – Six new metabolites produced by *Colletotrichum aotearoa* 09F0161, an endophytic fungus isolated from *Bredia oldhamii*. Natural Product Research 30, 251–258.
Hsieh SY, Goh TK, Kuo CH. 2021 – New species and records of *Helicosporium sensu lato* from Taiwan, with a reflection on current generic circumscription. Mycological Progress 20, 169–190.
Hsueh YP, Gronquist MR, Schwarz EM, Nath RD et al. 2017 – Nematophagous fungus *Arthrobotrys oligospora* mimics olfactory cues of sex and food to lure its nematode prey. eLife 6, e20023.
Hu DM, Cai L, Chen H, Bahkali AH, Hyde KD. 2010 – Four new freshwater fungi associated with submerged wood from Southwest Asia. Sydowia 62, 191–203.
Hu H, Guo H, Li E, Liu X et al. 2006 – Decaspirones F−I, bioactive secondary metabolites from the saprophytic fungus *Helicoma viridis*. Journal of Natural Products 69, 1672–1675.
Hu MJ, Grabke A, Schnabel G. 2015 – Investigation of the *Colletotrichum gloeosporioides* species complex causing peach anthracnose in South Carolina. Plant Disease 99, 797–805.
Hu X, Hoffmann DS, Wang M, Schuhmacher L et al. 2024 – GprC of the nematode-trapping fungus *Arthrobotrys flagrans* activates mitochondria and reprograms fungal cells for nematode hunting. Nature Microbiology 9, 1752–1763.
Huang F, Hou X, Dewdney MM, Fu Y et al. 2013 – *Diaporthe* species occurring on citrus in China. Fungal Diversity 61, 237–250.
Huang SK, Hyde KD, Jeewon R, Jayarama BD et al. 2019 – *Sordariomycetidae* and *Diaporthomycetidae*. Fungal Diversity 111, 443–572.
Huang SK, Hyde KD, Maharachchikumbura SS, McKenzie EH et al. 2021a – Taxonomic studies of *Coronophorales* and *Niessliaceae* (*Hypocreomycetidae*). Mycosphere 12, 875-992.
Huang SK, Hyde KD, Mapook A, Maharachchikumbura SS et al. 2021b – Taxonomic studies of some often over-looked *Diaporthomycetidae* and *Sordariomycetidae*. Fungal Diversity 111(1), 443–572.
Huang SK, Jeewon R, Hyde KD, Bhat DJ et al. 2018 – Beta-tubulin and Actin gene phylogeny supports *Phaeoacremonium ovale* as a new species from freshwater habitats in China. MycoKeys 41, 1–15.
Huang YT, Liaw SJ, Liao CH, Yang JL et al. 2008 – Catheter-related septicemia due to *Aureobasidium pullulans*. International Journal of Infectious Diseases 12(6), 137–139.
Hubka V, Dudova Z, Kubátová A, Frisvad JC et al. 2017 – Taxonomic novelties in *Aspergillus* section Fumigati: *A. tasmanicus* sp. nov., induction of sexual state in *A. turcosus* and overview of related species. Plant Systematics and Evolution 303, 787–806.
Hudson O, Buchholz M, Doyle V, Sundue MA. 2019 − Multilocus phylogeny of *Acrospermaceae*: New epibiotic species and placement of *Gonatophragmium*, *Pseudovirgaria*, and *Phaeodactylium* anamorphs. Mycologia 111(6), 1041–55.

Hughes SJ, Nag Raj TR. 1973 – New Zealand fungi: 20. *Fusichalara* gen. nov. New Zealand Journal of Botany 11(4), 661–671.
Hughes SJ. 1951a – Studies on microfungi. 5. *Acrotheca*. Mycological Papers 38, 1–8.
Hughes SJ. 1951b – Studies on micro-fungi. IV. Two fungi of Betula periderm. Mycological Papers, Commonwealth Mycological Institute 37, 1–17.
Hughes SJ. 1953 – Conidiophores, conidia, and classification. Canadian Journal of Botany 31(5), 577–659.
Hughes SJ. 1958 – Revisiones Hyphomycetum aliquot cum appendice de nominibus rejiciendis. Canadian Journal of Botany 36(6), 727–836.
Hughes SJ. 1972 – New Zealand fungi 17, pleomorphism in *Euantennariaceae* and *Metacapnodiaceae*, two families of sooty moulds. New Zealand Journal of Botany 10, 225–242.
Hughes SJ. 1976 – Sooty moulds. Mycologia 68, 451–691.
Hugot JP, Demanche C, Barriel V, Dei-Cas E et al. 2003 – Phylogenetic systematics and evolution of primate-derived *Pneumocystis* based on mitochondrial or nuclear DNA sequences comparison. Systems Biology 52, 735–744.
Huhndorf SM, Fernández DJ, Lodge DJ. 1999 – Noetropical *Ascomycetes* 9. *Jobellisia* species from Puerto Rico and elsewhere. Sydowia 51, 183–196.
Huhndorf SM, Fernández FA. 2005 – Teleomorph-anamorph connections: *Chaetosphaeria raciborskii* and related species, and their *Craspedodidymum*-like anamorphs. Fungal Diversity 19, 23–49.
Huhndorf SM, Greif M, Mugambi GK, Miller AN. 2008 – Two new genera in the *Magnaporthaceae*, a new addition to *Ceratosphaeria* and two new species of *Lentomitella*. Mycologia 100, 940–955.
Huhndorf SM, Miller AN, Fernández FA. 2004a – Molecular systematics of the *Sordariales*: the order and the family *Lasiosphaeriaceae* redefined. Mycologia 96(2), 368–387.
Huhndorf SM, Miller AN, Fernández FA. 2004b – Molecular systematics of the *Coronophorales* and new species of *Bertia*, *Lasiobertia* and *Nitschkia*. Mycological Research 108, 1384–1398.
Huhndorf SM, Miller AN, Greif M, Samuels GJ. 2009 – *Amplistroma* gen. nov. and its relation to *Wallrothiella*, two genera with globose ascospores and *Acrodontium*-like anamorphs. Mycologia 101, 904–919.
Huhndorf SM, Miller AN. 2008 – A new species of *Camarops* and phylogenetic analysis of related taxa in the *Boliniaceae*. North American Fungi 3, 231–239.
Huhndorf SM. 1992 – Neotropical *Ascomycetes* 1. *Valsonectria cinnamomi* in artificial culture. Mycologia 84, 642–649.
Huhndorf SM. 1994 – Neotropical *Ascomycetes* 5. *Hypsostromataceae*, a new family of *Loculoascomycetes* and *Manglicola samuelsii*, a new species from Guyana. Mycologia 86, 266–269.
Hujslová M, Kubátová A, Kostovčík M, Blanchette RA et al. 2014 – Three new genera of fungi from extremely acidic soils. Mycological Progress 13, 819−831.
Hujslová M, Kubátová A, Chudíčková M, Kolařík M. 2010 – Diversity of fungal communities in saline and acidic soils in the Soos National Natural Reserve, Czech Republic. Mycological Progress 9, 1–15.
Humphries Z, Seifert KA, Hirooka Y, Visagie CM. 2017 – A new family and genus in *Dothideales* for *Aureobasidium*-like species isolated from house dust. IMA Fungus 8, 299–315.
Huneck S, Porzel A, Schmidt J, Feige GB et al. 1993 – Crustinic acid, a new tridepside from *Umbilicaria custulosa*. Phytochemistry 32, 475–477.
Huneck S, Yoshimura I. 1996 – Identification of lichen substances. Springer Verlag, Berlin, Heidelberg, 493.
Huneck S. 1995 – The chemistry and chemotaxonomy of the lichen order *Arthoniales*, especially the family *Roccellaceae*. Cryptogamic Botany 5, 36–44.

Hung R, Lee S, Bennett JW. 2015 – Fungal volatile organic compounds and their role in ecosystems. Applied Microbiology and Biotechnology 99, 3395–3405.
Hurford C, Schneider M. (Eds.) 2007 – Monitoring Nature Conservation in Cultural Habitats: A Practical Guide and Case Studies. Springer Science & Business Media.
Hustad VP, Miller AN, Dentinger BTM, Cannon PF. 2013 – Generic circumscriptions in *Geoglossomycetes*. Persoonia: Molecular Phylogeny and Evolution of Fungi 31(1), 101–111.
Hustad VP, Miller AN, Moingeon JM, Priou JP. 2011 – Inclusion of *Nothomitra* in *Geoglossomycetes*. Mycosphere 2(6), 646–654.
Hustad VP, Miller AN. 2011 – Phylogenetic placement of four genera within the *Leotiomycetes* (*Ascomycota*). North American Fungi 6, 1–13.
Hustad VP, Miller AN. 2015 – Studies in the genus *Glutinoglossum*. Mycologia 107(3), 647–657.
Hutchison LJ, Sigler L, Hiratsuka Y. 1993 – *Hyphozyma lignicola* sp. nov., a yeast-like hyphomycete from black galls and cankers of trembling aspen (*Populus* tremuloides). Mycological Research 97, 1409–1415.
Hüttal W. 2021 – Echinocandins: structural diversity, biosynthesis, and development of antimycotics. Applied Microbiology and Biotechnology 105, 55–66.
Hyde KD, Al-Hatmi AM, Andersen B, Boekhout T et al. 2018a – The world's ten most feared fungi. Fungal Diversity 93, 161–194.
Hyde KD, Baldrian P, Chen Y, Chethana TKW et al. 2024a – Current trends, limitations and future research in the fungi. Fungal Diversity 125, 1–71.
Hyde KD, Bao DF, Hongsanan S, Chethana KT et al. 2021a – Evolution of freshwater *Diaporthomycetidae* (*Sordariomycetes*) provides evidence for five new orders and six new families. Fungal Diversity 107, 71–105.
Hyde KD, Borse BD. 1986 – Marine fungi from Seychelles V. *Biatriospora marina* gen. et sp. nov. from mangrove wood. Mycotaxon 26, 263–270.
Hyde KD, Cannon PF, Barr ME. 1997 – *Phaeochoraceae*, a new ascomycete family from palms. Systema Ascomycetum 15, 117–120.
Hyde KD, Cannon PF. 1999 – Fungi causing tar spots on palmae. Mycological Papers 175, 1–114.
Hyde KD, Chaiwan N, Norphanphoun C, Boonmee S et al 2018b – Mycosphere notes 169–224. Mycosphere 9, 271–430.
Hyde KD, de Silva NI, Jeewon R, Bhat DJ et al. 2020a – AJOM new records and collections of fungi: 1–100. Asian Journal of Mycology 3, 22–294.
Hyde KD, Dong Y, Phookamsak R, Jeewon R et al. 2020b – Fungal diversity notes 1151–1276: taxonomic and phylogenetic contributions on genera and species of fungal taxa. Fungal Diversity 100, 5–277.
Hyde KD, Fryar S, Tian Q, Bahkali AH et al. 2016a – Lignicolous freshwater fungi along a north−south latitudinal gradient in the Asian/Australian region; can we predict the impact of global warming on biodiversity and function? Fungal Ecology 19, 190−200.
Hyde KD, Goh TK, Lu BS, Alias SA. 1999 – Eleven new intertidal fungi from *Nypa fruticans*. Mycological Research 103(11), 1409–1422.
Hyde KD, Ho WH, Jones EBG, Tsui CKM et al. 2000 – *Torrentispora fibrosa* gen. et sp. nov. (*Annulatascaceae*) from freshwater habitats. Mycological Research 104, 1399–1403.
Hyde KD, Hongsanan S, Jeewon R, Bhat DJ et al. 2016b – Fungal diversity notes 367–490: Taxonomic and phylogenetic contributions to fungal taxa. Fungal Diversity 80(1), 1–270.
Hyde KD, Jones EBG. 1988 – Marine mangrove fungi. Marine Ecology 9, 15–33
Hyde KD, Jones EG, Liu JK, Ariyawansa H et al. 2013 – Families of *Dothideomycetes*: In loving memory of Majorie Phyllis Hyde (affectionately known as Mum or Marj), 29 August 1921–18 January 2013–without mum's determination, a character passed on to children, this treatise would never have been completed–KD Hyde. Fungal Diversity 63, 1–313.
Hyde KD, Jones EG. 1986 – Marine fungi from Seychelles. II. *Lanspora coronata* gen. et sp. nov. from driftwood. Canadian Journal of Botany 64(8), 1581–1585.

Hyde KD, Lee SY. 1998 – Ecology of mangrove fungi and their role in nutrient cycling: What gaps occur in our knowledge? Hydrobiologia 295, 107–118.
Hyde KD, Maharachchikumbura SS, Hongsanan S, Samarakoon MC et al. 2017a – The ranking of fungi: a tribute to David L. Hawksworth on his 70th birthday. Fungal Diversity 84, 1–23.
Hyde KD, McKenzie EHC, KoKo TW. 2011 – Towards incorporating anamorphic fungi in a natural classification – checklist and notes for 2010. Mycosphere 2(1), 1–88
Hyde KD, Nakagiri A. 1992 – Intertidal fungi from Australia. The genus *Swampomyces* including *S. triseptatus* sp. nov. Sydowia 44, 122–130.
Hyde KD, Noorabadi MT, Thiyagaraja V, He MQ et al. 2024b – The 2024 Outline of fungi and fungus-like taxa. Mycosphere 15(1), 5146–6239.
Hyde KD, Norphanphoun C, Abreu VP, Bazzicalupo A et al. 2017b – Fungal diversity notes 603–708: Taxonomic and phylogenetic notes on genera and species. Fungal Diversity 87, 1–235.
Hyde KD, Norphanphoun C, Chen J, Dissanayake AJ et al. 2020c – Thailand's amazing diversity – up to 96% of fungi in northern Thailand are novel. Fungal Diversity 93, 215–239
Hyde KD, Norphanphoun C, Ma J, Yang HD et al. 2023 – Mycosphere notes 387–412 – novel species of fungal taxa from around the world. Mycosphere 14(1), 663–744.
Hyde KD, Norphanphoun C, Maharachchikumbura S, Bhat D et al. 2020d – Refined families of *Sordariomycetes*. Mycosphere 11, 305–1059.
Hyde KD, Saleh A, Aumentado HD, Boekhout T et al. 2024c – Fungal numbers: global needs for a realistic assessment. Fungal Diversity 1–35.
Hyde KD, Stanley SJ, Steinke TD. 1996 – Fungi associated with leaf spots of palms. *Maculatifrondis aequatoriensis* gen. et sp. nov., with a *Cyclodomus* anamorph, and *Myelosperma parasitica* sp. nov. Mycological Research 100(12), 1509–1514.
Hyde KD, Suwannarach N, Jayawardena RS, Manawasinghe IS et al. 2021b – Mycosphere notes 325-344 – Novel species and records of fungal taxa from around the world. Mycosphere 12(1), 1101–1156.
Hyde KD, Swe A, Zhang KQ. 2014 – Nematode-Trapping Fungi. Springer.
Hyde KD, Tennakoon DS, Jeewon R, Bhat DJ et al. 2019 – Fungal diversity notes 1036–1150: taxonomic and phylogenetic contributions on genera and species of fungal taxa. Fungal Diversity 96, 1–242.
Hyde KD, Zhou DQ, Dalisay T. 2002 – Bambusicolous fungi: A review. Fungal Diversity 9, 1–14.
Hyde KD. 1988 – *Phomatospora acrostichi* sp. nov., a marine fungus on pinnae of *Acrostichum speciosum*. Transactions of the British Mycological Society 90(1), 135–138.
Hyde KD. 1991 – Fungal colonization of *Rhizophora apiculata* and *Xylocarpus granatum* poles in Kampong Kapok mangrove, Brunei. Sydowia 43, 31–38.
Hyde KD. 1992a – Fungi from decaying intertidal fronds of *Nypa fruticans*, including three new genera and four new species. Botanical Journal of the Linnean Society 110, 95–110.
Hyde KD. 1992b – Intertidal fungi from *Kandelia candel* including *Phomatospora kandelae* sp. nov. Transactions of the Mycological Society of Japan (Japan) 33, 313–316.
Hyde KD. 1993 – Fungi from palms. V. *Phomatospora nypae* sp. nov. and notes on marine fungi from *Nypa fruticans* in Malaysia. Sydowia 45, 199–203.
Hyde KD. 1997 – The genus *Roussoëlla*, including two new species from palms in Cuyabeno, Ecuador. Mycological Research 101(5), 609–616.
Ibrahim SR, Fadil SA, Fadil HA, Eshmawi BA et al. 2022 – Fungal naphthalenones; promising metabolites for drug discovery: Structures, biosynthesis, sources, and pharmacological potential. Toxins 14, 154.
Ibrahim SRM, Mohamed SGA, Sindi IA, Mohamed GA. 2021 – Biologically active secondary metabolites and biotechnological applications of species of the family *Chaetomiaceae* (*Sordariales*): an updated review from 2016 to 2021. Mycological Progress 20, 595–639.
Ihlen PG, Ekman S. 2002 – Outline of phylogeny and character evolution in *Rhizocarpon* (*Rhizocarpaceae*, lichenized *Ascomycota*) based on nuclear ITS and mitochondrial SSU ribosomal DNA sequences. Biological Journal of the Linnean Society 77(4), 535–546.

Ihlen PG. 1998 – The lichenicolous fungi on species of the genera *Baeomyces*, *Dibaeis*, and *Icmadophila* in Norway. The Lichenologist, 30(1), 27–57.
Ihlen PG. 2004 – A new species of *Lichenostigma* (*Lichenotheliaceae*, *Arthoniales*) from Scandinavia. The Lichenologist 36(3–4), 183–189.
Ikai K, Tomono H, Watanabe S. 1988 – Phaeohyphomycosis caused by *Phialophora richardsiae*. Journal of the American Academy of Dermatology, 19, 478–481.
Imai S. 1941 – *Geoglossaceae japoniae*. J Fac Agr Hokkaido ImpUniv 45, 155–264.
Imhoff JF. 2016 – Natural products from marine fungi – Still an underrepresented resource. Marine Drugs 14(1), 19.
Imshaug HA. 1957 – Alpine lichens of western United States and adjacent Canada. I. The Macrolichens. The Bryologist 60(3), 177–272.
Inácio CA, Cannon PF. 2008 – The genera of the *Parmulariaceae*. CBS biodiversity series, vol 8. CBS Fungal Biodiversity Centre, Utrecht.
Inácio J, Rodrigues MG, Sobral P, Fonseca Á. 2004 – Characterisation and classification of phylloplane yeasts from Portugal related to the genus *Taphrina* and description of five novel *Lalaria* species. FEMS Yeast Research 4(4-5), 541–555.
Inderbitzin P, Bostock RM, Trouillas FP, Michailides TJ. 2010 – A six locus phylogeny reveals high species diversity in *Botryosphaeriaceae* from California almond. Mycologia 102, 1350–1368.
Inderbitzin P, Landvik S, Abdel-Wahab MA, Berbee ML. 2001 – *Aliquandostipitaceae*, a new family for two new tropical ascomycetes with unusually wide hyphae and dimorphic ascomata. American Journal of Botany 88, 52–61.
Inderbitzin P, Lim SM, Volkmann-Kohlmeyer B, Kohlmeyer J et al. 2004 – The phylogenetic position of *Spathulospora* based on DNA sequences from dried herbarium material. Mycological Research 108, 737–748.
Index Fungorum 2023 – Available online: http://www.indexfungorum.org/Names/Names.asp.
Index Fungorum 2024 – Available online: http://www.indexfungorum.org/Names/Names.asp.
Index Fungorum 2025 – Available online: http://www.indexfungorum.org/Names/Names.asp.
Inoue M. 1982 – The genera *Lecidea*, *Lecidella* and *Huilia* (Lichens) in Japan I. Lecidea. Journal of science of the Hiroshima University. Series B. Div. 2, Botany 18(1), 1–55.
Intaraudom C, Punyain W, Bunbamrung N, Dramae A et al. 2019 − Antimicrobial drimane-phthalide derivatives from *Hypoxylon fendleri* BCC32408. Fitoterapia 138, 104353.
Isaka M, Yangchum A, Intamas S, Kocharin K et al. 2002 – Aigialomycins and related polyketide metabolites from the mangrove fungus *Aigialus parvus* BCC 5311. Tetrahedron 65, 4396–4403.
Ismaiel AA, Papenbrock J. 2015 – Mycotoxins: producing fungi and mechanisms of phytotoxicity. Agriculture 5, 492–537.
Ismailov AB, Urbanavichus GP, Yakovchenko LS, Urbanavichene IN. 2017 – The genus *Candelariella* (*Candelariaceae, Candelariales*) in the lichen flora of the Caucasus. Botanical Journal 102(6), 780–796.
Isola D, Scano A, Orrù G, Prenafeta-Boldú FX et al. 2021 – Hydrocarbon-contaminated sites: Is there something more than *Exophiala xenobiotica*? New insights into black fungal diversity using the long cold incubation method. Journal of Fungi 7, 817.
Isola D, Zucconi L, Onofri S, Caneva G et al. 2016 – Extremotolerant rock inhabiting black fungi from Italian monumental sites. Fungal Diversity 76(1), 75–96.
Itazaki H, Nagashima K, Sugita K, Yoshida H et al. 1990 – Solation and structural elucidation of new cyclotetrapeptides, trapoxins A and B, having detransformation activities as antitumor agents. The Journal of Antibiotics 43, 1524–1532.
Iturrieta-González I, García D, Gené J. 2021 – Novel species of *Cladosporium* from environmental sources in Spain. MycoKeys 77, 1.
Ivanova NV, DePriest PT, Bobrova VK, Troitsky AV. 1999 – Phylogenetic analisys of the lichen family *Umbilicariaceae* based on nuclear ITS1 and ITS2 rDNA sequences. The Lichenologist 31, 477–489.

Romeike J, Friedl T, Helms G, Ott S. 2002 – Genetic diversity of algal and fungal partners in four species of *Umbilicaria* (Lichenized *Ascomycetes*) along a transect of the Antarctic Peninsula. Molecular Biology and Evolution 19, 1209–1217.
Jackson TA. 2015 − Weathering, secondary mineral genesis, and soil formation caused by lichens and mosses growing on granitic gneiss in a boreal forest environment. Geoderma 251, 78−91.
Jacobs K, Holtzman K, Seifert KA. 2005 – Morphology, phylogeny and biology of *Gliocephalis hyalina*, a biotrophic contact mycoparasite of *Fusarium* species. Mycologia 97(1), 111–120.
Jaczevski A. 1922 – Materials or contributions for mycology and phytopathology in Russia. Discov Russ Mycol Flora 4, 3–15.
Jahns HM. 1973 – Anatomy, morphology, and development. The lichens, 3–58.
Jahns HM. 1982 – Luftverschmutzung und Krustenflechten im Frankfurter Stadtgebiet. Natur und Museum 112, 334–343.
Jaklitsch W, Baral HO, Lücking R, Lumbsch HT et al. 2016a – Syllabus of plant families-a. Engler's syllabus der Pflanzenfamilien part 1/2: *Ascomycota*, 13th ed. Borntraeger, Stuttgart, Germany.
Jaklitsch WM, Fournier J, Dai DQ, Hyde KD et al. 2015 – *Valsaria* and the *Valsariales*. Fungal Diversity 73, 159–202.
Jaklitsch WM, Fournier J, Rogers JD, Voglmayr H. 2014 – Phylogenetic and taxonomic revision of *Lopadostoma*. Persoonia 32, 52–82.
Jaklitsch WM, Fournier J, Voglmayr H. 2018 – Two unusual new species of *Pleosporales*: *Anteaglonium rubescens* and *Atrocalyx asturiensis*. Sydowia 70, 129–140.
Jaklitsch WM, Gardiennet A, Voglmayr H. 2016b − Resolution of morphology-based taxonomic delusions: *Acrocordiella*, *Basiseptospora*, *Blogiascospora*, *Clypeosphaeria*, *Hymenopleella*, *Lepteutypa*, *Pseudapiospora*, *Requienella*, *Seiridium* and *Strickeria*. Persoonia-Molecular Phylogeny and Evolution of Fungi 37(1), 82−105.
Jaklitsch WM, Réblová M, Voglmayr H. 2013 – Molecular systematics of *Woswasia atropurpurea* gen. et sp. nov. (*Sordariomycetidae*), a fungicolous ascomycete with globose ascospores and holoblastic conidiogenesis. Mycologia 105, 476–485.
Jaklitsch WM, Réblová M. 2015 – *Savoryellaceae* Jaklitsch & Réblová. Index Fungorum 209, 1.
Jaklitsch WM, Voglmayr H. 2011 – *Nectria eustromatica* sp. nov., an exceptional species with a hypocreaceous stroma. Mycologia 103, 209–218.
Jaklitsch WM, Voglmayr H. 2014 – Persistent hamathecial threads in the *Nectriaceae*, *Hypocreales*: *Thyronectria* revisited and re-instated. Persoonia 33, 182–211.
Jaklitsch WM, Voglmayr H. 2016 – Hidden diversity in *Thyridaria* and a new circumscription of the *Thyridariaceae*. Studies in Mycology 85, 35–64.
James PW, Vezda A. 1971 – *Melanophloea* P. James & Vezda, A new lichen genus. The Lichenologist 5, 89–91.
James TY, Kauff F, Schoch CL, Matheny PB et al. 2006 – Reconstructing the early evolution of fungi using a six-gene phylogeny. Nature 443(7113), 818–822.
Jami F, Slippers B, Wingfield MJ, Gryzenhout M. 2014 – *Botryosphaeriaceae* species overlap on four unrelated, native South African hosts. Fungal Biology 118, 168–179.
Janex-Favre MC. 1971 – Recherches sur l'ontogénie, l'organi-sation et les asques de quelques pyrénolichens. Revue Bryologique et Lichénologique 37, 421– 650.
Janex-Favre MC. 1974 – L'ontogénie et la structure des apothécies de l'Umbilicaria cylindrica. Revue Bryologique et Lichénologique 40, 59–86.
Jankowiak R, Strzałka B, Bilański P, Linnakoski R et al. 2017 – Two new *Leptographium* spp. reveal an emerging complex of hardwood-infecting species in the *Ophiostomatales*. Antonie van Leeuwenhoek 110, 1537–1553.
Jankowiak R, Szewczyk G, Bilański P, Jazłowiecka D et al. 2021 – Blue-stain fungi isolated from freshly felled Scots pine logs in Poland, including *Leptographium sosnaicola* sp. nov. Forest Pathology 51, e12672.

Janse M, de Hoog GS, Klerks N, van Dijk MAM et al. 2024 – Melanized fungi in bony fish species with Head and Lateral Line Erosion (HLLE) with a review of the literature on fungal fish diseases. One Health Mycology 1, 23–36.
Jany JL, Martin F, Garbaye J. 2003 – Respiration activity of ectomycorrhizas from *Cenococcum geophilum* and *Lactarius* sp. in relation to soil water potential in five beech forests. Plant and Soil 255, 487–494.
Jarvis SG, Woodward S, Taylor AFS. 2015 – Strong altitudinal partitioning in the distributions of ectomycorrhizal fungi along a short (300 m) elevation gradient. New Phytologist 206, 1145–1155.
Jatta A. 1911 – Lichenes (end) Flora Italica Cryptogama, Firenze Pars III. Fasc 4–6, 461–958.
Jayaram H, Marigowda V, Thara Saraswathi KJ. 2021 – Secondary metabolite production and terpenoid biosynthesis in endophytic fungi *Cladosporium cladosporioides* isolated from wild *Cymbopogon martinii* (Roxb.) Wats. Microbiology Research 12(4), 812–828.
Jayasiri SC, Ariyawansa HA, Jones EG, Kang JC et al. 2016 – Towards a natural classification of *Dothideomycetes*: 8. The genera *Cocconia*, *Dianesea*, *Endococcus* and *Lineostroma*. Phytotaxa 255(1), 66–74.
Jayasiri SC, Hyde KD, Jones EBG, Ariyawansa HA et al. 2017 – A new hysteriform *Dothideomycete* (*Gloniaceae*, *Pleosporomycetidae Incertae sedis*), *Purpurepithecium murisporum* gen. et sp. nov. on pine cone scales. Cryptogamie, Mycologie 38, 241–251.
Jayasiri SC, Hyde KD, Jones EBG, Derek P et al. 2018a – Taxonomic novelties of hysteriform *Dothideomycetes*. Mycosphere 9, 803–837.
Jayasiri SC, Hyde KD, Jones EBG, Jianchu Xu et al. 2018b – Seed decaying *Dothideomycetes* in Thailand: *Zeloasperisporium pterocarpi* sp. nov., (*Zeloasperisporiaceae*, *Zeloasperisporiales*) on carpel of *Pterocarpus* sp. (*Fabaceae*) seed pod. Asian Journal of Mycology 1(1), 106–113.
Jayasiri SC, Hyde KD, Jones EBG, McKenzie E et al. 2019 – Diversity, morphology and molecular phylogeny of *Dothideomycetes* on decaying wild seed pods and fruits. Mycosphere 10, 1–186.
Jayawardena RS, Ariyawansa HA, Singtripop C, Li YM et al. 2014 – A re-assessment of *Elsinoaceae* (*Myriangiales, Dothideomycetes*). Phytotaxa 176(1), 120–138.
Jayawardena RS, Bhunjun CS, Hyde KD, Gentekaki E et al. 2021a – *Colletotrichum*: Lifestyles, biology, morpho-species, species complexes and accepted species. Mycosphere 12(1), 519–669.
Jayawardena RS, Hyde KD, Chethana KWT, Daranagama DA et al. 2018 – Mycosphere Notes 102–168: saprotrophic fungi on Vitis in China, Italy, Russia and Thailand. Mycosphere 9, 1–114.
Jayawardena RS, Hyde KD, Damm U, Cai L et al. 2016 – Notes on currently accepted species of *Colletotrichum*. Mycosphere 7(8), 1192–1260.
Jayawardena RS, Hyde KD, de Farias AR, Bhunjun CS et al. 2021b – What is a species in fungal plant pathogens?. Fungal Diversity 109, 239–266.
Jayawardena RS, Hyde KD, Wang S, Sun YR et al. 2023 – Fungal diversity notes 1512–1610: taxonomic and phylogenetic contributions on genera and species of fungal taxa. Fungal Diversity 117(1), 1–272.
Jeffares DC, Rallis C, Rieux A, Speed D et al. 2015 – The genomic and phenotypic diversity of *Schizosaccharomyces pombe*. Nature Genetics 47(3), 235–241.
Jeffares DC. 2018 – The natural diversity and ecology of fission yeast. Yeast 35(3), 253–260.
Jenkins AE. 1925 – The Citrus scab fungus. Phytopathology 15, 99–104.
Jenkins AE. 1931 – Lima bean scab caused by *Elsinoë*. Journal of Agricultural Research 42, 13–23.
Jenkins AE. 1947 – A specific term for diseases caused by *Elsinoë* and *Sphaceloma*. Plant Disease Reporter 31, 71.
Jennings DH, Lysek G. 1999 – Fungal Biology: Understanding the Fungal Lifestyle, 2nd ed.; Bios Scientific Publishers Ltd.: Oxford, UK 1–166.
Jenssen, M, Rainsford P, Juskewitz E, Andersen J et al. 2021 – *Lulworthinone*, a new dimeric Naphthopyrone from a marine fungus in the family *Lulworthiaceae* with antibacterial activity

against clinical methicillin-resistant *Staphylococcus aureus* isolates. Frontiers in Microbiology 12.
Jha N, Aggarwal N. 2011 – First find of *Trichothyrites*, *Notothyrites* and *Frasnacritetrus* from Permian Gondwana sediments of Godavari Graben, India. Phytomorphology 61, 61–67.
Jia SJ, Zhang C, Luo ZD, Zhang S et al. 2018 – Differences in element concentrations between two lichens *Xanthoria mandschurica* and *Candelaria fibrosa* from Taihang mountains, Shanxi, China. Chinese Journal of Ecology 37(5), 1403–1409.
Jiang H, Phookamsak R, Xu J, Karunarathna S et al. 2020a – Taxonomic and phylogenetic characterizations reveal three new species of *Mendogia* (*Myriangiaceae*, *Myriangiales*). Mycological Progress 19, 41–51.
Jiang HB, Hyde KD, Yang EF, Kakumyan P et al. 2021a – Morphological and phylogenetic appraisal of *Ophioceras* (*Ophioceraceae*, *Magnaporthales*). PLoS ONE 16(8), e0253853.
Jiang L, Bao HY, Yang M. 2010 – Antitumor activity of a petroleum ether extract from *Paecilomyces hepiali* mycelium. Acta Edulis Fungi 17(4), 58–60
Jiang N, Fan XL, Tian CM, Crous PW. 2020b– Reevaluating *Cryphonectriaceae* and allied families in *Diaporthales*. Mycologia 112 (2), 267–292.
Jiang N, Fan XL, Tian CM. 2021b – Identification and characterization of leaf-inhabiting fungi from *Castanea* plantations in China. Journal of Fungi 7, 1–60.
Jiang P, Fu X, Niu H, Chen S, Liu F, Luo Y, Zhang D, Lei H. 2023 – Recent advances on *Pestalotiopsis* genus: Chemistry, biological activities, structure–activity relationship, and biosynthesis. Archives of Pharmacal Research 46, 449–499.
Jiang SH, Hawksworth DL, Lücking R, Wei JC. 2020c – A new genus and species of foliicolous lichen in a new family of *Strigulales* (*Ascomycota*: *Dothideomycetes*) reveals remarkable class-level homoplasy. IMA Fungus 11, 1.
Jiang SH, Lücking R, Liu HJ, Wei XL et al. 2022 – Twelve new species reveal cryptic diversification in foliicolous lichens of *Strigula s.lat.* (*Strigulales*, *Ascomycota*), Journal of Fungi 8, 2.
Jiang SH, Wei XL, Wei JC. 2017a – Two new species of *Strigula* (lichenised *Dothideomycetes*, *Ascomycota*) from China, with a key to the Chinese foliicolous species. MycoKeys 19, 31–42.
Jiang SH, Wei XL, Wei JC. 2017b – A new species and two new records of *Strigula* (lichenized *Ascomycota*) from China. Mycoscience 58, 391–397.
Jiang X, Xiang M, Liu XZ. 2017c – Nematode-trapping fungi. Microbiology Spectrum, 5, 10–1128.
Jiang Y, Dukik K, Muñoz JF, Sigler L et al. 2018 – Phylogeny, ecology and taxonomy of systemic pathogens and their relatives in *Ajellomycetaceae* (*Onygenales*): *Blastomyces*, *Emergomyces*, *Emmonsia*, *Emmonsiellopsis*. Fungal Diversity 90(1), 245–291.
Jie CY, Zhoua QX, Zhao WS, Jiang YL et al. 2013 – A new *Myrmecridium* species from Guizhou, China. Mycotaxon 124, 1–8.
Johnson GT. 1940 – Contributions to the study of the *Trypetheliaceae*. Annals of the Missouri Botanical Garden 27(1), 1–50.
Johnson KA. 2018 – Characterization and fungicide efficacy of North Carolina *Colletotrichum* populations causing *Glomerella* leaf spot and fruit rot on apple. North Carolina State University.
Johnston PR, Baschien C. 2020 – *Tricladiacea*e fam. nov. (*Helotiales, Leotiomycetes*). Fungal Systematics and Evolution 6, 233–242.
Johnston PR, Minter DW. 1989 − Structure and taxonomic significance of the ascus in the *Coryneliaceae*. Mycological Research 92(4), 422–430.
Johnston PR, Nguyen HDT, Park D, Hirooka Y. 2015 – *Harorepupu Aotearoa* (*Onygenales*) gen. sp. nov.; a threatened fungus from shells of *Powelliphanta* and *Paryphanta* snails (Rhytididae). IMA Fungus 6(1), 135–143.
Johnston PR, Park D, Baral HO, Galán R et al. 2014a – The phylogenetic relationships of *Torrendiella* and *Hymenotorrendiella* gen. nov. within the *Leotiomycetes*. Phytotaxa 117(1), 1–25.

Johnston PR, Park D, Bourdeau P, Eyssartier G. 2022 – A new species of *Cryptohymenium* (*Leotiomycetes, Helotiales*) from New Caledonia. Ascomycete.org 14 (4–5), 133–138.
Johnston[1] PR, Park D, Renner MA. 2019a – *Sphaeropezia leucocheila* sp. nov. (*Stictidaceae*): A liverwort pathogen from New Zealand. Phytotaxa 409(4), 222–226.
Johnston PR, Park D, Smissen R. 2017 – Comparing diversity of fungi from living leaves using culturing and high throughput environmental sequencing. Mycologia 109, 643–654.
Johnston PR, Park D. 2019 – New species of *Marthamyces* and *Ramomarthamyces* gen. nov. from New Zealand and the Cook Islands. Mycotaxon 134, 489–516.
Johnston PR, Quijada L, Smith CA, Baral HO et al. 2019b – A multigene phylogeny toward a new phylogenetic classification of *Leotiomycetes*. IMA Fungus 10, 1–22.
Johnston PR, Seifert KA, Stone JK, Rossman AY et al. 2014b – Recommendations on generic names competing for use in *Leotiomycetes* (*Ascomycota*). IMA Fungus 5, 91–120.
Johnston PR. 1985 – Anamorphs of the ostropalean genera *Schizoxylon* and *Acarosporina*. Mycotaxon 24, 349–360.
Johnston PR. 1990 – *Rhytismataceae* in New Zealand 3. The genus *Hypoderma*. New Zealand Journal Botany 28, 159−183.
Johnston PR. 2006 – *Rhytismatales* of Australia: the genus *Marthamyces*. Australian Systematic Botany 19, 135–146.
Jones EBG, Eaton RA. 1969 – *Savoryella lignicola* gen. and sp. nov. from water-cooling towers. Transactions of the British Mycological Society 52(1), 161–165.
Jones EBG, Hyde KD. 1988 – Methods for the study of mangrove marine fungi. 9–27, in Agate, Subramanian and Vannucci (eds.) Mangrove microbiology. Role of microorganisms in nutrient cycling of mangrove soils and water. UNDP/UNESCO, New Delhi.
Jones EBG, Hyde KD. 1992 – Taxonomic studies on *Savoryella* Jones et Eaton (*Ascomycotina*). Botanica Marina 35, 83–91.
Jones EBG, Johnson RG, Moss ST. 1983a – Taxonomic studies of the *Halosphaeriaceae*: *Corollospora* Werdermann. Botanical Journal of the Linnean Society 87, 193–212
Jones EBG, Klaysuban A, Pang K-L. 2008 – Ribosomal DNA phylogeny of marine anamorphic fungi: *Cumulospora varia*, *Dendryphiella* species and *Orbimyces spectabilis*. Raffles Bull Zool 19, 11–18.
Jones EBG, Le Campion-Alsumard T. 1970 – Marine fungi on polyurethane plates submerged in the sea. Nova Hedwigia 19, 567–590.
Jones EBG, Moss ST, Cuomo V. 1983b – Spore appendage development in the lignicolous marine pyrenomycetes *Chaetosphaeria chaetosa* and *Halosphaeria trullifera*. Transactions of British Mycological Society 80, 193–200.
Jones EBG, Pang KL, Abdel-Wahab MA, Scholz B et al. 2019 – An online resource for marine fungi. Fungal Diversity 96, 347–433.
Jones EBG, Pang KL. 2012 – Marine fungi and fungal-like organisms. Walter de Gruyter GmbH and Co. KG, Berlin/Boston.
Jones EBG, Ramakrishna S, Vikineswary S, Das D et al. 2022 – How do fungi survive in the sea and respond to climate change? Journal of Fungi 8, 291.
Jones EBG, Sakayaroj J, Suetrong S, Somrithipol S et al. 2009 – Classification of marine *Ascomycota*, anamorphic taxa and *Basidiomycota*. Fungal Diversity 35, 1–203.
Jones EBG, Suetrong S, Cheng WH, Rungjindamai N et al. 2014 – An additional fungal lineage in the *Hypocreomycetidae* (*Falcocladium* species) and the taxonomic revaluation of *Chaetosphaeria chaetosa* and *Swampomyces* species, based on morphology, ecology and phylogeny. Cryptogamie, Mycologie 35, 119–138.
Jones EBG, Suetrong S, Sakayaroj J, Bahkali AH et al. 2015 – Classification of marine *Ascomycota*, *Basidiomycota*, *Blastocladiomycota* and *Chytridiomycota*. Fungal Diversity 73, 1–72.

1

Jones EBG, To-anun C, Suetrong S, Boonyuen N. 2016 – Mycosphere Essays 12. Progress in the classification of the water–cooling tower ascomycete *Savoryella* and a tribute to John Savory: a review. Mycosphere 7(5), 570–581.
Jones EBG. 1963 – Observations on the fungal succession on wood test blocks submerged in the sea. Journal of the Institute of Wood Science 11, 14–23.
Jones EBG. 1994 – Fungal adhesion. Mycological Research 98, 961–981.
Jones EBG. 2006 – Form and function of fungal spore appendages. Mycoscience 47,167–183.
Jones KG, Blackwell M. 1996 – Ribosomal DNA sequence analysis places the yeast-like genus *Symbiotaphrina* within filamentous ascomycetes. Mycologia 88, 212–218.
Jones SG. 1935 – The structure of *Lophodermium pinastri* (Schard.) Chev. Annls Bot 49, 699−728.
Jong SC, Rogers JD. 1972 – Illustrations and descriptions of conidial states of some *Hypoxylon* species. Washington State Agricultural Experimental Station Technical Bulletin No. 71
Jönsson M, Edman M, Jansson S. 2008 – Identification and quantification of potential fungal biocontrol agents on coniferous seedlings in Swedish forest nurseries. Forest Pathology 38(5), 327–345.
Jordal JB, Holien H, Nordén B. 2022 – *Melaspilea bagliettoana* new to Fennoscandia. Graphis Scripta 34(1), 1–6.
Jørgensen PM, Andersen HL, Elvebakk A. 2019 – The genus *Massalongia* (lichenised ascomycetae) in the Southern Hemisphere. MycoKeys 60, 125.
Jørgensen PM. 1994 – Studies in the lichen family *Pannariaceae* VI: The taxonomy and phytogeography of *Pannaria* Del. *s. lat.* The Journal of the Hattori Botanical Laboratory 76, 197–206.
Joshi Y, Kumar P, Lal Yadav A, Suda N et al. 2020 – Distribution and diversity of lichenicolous fungi from western Himalayan Cold Deserts of India, including a new *Zwackhiomyces* species. Sydowia 73, 171–183.
Joshi Y, Nayal S, Tripathi M, Bisht K et al. 2015 – Distribution and diversity of lichenized fungi colonizing jageshwar group of temples, Almora, Uttarakhand. Proceedings of the National Academy of Sciences, India Section B: Biological Sciences 85(2), 545–554.
Joshi Y. 2022 – Three new species of lichenicolous fungi from India. Kew Bulletin 77, 333–340.
Jouraeva VA, Johnson DL, Hassett JP, Nowak DJ et al. 2006 – Role of sooty mold fungi in accumulation of fine-particle-associated PAHs and metals on deciduous leaves. Environmental Research 102, 272–282.
Ju Y, Rogers J. 1994 – Biological and developmental studies of *Xylobotryum andinum* (*Ascomycetes*, *Loculoascomycetes*). Cryptogamic Botany 4, 346–355.
Ju YM, Rogers JD, Hsieh HM. 2018 – *Xylaria* species associated with fallen fruits and seeds. Mycologia 110, 726–749.
Ju YM, Rogers JD, Huhndorf SM. 1966 – *Valsaria* and notes on *Endoxylina*, *Pseudothyridaria*, *Pseudovalsaria*, and *Roussoella*. Mycotaxon 58, 419–481.
Ju YM, Rogers JD. 1990 − *Astrocystis* reconsidered. Mycologia 82, 342–349.
Juel HO. 1902 – *Taphridium* Lagerh. und Juel, eine neue Gattung der Protomycetaceen. Bihang til Kongliga Svenska Vetenskaps-Akademiens Handlingar 27(16), 1–29.
Jumpponen A, Weber NS, Trappe JM, Cázares E. 1997 – Distribution and ecology of the ascomycete *Sarcoleotia globosa* in the United States. Canadian Journal of Botany 75(12), 2228–2231.
Jung P, Brust K, Schultz M, Büdel B et al. M 2021 – Opening the gap: rare lichens with rare cyanobionts – unexpected cyanobiont diversity in cyanobacterial lichens of the order *Lichinales*. Frontiers in Microbiology 12, 728378.
Junne T, Wong J, Studer C, Aust T et al. 2015 – Decatransin, a new natural product inhibiting protein translocation at the Sec61/SecYEG translocon. Journal of Cell Science. 128(6), 1217–1229.
Juravel E, Polacheck I, Isaacson B, Dagan A et al. 2023 – The distinction between dematiaceous molds and non-dematiaceous fungi in clinical and spiked samples treated with hydrogen peroxide using direct fluorescence microscopy. Journal of Fungi 9 (2), 227.

Jurzitza G. 1964 – Studien an der Symbiose der Anobiiden. II. Physiologische Studien am Symbionten von Lasioderma serricorne F. Arch Mikrobiol 49, 331–340.
Kabtani J, Militello M, Ranque S. 2022 – *Coniochaeta massiliensis* sp. nov. isolated from a clinical sampl28. Journal of Fungi 8(10), 999.
Kaishian P, Lubbers M, de Groot M, Schilthuizen M et al. 2022 – Definitions of parasites and pathogens through time. Authorea.
Kalb K, Aptroot A. 2021 – New lichens from Africa. Archive for Lichenology 28, 1–12.
Kalgutkar RM, Jansonius J. 2000 – Synopsis of fossil fungal spores, mycelia and fructifications. AASP Contributions Series, Number 39. American Association of Stratigraphic Palynologists Foundation, Dallas, Texas.
Kalgutkar RM, Nambudiri EMV, Tidwell WD. 1993 – *Diplodites sweetii* sp. nov. from the Late Cretaceous (Maastrichtian) Deccan Intertrappean Beds of India. Review of Palaeobotany and Palynology 77, 107–118.
Kamauchi H, Shiraishi Y, Kojima A, Kawazoe N et al. 2018 − *Isoindolinones*, *phthalides*, and a naphthoquinone from the fruiting body of *Daldinia concentrica*. Journal of Natural Products 81, 1290–4.
Kandasamy D, Gershenzon J, Hammerbacher A. 2016 – Volatile organic compounds emitted by fungal associates of conifer bark beetles and their potential in bark beetle control. Journal of Chemical Ecology 42, 952–969.
Kandasamy D, Zaman R, Nakamura Y, Zhao T et al. 2023 – Conifer-killing bark beetles locate fungal symbionts by detecting volatile fungal metabolites of host tree resin monoterpenes. PLoS biology 21, e3001887.
Kandemir AH, Dukik K, de Melo Teixeira M, Stielow JB et al. 2022 – Phylogenetic and ecological reevaluation of the order *Onygenales*. Fungal Diversity 115(1), 1–72.
Kandemir AH. 2022 – Taxonomy and biodiversity of *Onygenales*. Radboud University Nijmegen
Kang HJ, Sigler L, Lee J, Gibas CFC et al. 2010 – *Xylogone ganodermophthora* sp. nov., an ascomycetous pathogen causing yellow rot on cultivated mushroom *Ganoderma lucidum* in Korea. Mycologia 102, 1167–1184.
Kang JC, Hyde KD, Kong RYC. 1999 – Studies on *Amphisphaeriales*: The genera excluded from the *Amphisphaeriaceae*, *Cainiaceae* and *Clypeosphaeriaceae*. Fungal Diversity 2, 135–151.
Kantvilas G, Lumbsch HT. 2009 – *Meridianelia*, a new genus in the *Elixiaceae* (*Ascomycota*) from Tasmania. The Lichenologist 41(3), 261–270.
Kantvilas G, Lumbsch HT. 2012 – Reappraisal of the genera of *Megalosporaceae* (*Teloschistales*, *Ascomycota*). Australian Systematic Botany 25(3), 210–216.
Kantvilas G, McCarthy PM. 2003 – *Hueidea* (*Fuscideaceae*), a new lichen genus from alpine Australia. The Lichenologist 35(5-6), 397–407.
Kantvilas G, Vězda A. 1996 – The lichen genus *Sarrameana*. Nordic Journal of Botany 16(3), 325–333.
Kantvilas G. 1999 – A new species of *Schaereria* from Tasmania. The Lichenologist 31(3), 231–238.
Kantvilas G. 2000 – Additions from the Southern Hemisphere to the lichen genus *Loxospora*. Herzog 14, 35–38.
Kao MR, Kuo HW, Lee CC, Huang KY et al. 2019 – *Chaetomella raphigera* β-glucosidase D2-BGL has intriguing structural features and a high substrate affinity that renders it an efficient cellulase supplement for lignocellulosic biomass hydrolysis. Biotechnology for Biofuels 12(1), 1–18.
Karakehian JM, Pennycook SR, Rudman NA, Knierim M et al. 2023 – (2965–2967) Proposals to conserve the names *Mellitosporium* with a conserved type, and *Mellitosporiella* (Fungi, *Ascomycota*, *Marthamycetales*) with those spellings and to conserve the name *Mellitosporium versicolor* with a conserved type. TAXON 72, 923–925.
Karakehian JM, Quijada L, Friebes G, Tanney JB et al. 2019 – Placement of *Triblidiaceae* in *Rhytismatales* and comments on unique ascospore morphologies in *Leotiomycetes* (Fungi, *Ascomycota*). MycoKeys 54, 99.

Karimi O, Chethana KWT, Farias ARG, Li QR. 2023 – Two new records of *Xylariales* species from Northern Thailand. Phytotaxa 598(3), 187−205.
Karmacharya N, Upreti DK, Chettri MK. 2022 – Distribution pattern of corticolous lichens in different areas of Kathmandu valley, Nepal. Banko Janakari 32(2), 3–18.
Kärnefelt I. 1989 – Morphology and phylogeny in the *Teloschistales*. Cryptogam. Bot 1, 147–203.
Kärnefelt I. 1990 – Isidiate taxa in the *Teloschistales* and their ecological and evolutionary significance. The Lichenologist 22(3), 307–320.
Karsten H. 1869 – Chemismus der Pflanzenzelle. Vienna: Wilhelm Braumüller. 90.
Karsten PA. 1871 – Mycologia fennica. I. Discomycetes, Helsingfors
Karsten PA. 1873 – Mycologia fennica, Pars secunda *Pyrenomycetes*. Bidrag till Ka¨nnedom av Finlands Natur och Folk 23, 1–252.
Karsten PA. 1885 – Revisio monographica atque synopsis *Ascomycetum* in Fennia hucusque detectorum. Acta Societatis Pro Fauna et Flora Fennica 2(6), 1–174.
Kauff F, Bachran A, Schultz M, Hofstetter V et al. 2018 – Molecular data favours a monogeneric *Peltulaceae* (*Lichinomycetes*). The Lichenologist 50(3), 313–327.
Kauff F, Büdel B. 2005 – Ascoma ontogeny and apothecial anatomy in the *Gyalectaceae* (*Ostropales*, *Ascomycota*) support the re-establishment of the *Coenogoniaceae*. The Bryologist 108(2), 272–281.
Kauff F, Lutzoni F. 2002 – Phylogeny of *Gyalectales* and *Ostropales* (*Ascomycota*, Fungi): among and within order relationships based on nuclear ribosomal RNA small and large subunits. Molecular Phylogenetics and Evolution 25, 138–156.
Kawamukai M. 2009 – Biosynthesis and bioproduction of coenzyme Q10 by yeasts and other organisms. Biotechnology and applied biochemistry 53(4), 217–226.
Kazemzadeh Chakusary M, Mohammadi H, Khodaparast S. 2017 – Decline-associated *Phaeoacremonium* species occurring on forest trees in the north of Iran. Forest pathology 47, e12368.
Keely SP, Fischer JM, Cushion MT, Stringer JR. 2004 – Phylogenetic identification of *Pneumocystis murina* sp. nov., a new species in laboratory mice. Microbiology 150, 1153–1165.
Keely SP, Fischer JM, Stringer JR. 2003 – Evolution and speciation of *Pneumocystis*. Journal of Eukaryotic Microbiology 50, S624–S626.
Keissler K von. 1930 – Rabenhorst's Kryptogamen-Flora, Pilze - Die Flechtenparasiten 8, 1–712
Keissler K. 1937 – *Pyrenulaceae*, *Trypetheliaceae*, *Pyrenidaceae*, *Xanthopyreniaceae*, *Mycoporaceae* und *Coniocarpaceae*, Rabenh. Krypt.
Keizer G. 1990 – Twee opvallende zeldzame Ascomyceten: *Catinella olivacea* en Jafneadelphus amethystinus. Coolia 33, 58–62.
Kekuda TP, Vinayaka KS, Sachin MB. 2018 – Chemistry, ethnobotanical uses and biological activities of the lichen genus *Heterodermia* Trevis. (*Physciaceae*; *Lecanorales*; *Ascomycota*): A comprehensive review. Journal of Applied Pharmaceutical Science 8(5), 148–155.
Keller NP, Turner G, Bennett JW. 2005 – Fungal secondary metabolism - from biochemistry to genomics. Nature Reviews Microbiology 3, 937–947.
Kellogg CA, Griffin DW. 2006 – Aerobiology and the global transport of desert dust. Trends in Ecology & Evolution 21, 638–644.
Kern H, Naef-Roth S. 1975 – Zur Bildung von Auxinen und Cytokininen durch *Taphrina*-arten. Phytopathologische Zeitschrift 83, 193–222.
Khalid AN, Zulfiqar R. 2023 – A new species of the genus *Verrucaria* (lichenized *Ascomycetes*: *Verrucariaceae*) from Kohistan district, Pakistan. Plant Systematics and Evolution 309(3), 1–6.
Khan KH, Kluting K, Tångrot J, Urbina H et al. 2020 – Naming the untouchable – environmental sequences and niche partitioning as taxonomical evidence in fungi. IMA Fungus 11, 23.
Khan Z, Gené J, Ahmad S, Cano J et al. 2013 – *Coniochaeta polymorpha*, a new species from endotracheal aspirate of a preterm neonate, and transfer of *Lecythophora* species to *Coniochaeta*. Antonie van Leeuwenhoek 104, 243–252.

Khemmuk W. 2017 – Plant pathogenic *Magnaporthales* in Australia, with particular reference to *Pyricularia oryzae* on wild and cultivated rice. Doctoral dissertation, University of Queensland.
Khodosovtsev A, Kondratyuk S, Kärnefelt I. 2004 – *Candelariella boikoi*, a new lichen species from Eurasia. Graphis Scripta 16(1), 11–15.
Khodosovtsev AE. 2005 – The genus *Candelariella* (*Candelariaceae*, *Lecanorales*) of the Southern Ukraine. Novitates Systematicae Plantarum non Vascularium 39, 265–281.
Khodosovtsev AYe, Darmostuk VV 2017a – *Collemopsidium kostikovii* sp. nov. (*Collemopsidales*, *Xanthopyrenaceae*), a new algicolous fungus on terricolous *Nostoc* crust from Ukraine. Ukrainian Botanical Journal 74(5), 431–434.
Khodosovtsev AYe, Darmostuk VV. 2017b – *Zwackhiomyces polischukii* sp. nov. and other noteworthy lichenicolous fungi from Ukraine. Polish Botanical Journal 62(1), 27–35.
Kim MS, Lee KA. 2006 – Antithrombic activity of methanolic extract of *Umbilicaria esculenta*. Journal of Ethnopharmacology 105, 342–345.
Kim S, Lee H, Lee M, Lee T. 2006 – Efficient synthesis of the immunosuppressive agent FTY720. Synthesis 2006(05), 753-755.
Kim S, Shin DS, Lee T, Oh KB. 2004 – Periconicins, two new fusicoccane diterpenes produced by an endophytic fungus *Periconia* sp. with antibacterial activity. Journal of Natural Products 67, 448–450.
Kimbrough JW. 1970 – Current trends in the classification of *Discomycetes*. The Botanical Review 36, 91–161.
Kimbrough JW. 1981 – The discomycete centrum. In *Ascomycete systematics: the Luttrellian concept* (92–101). New York, NY: Springer New York.
King D, Pasarell L, Dixon DM, McGinnis MR et al. 1993 – A phaeohyphomycotic cyst and peritonitis caused by *Phialemonium* species and a reevaluation of its taxonomy. Journal of Clinical Microbiology 31, 1804–1810.
Kino T, Hatanaka H, Hashimoto M, Nishiyama M et al. 1987 – FK-506, a novel immunosuppressant isolated from a *Streptomyces* I. Fermentation, isolation, and physico-chemical and biological characteristics. The Journal of antibiotics 40(9), 1249–1255.
Kirk PM, Cannon PF, David JC, Stalpers JA 2001 – Ainsworth & Bisby's dictionary of the fungi, 9th edn. CABI, Wallingford.
Kirk PM, Cannon PF, Minter DW, Stalpers JA, 2008b – Dictionary of the Fungi. CABI International, Wallingford, UK.
Kirk PM, Cannon PF, Minter DW, Stalpers JA. 2008a – Ainsworth & Bisby's Dictionary of the Fungi. CABI, Wallingford, Oxon, UK.
Kirk PM, Spooner BM. 1989 – *Ascomycetes* on leaf litter of *Laurus nobilis* and *Hedera helix*. Mycological Research 92, 335–346.
Kirk PM. 1984 – New or interesting microfungi XII. A new species of *Conioscypha* (*Hyphomycetes*). Transactions of the British Mycological Society 82: 177e178.
Kirk PM. 2015 – Nomenclatural novelties. Index Fungorum 265, 1.
Kirschner R. 2003 – Two new species of *Pyxidiophora* associated with bark beetles in Europe. Mycological Progress 2, 209–218.
Kirschstein W. 1924 – Beiträge zur Kenntnis der Ascomyeeten. Verhandlungen des Botanischen Vereins der Provinz Brandenburg 66, 23–29.
Kirschstein W. 1936 – Beiträge zur Kenntnis der Ascomyceten und ihrer Nebenformen besonders aus der Mark Brandenburg und dem Bayerischen Walde. Ann Mycol 34, 180–210.
Kiss L, Kovács GM, Bóka K, Bohár G et al. 2018 – Deciphering the biology of *Cryptophyllachora eurasiatica* gen. et sp. nov., an often cryptic pathogen of an allergenic weed, *Ambrosia artemisiifolia*. Scientific Reports 8, 10806.
Kjoller A, Struwe S. 1982 – Microfungi in ecosystems: fungal occurrence and activity in litter and soil. Oikos 39, 389–422.

Klar AJ. 2013 – *Schizosaccharomyces japonicus* yeast poised to become a favorite experimental organism for eukaryotic research. G3: Genes, Genomes, Genetics 3(10), 1869–1873.
Klaubauf S, Tharreau D, Fournier E, Groenewald JZ et al. 2014 – Resolving the polyphyletic nature of *Pyricularia* (*Pyriculariaceae*). Studies in mycology 79(1), 85–120.
Klepzig KD, Six DL. 2004 – Bark beetle-fungal symbiosis: context dependency in complex associations. Symbiosis.
Knudsen K, Breuss O, Kocourková J. 2014 – A new lichenicolous *Heteroplacidium* (*Verrucariaceae*) from the deserts of southern California. Opuscula Philolichenum 13, 26–33.
Knudsen K, Kocourková J. 2013 – Lichenological notes 6: nomenclatural acts. Mycotaxon, 124(1), 353–359.
Knudsen K, Kocourková J. 2014 – A new species of *Lecidea* (*Lecideaceae*, Lichenized *Ascomycetes*) from the mountains of California. Opuscula Philolichenum 13, 80–83.
Knudsen K, Lendemer JC, Harris RC. 2011 – Lichens and lichenicolous fungi - no. 15: miscellaneous notes on species from eastern North America. Opuscula Philolichenum
Knudsen K, Lendemer JC. 2016 – A new perspective on *Melanophloea*, *Thelocarpella* and *Trimmatothelopsis*: species previously placed in multiple families are united within a single genus in the *Acarosporaceae*. The Bryologist 119(3), 266–279.
Kobayashi E, Ando K, Nakano H, Iida T et al. 1989 – *Calphostins* (UCN-1028), novel and specific inhibitors of protein kinase C.I. Fermentation, isolation, physico-chemical properties and biological activities. The Journal of antibiotics 42, 1470–1474.
Kobayasi Y, Shimizu D. 1960 – Monographic studies of *Cordyceps* 1. Group parasitic on *Elaphomyces*. Bulletin of the National Science Museum Tokyo 5, 69–85.
Kobayasi Y. 1941 – The genus *Cordyceps* and its allies. Science Reports of the Tokyo Bunrika Daigaku (Section B no. 84)5, 53–260.
Kobayasi Y. 1982 – Keys to the taxa of the genera *Cordyceps* and *Torrubiella*. Transactions of the Mycological Society of Japan 23, 329–364.
Koch J, Pang KL, Jones EBG. 2007 – *Rostrupiella danica* gen. et sp. nov., a *Lulworthia*-like marine lignicolous species from Denmark and the USA
Kocourková-Horáková J. 1998 – Distribution and ecology of the genus *Thelocarpon* (*Lecanorales*, *Thelocarpaceae*) in the Czech Republic. Czech Mycology 50(4), 271–302.
Kodsueb R, Jeewon R, Vijaykrishna D, Eric M et al. 2006 – Systematic revision of *Tubeufiaceae* based on morphological and molecular data. Fungal Diversity 21, 105–130.
Koenig H, Ball C, de Bie`vre C. 1997 – First European cases of onychomycosis caused by *Onychocola canadensis*. Journal of Medical and Veterinary Mycology 35, 71–72.
Koerber GW. 1855 – Systema Lichenum Germaniae. Breslau, 458 pp.
Koerber GW. 1865 – Parerga Lichenologica. Breslau 3, Verlag Von Eduard Trewend p, 282
Kogej T, Wheeler MH, Lanišnik Rižner T, Gunde-Cimerman N. 2004 – Evidence for 1, 8-dihydroxynaphthalene melanin in three halophilic black yeasts grown under saline and non-saline conditions. FEMS Microbiology Letters 232, 203–209.
Kohler A, Kuo A, Nagy LG, Morin E et al. 2015 – Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists. Nature Genetics 47, 410–415.
Kohlmeyer J, Hawksworth DL, Volkmann-Kohlmeyer B – 2004 – Observations on two marine and maritime "borderline" lichens: *Mastodia tessellata* and *Collemopsidium pelvetiae*. Mycological Progress 3, 51–56.
Kohlmeyer J, Kohlmeyer E. 1965 – New marine fungi from mangrove and trees along eroding shorelines. Nova Hedwigia 9, 89–104
Kohlmeyer J, Kohlmeyer E. 1967 – Icones Furgorum Maris Fasc. 4 & 5. Lehre: J. Cramer.
Kohlmeyer J, Kohlmeyer E. 1975 – Biology and geographical distribution of *Spathulospora* species. Mycologia 67, 629–637.
Kohlmeyer J, Kohlmeyer E. 1979 – Marine Mycology. The Higher Fungi. New York and London: Academic Press.

Kohlmeyer J, Spatafora JW, Volkmann-Kohlmeyer B. 2000 – *Lulworthiales*, a new order of marine Ascomycota. Mycologia 92, 453–458.
Kohlmeyer J, Volkmann-Kohlmeyer B, Eriksson O. 1995 – Fungi on *Juncus roemerianus*. 3. New ascomycetes. Botanica Marina 38, 175–186.
Kohlmeyer J, Volkmann-Kohlmeyer B, Eriksson OE 1997 – Fungi on *Juncus roemerianus* 9. New obligate and facultative marine *Ascomycotina*. Botanica Marina 40, 291–300.
Kohlmeyer J, Volkmann-Kohlmeyer B. 1987a – *Koralionastetaceae* fam. nov. (*ascomycetes*) from coral rock. Mycologia 79, 764–778.
Kohlmeyer J, Volkmann-Kohlmeyer B. 1987b – Marine fungi from Belize with a description of two new genera of *Ascomycetes*. Botanica Marina 30, 195–204.
Kohlmeyer J, Volkmann-Kohlmeyer B. 1989 – Hawaiian marine fungi, including two new genera of *Ascomycotina*. Mycological Research 92, 410–421.
Kohlmeyer J, Volkmann-Kohlmeyer B. 1990 – New species of *Koralionastes* (*Ascomycotina*) from the Caribbean and Australia. Canadian Journal of Botany 68(7), 1554–1559.
Kohlmeyer J, Volkmann-Kohlmeyer B. 1990b – Revision of marine species of *Didymosphaeria* (*Ascomycotina*). Mycological Research 94(5), 685–690.
Kohlmeyer J, Volkmann-Kohlmeyer B. 1996 – Fungi on *Juncus roemerianus*. 6. *Glomerobolus* gen. nov., the first ballistic member of *Agonomycetales.* Mycologia 88(2), 328–337.
Kohlmeyer J, Volkmann-Kohlmeyer B. 2003 – Marine *ascomycetes* from algae and animal hosts. Botanica Marina 46, 285–306.
Kohlmeyer J. 1960 – Wood-inhabiting marine fungi from the Pacific Northwest and California. Nova Hedwigia 2, 293–343.
Kohlmeyer J. 1963 – Fungi marini novi vel critici. Nova Hedwigia 6, 297–329.
Kohlmeyer J. 1972 – A revision of *Halosphaeriaceae*. Canadian Journal of Botany 50, 1951–1963.
Kohlmeyer J. 1973 – *Spathulosporales*, a new order and possible missing link between *Laboulbeniales* and *Pyrenomycetes*. Mycologia 65(3), 614–647.
Kohlmeyer J. 1975 – Revision of algicolous *Zigonella* spp. and description of *Pontogenia* gen. nov. (*Ascomycetes*). Botanische Jahrb ü cher f ü r Systematik 96, 200–211.
Kohno J, Hirano N, Sugawara K, Nishio M et al. 2001 – Structure of TMC-69, a new antitumor antibiotic from *Chrysosporium* sp. TC 1068. Tetrahedron 57(9), 1731–1735.
Kokaew J, Manoch L, Worapong J, Chamswarng C et al. 2011 – *Coniochaeta ligniaria* an endophytic fungus from *Baeckea frutescens* and its antagonistic effects against plant pathogenic fungi. Thai Journal of Agricultural Science 44, 123–131.
Kolařík M, Hulcr J. 2009 – Mycobiota associated with the ambrosia beetle *Scolytodes unipunctatus* (*Coleoptera*: *Curculionidae*, *Scolytinae*). Mycological Research 113, 44–60.
Kolařík M, Spakowicz DJ, Gazis R, Shaw J et al. 2017 – *Biatriospora* (*Ascomycota*: *Pleosporales*) is an ecologically diverse genus including facultative marine fungi and endophytes with biotechnological potential. Plant Systematics and Evolution 303, 35–50.
Komposch H, Hafellner J. 2000 – Diversity and vertical distribution of lichens in a Venezuelan tropical lowland rain forest. Selbyana 21, 11–24.
Komposch H, Hafellner J. 2003 – Species composition of lichen dominated corticolous communities: a lowland rain forest canopy compared to an adjacent shrubland in Venezuela. Bibliotheca lichenologica 86, 351–367.
Kondratyuk SY, Lokos L, Farkas E, Oh SO, Hur JS. 2015 – New and noteworthy lichen-forming and lichenicolous fungi 2. Acta Botanica Hungarica 57(1-2), 108–142.
Kondratyuk SY, Lőkös L, Halda JP, Farkas E et al. 2018 – New and noteworthy lichen-forming and lichenicolous Fungi 7. Acta Botanica Hungarica 60(1–2), 115–184.
Kondratyuk SY, Lőkös L, Halda JP, Roux C et al. 2017 – New and noteworthy lichen-forming and lichenicolous fungi 6. Acta Botanica Hungarica 59(1–2), 137–260.
Kondratyuk SY, Lőkös L, Jeong M-H, Oh SO et al. 2020 –Contributions to molecular phylogeny of lichen-forming fungi, 1. The family *Candelariaceae*. Acta Botanica Hungarica 62(3–4), 293–307.

Kondratyuk SY, Lőkös L, Kondratiuk AS, Kärnefelt I et al. 2022 – Contributions to molecular phylogeny of lichens 3: New monophyletic branches of the *Trapeliaceae* and *Xylariaceae*. Acta Botanica Hungarica 64(1–2), 97–135.

Konrad M, Grasse AV, Tragust S, Cremer S. 2015 – Anti-pathogen protection versus survival costs mediated by an ectosymbiont in an ant host. Proceedings of the Royal Society B: Biological Sciences 282(1799), 20141976.

Konta S, Hongsanan S, Eungwanichayapant PD, Liu JK et al. 2017 – *Leptosporella* (*Leptosporellaceae* fam. nov.) and *Linocarpon* and *Neolinocarpon* (*Linocarpaceae* fam. nov.) are accommodated in *Chaetosphaeriales*. Mycosphere 8, 1943–1974.

Konta S, Hongsanan S, Tibpromma S, Thongbai B et al. 2016 – An advance in the endophyte story: *Oxydothidaceae* fam. nov. with six new species of *Oxydothis*. Mycosphere 7, 1425–1446.

Konta S, Hyde KD, Phookamsak R, Xu JC et al. 2020 − Polyphyletic genera in *Xylariaceae* (*Xylariales*): *Neoxylaria* gen. nov. and *Stilbohypoxylon*. Mycosphere 11(1), 2629−2651.

Konta S, Tibpromma S, Karunarathna SC, Samarakoon MC, Steven LS, Mapook A, Boonmee S, Senwanna C, Balasuriya A, Eungwanichayapant PD, Hyde KD 2023 – Morphology and multigene phylogeny reveal ten novel taxa in *Ascomycota* from terrestrial palm substrates (*Arecacea*e) in Thailand. Mycosphere 14(1), 107–152.

Koodalugodaarachchi V, Chethana KT, Jayawardena RS, Bundhun D et al. 2024 – New records of pestalotioid species associated with leaf spot disease on *Camellia sinensis* from Northern Thailand. Phytotaxa 647, 91–114.

Körber GW. 1855 – Systema Lichenum Germaniae. Trewendt & Granier, Breslau, Germany.

Korf RF, Lizon P. 2000 – Validation of Nannfeldt's ordinal name *Helotiales*. Mycotaxon 75, 501–502.

Korf RP, Abawi GS. 1971 – On *Holwaya*, *Crinula*, *Claussenomyces*, and *Corynella*. Canadian Journal of Botany 49(11), 1879–1883.

Korf RP, Lizon P. 2001 – The status of the ordinal name *Leotiales*. Czech Mycology, 52(4), 255–257.

Korf RP. 1973 – *Discomycetes* and *Tuberales*. In: Ainsworth GC, Sparrow FK, Sussman AS (eds.) The fungi: an advanced treatise. Vol. IVA. Academic Press, New York 249–319.

Korf RP. 1986 – Proposal to reject the generic name *Helotium* Tode: E. M. Fries under Art. 69.1 (Fungi). Taxon 35, 737–738.

Kosanić M, Ranković B, Stanojković T, Rančić A et al. 2014 – *Cladonia* lichens and their major metabolites as possible natural antioxidant, antimicrobial and anticancer agents. LWT - Food Science and Technology 59(1), 518–525.

Koukol O, Hofmann TA, Piepenbring M. 2017 – *Dendroseptoria mucilaginosa*: A new anamorphic fungus with stauroconidia and phylogenetic placement of *Dendroseptoria*. Mycological Progress 16, 1065–1070.

Koukol O, Kolařík M, Kolářová Z, Baldrian P. 2012 – Diversity of foliar endophytes in wind-fallen *Picea abies* trees. Fungal Diversity 54, 69–77.

Kraichak E, Crespo A, Divakar PK, Leavitt SD et al. 2017 – A temporal banding approach for consistent taxonomic ranking above the species level. Scientific Reports 7, 2297.

Kraichak E, Huang JP, Nelsen M, Leavitt SD et al. 2018a – *Sporastatiales* Lumbsch & Leavitt. Index Fungorum 375, 1.

Kraichak E, Huang JP, Nelsen M, Leavitt SD et al. 2018b – A revised classification of orders and families in the two major subclasses of *Lecanoromycetes* (*Ascomycota*) based on a temporal approach. Botanical Journal of the Linnean Society 188(3), 233–249.

Krajicek BJ, Thomas CF, Limper AH. 2009 – *Pneumocystis* pneumonia: current concepts in pathogenesis, diagnosis, and treatment. Clinics in Chest Medicine 30(2), 265–278.

Kralj A, Kehraus S, Krick A, Eguereva E et al. 2006 − Arugosins G and H: Prenylated Polyketides from the Marine-Derived Fungus *Emericella nidulans* var. *acristata*. Journal of natural products 69(7), 995−1000.

Kramer CL 1973 – *Protomycetales* and *Taphrinales*. In G.C. Ainsworth, F.K. Sparrow and A.S. Sussman (Eds.), The Fungi – an Advanced Treatise, Vol. IVA (pp. 33–41) New York: Academic Press.
Kramer CL. 1958 – A new genus in the *Protomycetaceae*. Mycologia 50 (6), 916–926.
Kramer CL. 1987 – The *Taphrinales*. In G.S. de Hoog, M.Th. Smith and A.C.M. Weijman (Eds.), The Expanding Realm of Yeast-like Fungi. Studies in Mycology 30, 151–166.
Kraus C, Damm U, Bien S, Voegele RT et al. 2020 – New species of *Phaeomoniellales* from a German vineyard and their potential threat to grapevine (*Vitis vinifera*) health. Fungal Systematics and Evolution 6(1), 139–155.
Krause RA, Webster RK. 1972 – The morphology, taxonomy, and sexuality of the rice stem rot fungus, *Magnaporthe salvinii* (*Leptosphaeria salvinii*). Mycologia 64(1), 103–114.
Kredics L, Hatvani L, Manczinger L, Vágvölgyi C et al. 2011 – Molecular detection of human fungal pathogens. CRC Press 1–958.
Kreger-van Rij NJW. 1984 – Yeasts (pp. 45-103). Amsterdam: Elsevier.
Krempelhuber A von. 1875 – Lichenes quos legit O. Beccari in insulis Borneo et Singapore annis 1866 et 1867. Nuovo Giornale Botanico Italiano 7, 5–67.
Krings M, Taylor TT, Dotzler N. 2012 – Fungal endophytes as a driving force in land plant evolution: evidence from the fossil record. In: Southworth D (ed) Biocomplexity of plant-fungal interactions. Wiley 5–27.
Krishna KV, Ulhas RS, Malaviya A. 2024 – Bioactive compounds from *Cordyceps* and their therapeutic potential. Critical reviews in biotechnology 44(5), 753–773.
Krohn K, Sohrab MH, van Ree T, Draeger S et al. 2008 – Dinemasones A, B and C–new bioactive metabolites from the endophytic fungus *Dinemasporium strigosum*. Eur. J. Org. Chem. 33, 5638–5646.
Krungkrai J, Webster HK, Yuthavong Y. 1990 – Folate and cobalamin metabolism in *Plasmodium falciparum*. Parasitology Today 6, 388–391.
Kruys A, Eriksson OE, Wedin M. 2006 – Phylogenetic relationships of coprophilous *Pleosporales* (*Dothideomycetes*, *Ascomycota*), and the classification of some bitunicate taxa of unknown position. Mycological Research 110, 527–536.
Kruys Å, Huhndorf SM, Miller AN. 2015 – Coprophilous contributions to the phylogeny of *Lasiosphaeriaceae* and allied taxa within *Sordariales* (*Ascomycota*, Fungi). Fungal Diversity 70, 101–113.
Kruys ÅN. 2005 – Phylogenetic relationships and species richness of coprophilous *Ascomycetes*. Doctoral thesis, Publikationer från Umeå universitet.
Kruys N, Jonsson BG. 1997 – Insular patterns of calicioid lichens in a boreal old-growth forest-wetland mosaic. Ecography 20, 605–613.
Krzewicka B, García MA, Johansen SD, Sancho L et al. 2009 – Morphological and nuclear ribosomal DNA data support distinguishing two new species of *Umbilicaria* (*Umbilicariaceae*, *Ascomycota*) from Europe. The Lichenologist 41(6), 631–648.
Krzysiak AJ. 2006 – The isolation and characterization of natural products from marine plants and microorganisms (Doctoral dissertation, University of North Carolina at Wilmington).
Kubiak D, Kukwa M, Motiejunaite J. 2003 – Notes on *Pycnora sorophora* (*Lecanoraceae*, lichenised *Ascomycota*) in Poland and Lithuania. Botanica Lithuanica 9(4), 371–378.
Kuehn HH. 1958 – A preliminary survey of the *Gymnoascaceae*. I. Mycologia 50(3), 417–439.
Kuehn KA, Gessner MO, Wetzel RG, Suberkropp K. 1999 – Decomposition and CO_2 evolution from standing litter of the emergent macrophyte *Erianthus giganteus*. Microbial Ecology 38, 50–57.
Kühlwein H, Jurzitza G. 1961 – Studien an der Symbiose der Anobiiden. 1. Mitteilung: Die Kultur des Symbionten von Sitodrepa panicea L. Arch Mikrobiol 40, 247–260.
Kuhnert E, Surup F, Herrmann J, Huch V et al. 2015 − Rickenyls A–E, antioxidative terphenyls from the fungus *Hypoxylon rickii* (*Xylariaceae*, *Ascomycota*). Phytochemistry 118, 68−73.

Kukwa M, Kubiak D. 2007 – Six sorediate crustose lichens new to Poland. Mycotaxon 102, 155–164.
Kukwa M. 2011 – The lichen genus *Ochrolechia* in Europe. Fundacja Rozwoju Uniwersytetu Gdańskiego, Gdańsk, 309.
Kularathnage ND, Tennakoon DS, Zhu X, Zhou J et al. 2023 – Reinstating *Dyfrolomyces* and introducing *Melomastia pyriformis* sp. nov. (*Pleurotremataceae*, *Dyfrolomycetales*) from Guangdong Province, China. Current Research in Environmental & Applied Mycology 13(1), 426–438.
Kumar CG, Mongolla P, Joseph J, Nageswar Y et al. 2010 – Antimicrobial activity from the extracts of fungal isolates of soil and dung samples from Kaziranga National Park, Assam, India. Journal de Mycologie Médicale 20(4), 283–289.
Kumar TA, Healy R, Spatafora JW, Blackwell M et al. 2012 – *Orbilia* ultrastructure, character evolution and phylogeny of *Pezizomycotina*. Mycologia 104(2), 462–476.
Kumarihamy M, Ferreira D, Croom EM Jr, Sahu R et al. 2019 − Antiplasmodial and cytotoxic cytochalasins from an endophytic fungus, *Nemania* sp. UM10M, isolated from a diseased *Torreya taxifolia* leaf. Molecules 24, 777.
Kunze G, Schmidt JC. 1823 – Mykologische Hefte (Leipzig) 2, 92.
Kuo CH, Goh TK. 2021 – Two new species and one new record of *Xenosporium* with ellipsoidal or ovoid conidia from Taiwan. Mycologia 113, 434–449.
Kuo CY, Tay RJ, Lin HC, Juan SC et al. 2024 – The nematode-trapping fungus *Arthrobotrys oligospora* detects prey pheromones via G protein-coupled receptors. Nature Microbiology 9, 1738–1751.
Kureljušić B, Milićević V, Ćirović D, Kuručki M. 2022 – First Molecular Detection of *Pneumocystis* spp. in the Golden Jackal (*Canis aureus*). The Journal of Wildlife Diseases 58(4), 897–901.
Kureljušić B, Weissenbacher-Lang C, Nedorost N, Stixenberger D et al. 2016 – Association between *Pneumocystis* spp. and co-infections with *Bordetella bronchiseptica*, *Mycoplasma hyopneumoniae* and *Pasteurella multocida* in Austrian pigs with pneumonia. The Veterinary Journal 207, 177–179.
Kurniawati E, Zhang H, Chukeatirote E, Sulistyowati L et al. 2010 – Diversity of freshwater ascomycetes in freshwater bodies at Amphoe Mae Chan, Chiang Rai. Cryptogamie, Mycologie 31(3), 323–331.
Kurtzman CP, Robnett CJ. 1991 – Phylogenetic relationships among species of *Saccharomyces*, *Schizosaccharomyces*, *Debaryomyces* and *Schwanniomyces* determined from partial ribosomal RNA sequences. Yeast 7(1), 61–72.
Kurtzman CP, Robnett CJ. 1994 – Orders and families of ascosporogenous yeasts and yeast-like taxa compared from ribosomal RNA sequence similarities. Ascomycete systematics: problems and perspectives in the nineties 249–258.
Kurtzman CP, Sugiyama J. 2001 – Ascomycetous yeasts and yeastlike taxa. In D.J. McLaughlin, E.G. McLaughlin and P.A. Lemke (Eds.), The Mycota. Vol. VII Part A Systematics and Evolution (pp. 179–200) Berlin: Springer-Verlag.
Kurtzman CP, Sugiyama J. 2015 – *Saccharomycotina* and *Taphrinomycotina*: The yeasts and yeastlike fungi of the *Ascomycota*. In D. McLaughlin, J. Spatafora (Eds.), The Mycota (A Comprehensive Treatise on Fungi as Experimental Systems for Basic And Applied Research) (Second edition) Vol. 7B Systematics and Evolution (pp. 3-33) Berlin/Heidelberg: Springer.
Kurtzman CP. 1993 – Systematics of the ascomycetous yeasts assessed from ribosomal RNA sequence divergence. Antonie van Leeuwenhoek International Journal of General and Molecular Microbiology 63 (2), 165–174.
Kurtzman CP. 1994 – *Endomycetales*, *Protomycetales*, and *Taphrinales*. Ascomycete Systematics: Problems and Perspectives in the Nineties, 361–363.
Kurtzman CP. 1998 – Discussion of teleomorphic and anamorphic ascomycetous yeasts and a key to genera. In The Yeasts (pp. 111–121). Elsevier.

Kurtzman CP. 2011 – *Protomyces* Unger (1833). In C.P. Kurtzman, J.W. Fell and T. Boekhout (Eds.) The Yeasts, a Taxonomic Study (Fifth Edition), Vol. 2 (pp. 725-731) Amsterdam: Elsevier.
Kutleša M, Mlinarić-Missoni E, Hatvani L, Voncina D et al. 2012 – Chronic fungal meningitis caused by *Aureobasidium proteae*. Diagnostic Microbiology and Infectious Disease 73(3), 271–272.
Kutorga E, Hawksworth D. 1997 – A reassessment of the genera referred to the family *Patellaraceae* (*Ascomycota*). Systema Ascomycetum 15, 1–110.
Kwak YS, Weller DM. 2013 – Take-all of wheat and natural disease suppression: a review. The Plant Pathology Journal 29(2), 125–135.
Kwok S, White TJ, Taylor JW. 1986 – Evolutionary relationships between fungi, red algae, and other simple eukaryotes inferred from total DNA hybridizations to a cloned basidiomycete ribosomal DNA. Experimental Mycology 10(3), 196–204.
Kylle R, Jaenecke KA, Robert WP. 2020 – Ambrosia beetle (*Coleoptera*: *Curculionidae*) communities and frass production in ‘Ōhi‘a (*Myrtales*: *Myrtaceae*) infected with *Ceratocystis* (*Microascales*: *Ceratocystidaceae*) fungi responsible for rapid ‘Ōhi‘a death. Environmental Entomology 49(6), 1345–1354.
Laakkonen J, Fisher RN, Case TJ. 2001 – *Pneumocystosis* in wild small mammals from California. Journal of Wildlife Diseases 37, 408–412.
Laakkonen J, Sukura A, Haukisalmi V, Henttonen H. 1993 – *Pneumocystis carinii* and helminth parasitism in shrews *Sorex araneus* and *Sorex caecutiens*. Journal of Wildlife Diseases 29, 273–277.
Laakkonen J, Sukura A. 1997 – *Pneumocystis carinii* of the common shrew, *Sorex araneus*, shows a discrete phenotype. Journal of Eukaryotic Microbiology 44, 117–121.
Laakkonen J. 1998 – *Pneumocystis carinii* in wildlife. International Journal of Parasitology 28, 241–252.
Labandiera CC, Sepkoski JJJR. 1993 – Insect diversity in the fossil record. Science 261, 310–315.
Labuda R, Bernreiter A, Hochenauer D, Kubátová A et al. 2021 – Molecular systematics of *Keratinophyton*: the inclusion of species formerly referred to *Chrysosporium* and description of four new species. IMA Fungus 12(1), 17.
Lacerda LT, Gusmão LFP, Rodrigues A. 2018 – Diversity of endophytic fungi in *Eucalyptus* microcorys assessed by complementary isolation methods. Mycological Progress 17, 719–727.
Lackner M, Hoog GS de, Yang L, Moreno LF et al. 2014 – Proposed nomenclature for *Pseudallescheria*, *Scedosporium* and related genera. Fungal Diversity 67, 1–10.
Lad S, Rajeshkumar KC, Sruthi OP, Ashtekar N et al. 2022 – Resolving the phylogenetic placement of *Gangliostilbe* in the family *Xenospadicoidaceae* (*Xenospadicoidales*). MycoAsia 2022/01.
LaGreca S, Lumbsch HT. 2001 – The phylogenetic position of the *Candelariaceae* (*Lecanorales*) inferred from anatomical and molecular data. Bibliotheca Lichenologica 78, 211–222.
LaGreca S. 2006 – Notes on the chemistry of *Maronea constans* and *Maronea polyphaea* (*Fuscideaceae*). The Lichenologist 38(6), 595–598.
Lai D, Li J, Zhao S, Gu G et al. 2021 – Chromone and isocoumarin derivatives from the endophytic fungus *Xylomelasma* sp. Samif07, and their antibacterial and antioxidant activities. Natural Product Research 35(22), 4616–4620.
Lam JK, Sargent MV, Elix JA, Smith DO. 1972 – Synthesis of valsarin and 5, 7-dichloroemodin. Journal of the Chemical Society, Perkin Transactions 1, 1466–1470.
Lamb IM. 1954 – Studies in frutescent *Lecideaceae* (lichenized *Discomycetes*). Rhodora 56, 105–153.
Lambert C, Pourmoghaddam MJ, Cedeño-Sanchez M, Surup F et al. 2021 − Resolution of the *Hypoxylon fuscum* complex (*Hypoxylaceae*, *Xylariales*) and discovery and biological characterization of two of its prominent secondary metabolites. Journal of Fungi 7(2), 131.
Landvik S, Eriksson OE, Gargas A, Gustafsson P. 1993 – Relationships of the genus *Neolecta* (*Neolectales* ordo nov., *Ascomycotina*) inferred from 18S rDNA sequences. Systema Ascomycetum 11, 107–118.

Landvik S, Eriksson OE. 1994 – Relationship of *Tuber*, *Elaphomyces*, and *Cyttaria* (*Ascomycotina*), inferred from 18S rDNA studies. In: Hawksworth DL (ed) Ascomycetes systematics: problems and perspectives in the nineties. Plenum Press, New York

Landvik S, Schumacher TK, Eriksson OE, Moss ST. 2003 – Morphology and ultrastructure of *Neolecta* species. Mycological Research 107(9), 1021–1031.

Lange OL, Büdel B, Meyer A, Kilian E. 1993 – Further evidence that activation of net photosynthesis by dry cyanobacterial lichens requires liquid water. The Lichenologist 25, 175–189.

Langeron M, Vanbreuseghem R. 1965 – Outline of mycology. Pitman & Sons, London, UK.

Lantz H, Johnston PR, Park D, Minter DW. 2011 – Molecular phylogeny reveals a core clade of *Rhytismatales*. Mycologia 103, 57–74.

Larson DW, Carey CK. 1986 – Phenotypic variation with "individual" lichen thalli. American Journal of Botany 73, 214–223.

Latinne A, Chen HW, Kuo CC, Lorica R et al. 2021. Revisiting the *Pneumocystis* host specificity paradigm and transmission ecology in wild Southeast Asian rodents. Infection, Genetics and Evolution 93, 104978.

Lawrence DP, Peduto Hand F, Gubler WD et al. 2017 – *Botryosphaeriaceae* species associated with dieback and canker disease of bay laurel in northern California with the description of *Dothiorella californica* sp. nov. Fungal Biology 121, 347–360.

Lawrey JD, Diederich P, Nelsen MP, Sikaroodi M et al. 2011 – The obligately lichenicolous genus *Lichenoconium* represents a novel lineage in the *Dothideomycetes*. Fungal Biology 115, 176–187.

Lazzizera C, Frisullo S, Alves A, Lopes J et al. 2008 – Phylogeny and morphology of *Diplodia* species on olives in Southern Italy and description of *Diplodia olivarum* sp. nov. Fungal Diversity 31, 63–71.

Le Gal M. 1946 – Les Discomyce` tes subopercule´ s. Bull Soc Mycol France 62, 218–240.

Le Pogam P, Le Lamer AC, Siva B, Legouin B et al. 2016 – Minor pyranonaphthoquinones from the apothecia of the lichen *Ophioparma ventosa*. Journal of Natural Products 79(4), 1005–1011.

Lee HB, Park JY, Jung HS, Summerbell RC. 2006 – *Phaeomoniella zymoides* and *Phaeomoniella pinifoliorum* spp. nov., new acid-tolerant epiphytic fungi isolated from pine needles in Korea. Mycologia 98, 598–611.

Lee S, Hanlin RT. 1999. Phylogenetic relationships of *Chaetomium* and similar genera based on ribosomal DNA sequences. Mycologia 91, 434–442.

Lee SM, Kim DS, Lee KS, Lee CK et al. 2013 – Antibiotic Properties of *Helicosporium* sp. KCTC 0635BP to *Rhizoctonia solani* AG2-2 IV. Weed & Turfgrass Science 2, 202–206.

Lee SQE, Tan TS, Kawamukai M, Chen ES. 2017 – Cellular factories for coenzyme Q 10 production. Microbial Cell Factories 16, 1–16.

Lee T, Yun SH, Hodge K, Humber R et al. 2001 – Polyketide synthase genes in insect-and nematode-associated fungi. Applied Microbiology and Biotechnology 56, 181–187.

Lei HM, Wang JT, Hu QY, Li CQ et al. 2023 – 2-Furoic acid associated with the infection of nematodes by *Dactylellina haptotyla* and its biocontrol potential on plant root-knot nematodes. Microbiology Spectrum 11(5), e0189623.

Lei LR, Gong LQ, Jin MY, Wang R et al. 2022 – Research advances in the structures and biological activities of secondary metabolites from *Talaromyces*. Frontiers in Microbiology 13, 984801.

Leightley LE. 1980 – Wood decay activities of marine fungi. Botanica Marina 23, 387–395.

Lendemer JC, Hodkinson BP. 2013 – A radical shift in the taxonomy of *Lepraria* sl: molecular and morphological studies shed new light on the evolution of asexuality and lichen growth form diversification. Mycologia 105(4), 994–1018.

Lendemer JC, Westberg M. 2010 – *Candelariella xanthostigmoides* in North America. Opuscula Philolichenum 8, 75–81.

Leong WF, Tan TK, Jones EBG. 1991 – Fungal colonization of submerged *Bruguiera cylindrica* and *Rhizophora apiculata* wood. Botanica Marina 34, 69–76

Lestari AS, Ekanayaka AH, Chethana KW. 2023 – Phytopathogenic *Discomycetes*, their economic impacts and control applications. Journal of Fungal Biology 13(1), 299–346.
Leupold U. 1970 – Genetical methods for *Schizosaccharomyces pombe*. In Methods in cell biology (Vol. 4, pp. 169–177). Academic Press.
Leupold U. 1987 – Sex appeal in fission yeast. Current genetics 12, 543–545.
Lewkowicz AG, Hartshorn J. 1998 – Terrestrial record of rapid mass movements in the Sawtooth Range, Ellesmere Island, Northwest Territories, Canada. Canadian Journal of Earth Science 35, 55–64.
Li CS, Li XM, Gao SS, Lu YH et al. 2013 – Cytotoxic anthranilic acid derivatives from deep sea sediment-derived fungus *Penicillium paneum* SD-44. Marine Drugs 11, 3068–3076.
Li DM, De Hoog GS, Saunte DL, van den Ende AG et al. 2008 – *Coniosporium epidermidis* sp. nov., a new species from human skin. Studies in Mycology 61, 131–136.
Li GJ, Hyde KD, Zhao RL, Hongsanan S et al. 2016a – Fungal diversity notes 253–366: taxonomic and phylogenetic contributions to fungal taxa. Fungal Diversity 78, 1–237.
Li H, Sun G, Batzer JC, Crous PW et al. 2011 – *Scleroramulariagen*. nov. associated with sooty blotch and flyspeck of apple and pawpaw from the Northern Hemisphere. Fungal Diversity 46, 53–66.
Li HY, Sun GY, Zhai XR, Batzer JC et al. 2012 – *Dissoconiaceae* associated with sooty blotch and flyspeck on fruits in China and the United States. Persoonia 28, 113–125.
Li J, Wang WX, Chen HP, Li ZH et al. 2019a − (±)-Xylaridines A and B, highly conjugated alkaloids from the fungus *Xylaria longipes*. Organic Letters 21, 1511–4.
Li J, Wang WX, Li ZH, He J et al. 2019b − Xylaridines C and D, unusual thiopyranodipyridine alkaloids from the fungus *Xylaria longipes*. Organic Letters 21, 6145–8.
Li J, Yang JY, Xu KC, Sun YX et al. 2016b – First report of *Ceratocystis fimbriata* causing leaf blight on *Alocasia macrorrhiza* in China. Plant Disease 100, 2172.
Li J, Zou C, Xu J, Ji X et al. 2015 – Molecular mechanisms of nematode-nematophagous microbe interactions: basis for biological control of plant-parasitic nematodes. Annual Review of Phytopathology 53(1), 67–95.
Li JC, Wu HX, Li Y, Li XH et al. 2022a – Taxonomy, Phylogenetic and Ancestral Area Reconstruction in *Phyllachora*, with Four Novel Species from Northwestern China. Journal of Fungi 8, 520.
Li L, Du HZ, Thiyagaraja V, Bhat DJ et al. 2024 – Two novel freshwater hyphomycetes, in *Acrogenospora* (*Minutisphaerales*, *Dothideomycetes*) and *Conioscypha* (*Conioscyphales*, *Sordariomycetes*) from Southwestern China. MycoKeys 101, 249–273.
Li LL, Shen HW, Bao DF, Wanasinghe DN et al. 2022b – The plethora of *Tubeufiaceae* in lakes of the northwestern Yunnan plateau, China. Frontiers in Microbiology 13, 1056669.
Li M, Raza M, Song S, Hou LW et al. 2023a – Application of culturomics in fungal isolation from mangrove sediments. Microbiome 11, 272.
Li M, Yuan C, Zhang X, Pang W et al. 2023b – The transcriptional responses of ectomycorrhizal fungus, *Cenococcum geophilum*, to drought stress. Journal of Fungi 9(1), 15.
Li WJ, Maharachchikumbura SS, Li QR, Bhat DJ, Camporesi E et al. 2015 – Epitypification of *Broomella vitalbae* and introduction of a novel species of *Hyalotiella*. Cryptogamie, Mycologie 36, 93–108.
Li WJ, McKenzie EH, Liu JKJ, Bhat DJ et al. 2020 – Taxonomy and phylogeny of hyaline-spored coelomycetes. Fungal Diversity 100(1), 279–801.
Li WL, Liang RR, Dissanayake AJ, Liu JK. 2023c – Mycosphere Notes 413–448: *Dothideomycetes* associated with woody oil plants in China. Mycosphere 14, 1436–1529.
Li WL, Maharachchikumbura SSN, Cheewangkoon R, Liu JK. 2022c – Reassessment of *Dyfrolomyces* and four new species of *Melomastia* from Olive (*Olea europaea*) in Sichuan Province, China. Journal of Fungi 8, 76.

Li Y, Huang YT, Kasson MT, Macias AM et al. 2018 – Specific and promiscuous ophiostomatalean fungi associated with *Platypodinae ambrosia* beetles in the southeastern United States. Fungal Ecology 35, 42–50.
Li Y, Hyde KD, Jeewon R, Cai L et al. 2005 – Phylogenetics and evolution of nematode-trapping fungi (*Orbiliales*) estimated from nuclear and protein coding genes. Mycologia 97(5), 1034–1046.
Li Y, Steenwyk JL, Chang Y, Wang Y et al. 2021a – A genome-scale phylogeny of Fungi; insights into early evolution, radiations, and the relationship between taxonomy and phylogeny. Current Biology 31, 1653–1665.
Li YJ, Wei MJ, Zhang H. 2021b – Antimicrobial acticities of solid fermentation extracts from 29 freshwater fungi. Journal of Kunming University of Science and Technology (Natural Science). 46, 137–146.
Li YY. 2019 – Removal of heavy metal Cr(Ⅵ) by *Trichoderma hamatum* BSL01. Harbin: Master's Thesis of Northeast Forestry University.
Liang Y, Xu W, Liu C, Zhou D et al. 2019 − Eremophilane sesquiterpenes from the endophytic fungus *Xylaria* sp. GDG-102. Natural product research 33(9), 1304−1309.
Libert MA. 1834 – Plantae Cryptogamae, quas in Arduenna collegit. Fasc 3, 272
Liew EC, Aptroot A, Hyde KD. 2000 − Phylogenetic significance of the pseudoparaphyses in *Loculoascomycete* taxonomy. Molecular Phylogenetics and Evolution 16(3), 392−402.
Lin CG, McKenzie EHC, Bhat DJ, Liu JK et al. 2018 – *Pseudodactylaria brevis* sp. nov. from Thailand confirms the status of *Pseudodactylariaceae*. Phytotaxa 369(4), 241–250.
Lin CG, McKenzie EHC, Liu JK, Jones EBG et al. 2019a – Hyaline-spored chaetosphaeriaceous hyphomycetes from Thailand and China, with a review of the family *Chaetosphaeriaceae*. Mycosphere 10, 655–700.
Lin SF, Li CK, Chung YP. 2019b – Identification of a novel lactose oxidase in *Myrmecridium flexuosum* NUK-21. FEBS Open Bio 9, 364–373.
Lin YR, Li Z, Liang SW, Yu SM. 1995 – Thirteen species of *Rhytismatales* on conifers from the northern part of the country. Mycosystema 14, 179–183.
Lin YR, Xu ZS, Yie GB, Wang SJ. 2004 – Additional species of *Lophodermium* Chev. from China I. Mycosystema 23 (1), 14−17.
Lin YR. 1987 – Study on the needle cast fungus of pine, *Lophodermium pinastri*. Journal of Anhui Agricultural University 4, 21–28+79.
Lin YR. 2012 – Flora Fungrorum Sinicorum VOL.40 *Rhytismatales*. Science Press, Beijing 1–261.
Linaldeddu BT, Deidda A, Scanu B, Franceschini A et al. 2015 – Diversity of *Botryosphaeriaceae* species associated with grapevine and other woody hosts in Italy, Algeria and Tunisia, with descriptions of *Lasiodiplodia exigua* and *Lasiodiplodia mediterranea* sp. nov. Fungal Diversity 71, 201–214.
Lindau G. 1896 − Hysterineae, in Engler & Prantl. Die Naturiichen Pftanzenfamilien 276−277.
Lindau G. 1897a – Pyrenomycetineae, Laboulbeniineae. In: Engler A, Prantl K (eds) Die Natu¨rlichen Pflanzenfamilien, vol 1(1). Verlag von Wilhelm Engelmann, Leipzig, 321–505.
Lindau G. 1897b – *Sphaeriales*. In: Engler A, Prantl K (eds), Die natürlichen Pflanzenfamilien 1(1), 384–491.
Lindau G. 1987 – *Hypocreales*. Engler HA, Prantl KA (eds.). Die Natürlichen Pflanzenfamilien. part I, section 1. Leipzig: Verlag W. Engelman, pp. 343–372.
Lindau. 1897c– Engler Prantl Nat Pflanzenfam Teil I (Leipzig) 1(1), 373.
Lindemuth R, Wirtz N, Lumbsch HT. 2001 – Phylogenetic analysis of nuclear and mitochondrial rDNA sequences supports the view that *Loculoascomycetes* (*Ascomycota*) are not monophyletic. Mycological Research 105, 1176–1181.
Linder DH. 1929 – A monograph of the helicosporous fungi imperfecti. Annals of the Missouri botanical Garden 16, 227–388.
Lindner P. 1893 – *Schizosaccharomyces pombe* n. sp., ein neuer Gährungserreger. Wochenschrift für Brauerei 10, 1298–300.

Lindquist JC, Alippi HE. 1964 – Un nuevo género de hongo parásito de Tropaeolum majus: *Acroconidiella tropaeoli* (Bond) nov. comb., sinónimo *Heterosporium tropaeoli* Bond. Darwiniana 607–614.
Lindsay WL. 1857 – Monograph of the genus *Abrothallus* (De Notaris and Tulasne emend.). Journal of Cell Science 5, 27–63.
Lingham RB, Silverman KC, Bills GF, Cascales C et al. 1993 – *Chaetomella acutiseta* produces chaetomellic acids A and B which are reversible inhibitors of farnesyl-protien transferase. Applied Microbiology and Biotechnology 40, 370–374.
Lini KM, Jacob T, Neeta NN. 2021 – *Marthomamyces* gen. nov. (*Asterinales*, *Lembosiaceae*) from Southern Western Ghats, India. Asian Journal of Mycology 4, 35–41.
Link HF. 1809 – Observationes in ordines plantarum naturales. Mag Ges Naturf Freunde Berlin 3, 3–42.
Link HF. 1833 – Handbuch zur Erkennung der nutzbarsten und am häufigsten vorkommenden Gewächse. Theil 3. – Berlin: in der Haude und Spenerschen Buchhandlung (S. J. Joseepy), 536.
Linnaeus C. 1753 – Species Plantarum Vol. 2. Stockholm: L. Salvius.
Linnaeus C. 1763 – Species Plantarum, ed. 2. Vol. 2. Stockholm: L. Salvius.
Liška J, Palice Z, Slavíková Š. 2008 – Checklist and Red List of lichens of the Czech Republic. Preslia 80, 151–182.
Litz CE, Cavagnolo RZ. 2010 – Polymerase chain reaction in the diagnosis of onychomycosis: a large, single-institute study. British Journal of Dermatology 163, 511–514.
Liu B, Liu XZ, Zhuang WY, Baral HO. 2006 – Orbiliaceous fungi from Tibet, China. Fungal Diversity 22, 107–120.
Liu B, Liu XZ, Zhuang WY. 2005 – *Orbilia querci* sp. nov. and its knob-forming nematophagous anamorph. FEMS Microbiology Letters 245, 99–105.
Liu B. 2006 – Taxonomy and Molecular Phylogenetics of the Family *Orbiliaceae* in China. PhD Dissertation, Institute of Microbiology, Chinese Academy of Sciences, Beijing, China.
Liu D, Hur JS. 2018 – *Candelaria asiatica*, an ignored new species from South Korea. Mycobiology 46(4), 305–310.
Liu D, Wang L, Wang XY, Hur JS. 2019a – Two new species of the genus *Candelariella* from China and Korea. Mycobiology 47(1), 40–49.
Liu F, Hu DM, Cai L. 2012a – *Conlarium duplumascospora* gen. et. sp. nov. and *Jobellisia guangdongensis* sp. nov. from freshwater habitats in China. Mycologia 104, 1178–1186.
Liu HJ, Wang JG, Xia Y, Yang MJ et al. 2017a – Elemental compositions of lichens from Duolun County, Inner Mongolia, China: Origin, road effect and species difference. Scientific Reports 7(1), 5598.
Liu J, Hu Y, Luo X, Castañeda-Ruíz RF et al. 2023a – Molecular Phylogeny and Morphology Reveal Four Novel Species of *Corynespora* and *Kirschsteiniothelia* (*Dothideomycetes*, *Ascomycota*) from China: A Checklist for *Corynespora* Reported Worldwide. Journal of Fungi 9(1), 107.
Liu JK, Hyde KD, Jeewon R, Phillips AJL et al. 2017b – Ranking higher taxa using divergence times: A case study in *Dothideomycetes*. Fungal Diversity 84(1), 75–99.
Liu JK, Hyde KD, Jones EBG, Ariyawansa HA et al. 2015a – Fungal diversity notes 1–110: Taxonomic and phylogenetic contributions to fungal species. Fungal Diversity 72, 1–197.
Liu JK, Lu Y, Cheewangkoon R, To-Anun C. 2018b – Phylogeny and morphology of *Helicotubeufia* gen. nov., with three new species in *Tubeufiaceae* from aquatic habitats. Mycosphere 9(3), 495–509.
Liu JK, Luo ZL, Liu NG, Cheewangkoon R et al. 2018a – Two novel species of *Paradictyoarthrinium* from decaying wood. Phytotaxa 338, 285–293.
Liu JK, Phookamsak R, Dai DQ, Tanaka K et al. 2014a – *Roussoellaceae*, a new pleosporalean family to accommodate the genera *Neoroussoella* gen. nov., *Roussoella* and *Roussoellopsis*. Phytotaxa 181, 1–33.

Liu JK, Phookamsak R, Doilom M, Wikee S et al. 2012b –Towards a natural classification of *Botryosphaeriales*. Fungal Diversity 57, 149–210.
Liu JK, Yang J, Maharachchikumbura SSN, McKenzie EH et al. 2016a – Novel chaetosphaeriaceous hyphomycetes from aquatic habitats. Mycological Progress 15, 1157–1167.
Liu N, Ariyawansa H, Hyde K, Maharachchikumbura S et al. 2016b – Perspectives into the value of genera, families and orders in classification. Mycosphere 7(11), 1649–1668.
Liu N, Xu S, Yao X, Zhang G et al. 2016c – Studies on the Control of Ascochyta Blight in Field Peas (*Pisum sativum* L.) Caused by Ascochyta pinodes in Zhejiang Province, China. Frontiers in Microbiology 7, 481.
Liu NG, Hyde KD, Sun YR, Bhat DJ et al. 2024 – Notes, outline, taxonomy and phylogeny of brown-spored hyphomycetes. Fungal Diversity 129, 1–281.
Liu NG, Lu YZ, Bhat DJ, McKenzie EH et al. 2019b – *Kevinhydea brevistipitata* gen. et sp. nov. and *Helicoma hydei* sp. nov., (*Tubeufiaceae*) from decaying wood habitats. Mycological Progress 18, 671–682.
Liu R, Li D, Zhang Z, Liu S et al. 2023b – Morphological and phylogenetic analyses reveal two new species and a new record of Apiospora (*Amphisphaeriales*, *Apiosporaceae*) in China. MycoKeys 95, 27.
Liu S, Su H, Su X, Zhang F et al. 2014b – *Arthrobotrys xiangyunensis*, a novel nematode-trapping taxon from a hot-spring in Yunnan Province, China. Phytotaxa 174(2), 89–96.
Liu Y, Hall BD. 2004 – Body plan evolution of *Ascomycetes*, as inferred from an RNA polymerase II phylogeny. Proc. Natl. Acad. Sci. U.S.A. 101, 4507– 4512.
Liu Y, Kurtán T, Mándi A, Weber H et al. 2018b − A novel 10-membered macrocyclic lactone from the mangrove-derived endophytic fungus *Annulohypoxylon* sp. Tetrahedron Letters 59, 632–6.
Liu Y, Leigh JW, Brinkmann H, Cushion MT et al. 2009 – Phylogenomic analyses support the monophyly of *Taphrinomycotina*, including *Schizosaccharomyces* fission yeasts. Molecular Biology and Evolution 26, 27–34.
Liu Y, Rocourt M, Pan S, Liu C et al. 1992 – Sequence and variability of the 5.8S and 26S rRNA genes of *Pneumocystis carinii*. Nucleic Acids Research 20(14), 3763–3772.
Liu Y, Wang J, Wang W, Zhang H et al. 2015b – The chemical constituents and pharmacological actions of *Cordyceps sinensis*. Evidence‐Based Complementary and Alternative Medicine 2015(1), 575063.
Liu Y. 2019 – Study on secondary metabolites and biological activities of fungus *Aspergillus ochraceus*. Qingdao:Master's Thesis of Qingdao University of Technology.
Liu ZG, Bao L, Liu HW, Ren JW et al. 2017c – Chemical diversity from the Tibetan Plateau fungi *Penicillium kongii* and *P. brasilianum*. Mycology 9(1), 10–19.
Llano GA. 1950 – A monograph of the lichen family *Umbilicariaceae* in the Western Hemisphare. Washington D. C.
Llewellyn T, Nowell RW, Aptroot A, Temina M et al. 2023 – Metagenomics shines light on the evolution of "sunscreen" pigment metabolism in the *Teloschistales* (lichen-forming *Ascomycota*). Genome Biology and Evolution 15(2), evad002.
Lloyd CG. 1920 – Mycological notes 62. Mycological Writings 6, 904–944.
Lloyd CG. 1925 – Mycological notes 75. Mycological Writings 7, 1349–1364.
Löbs AK, Schwartz C, Wheeldon I. 2017 – Genome and metabolic engineering in non-conventional yeasts: current advances and applications. Synthetic and systems biotechnology 2(3), 198–207.
Lobuglio KF, Pfister DH. 2010 – Placement of *Medeolaria farlowii* in the *Leotiomycetes*, and comments on sampling within the class. Mycological Progress 9, 361–368.
Lobuglio KF, Pfister DH. 2013 – Systemic infection of *Medeola virginiana* (*Liliaceae*) by the fungus *Medeolaria farlowii* (*Ascomycota*: *Leotiomycetes*). Mycosystema 32(3), 342–346.
Locquin M. 1984a – Mycologie générale et structurale 1–551.
Locquin MV. 1984b – Mycologie ge´ne´rale et structurale: 202. Masson,Paris.

Lohman ML. 1932 – Three new species of *Mytilidion* in the proposed subgenus *Lophiopsis.* Mycologia 24, 477–484.
Lohman ML. 1933 – *Hysteriaceae*: Life histories of certain species. Papers of the Michigan Academy of Science Arts & Letters 17, 229–288.
Lõhmus P, Marmor L, Jüriado I, Suija A et al. 2019 – Red List of Estonian lichens: revision in 2019. Folia Cryptogamica Estonica 56, 63–76.
Lohtander K, Källersjö M, Moberg R, Tehler A. 2000 – The family *Physciaceae* in Fennoscandia: phylogeny inferred from ITS sequences. Mycologia 92(4), 728–735.
Lombard L, van der Merwe NA, Groenewald J Z, Crous PW. 2015 – Generic concepts in *Nectriaceae*. Studies in Mycology 80, 189–245.
Lorch JM, Meteyer CU, Behr MJ, Boyles JG et al. 2011 – Experimental infection of bats with *Geomyces destructans* causes white-nose syndrome. Nature 480(7377), 376–378.
Low M, Berggren A, Morgan KJ, Alley MR. 2005 – *Aspergillosis* in a North Island robin (*Petroica longipes*). The New Zealand Veterinary Journal 53, 462–464.
Lu LL, Weil AA, Wiederhold N, Sutton DA et al. 2015 – Probable case of *Cephalotheca foveolata* bloodstream infection. JMM Case Reports 2(4), e000045.
Lu Y, Kang J. 2020 – Research progress on helicosporous hyphomycetes. Journal of Fungal Research 18, 304–314.
Lu YZ, Boonmee S, Bhat DJ, Hyde KD et al. 2017a – – *Helicosporium luteosporum* sp. nov. and *Acanthohelicospora aurea* (*Tubeufiaceae*, *Tubeufiales*) from terrestrial habitats. Phytotaxa 319, 241–253.
Lu YZ, Boonmee S, Dai DQ, Liu JK et al. 2017b – Four new species of *Tubeufia* (*Tubeufiaceae*, *Tubeufiales*) from Thailand. Mycological Progress 16, 403–417.
Lu YZ, Boonmee S, Liu JK, Hyde KD et al. 2017c – Novel *Neoacanthostigma* species from aquatic habitats. Cryptogamie, Mycologie 38, 169–190.
Lu YZ, Boonmee S, Liu JK, Hyde KD et al. 2018a – Multi-gene phylogenetic analyses reveals *Neohelicosporium* gen. nov. and five new species of helicosporous hyphomycetes from aquatic habitats. Mycological Progress 17, 631–646.
Lu YZ, Liu JK, Hyde KD, Jeewon R et al. 2018b – A taxonomic reassessment of *Tubeufiales* based on multi-locus phylogeny and morphology. Fungal Diversity 92, 131–344.
Lu YZ, Ma J, Xiao XJ, Zhang LJ et al. 2022 – Four new species and three new records of helicosporous hyphomycetes from China and their multi-gene phylogenies. Frontiers in Microbiology 13, 1053849.
Lu ZY, Lin ZJ, Wang WL, Du L et al. 2008 – Citrinin dimers from the halotolerant fungus *Penicillium citrinum* B-57. Journal of Natural Products 71, 543–546
Lücking R, Grube M. 2002 – Facultative parasitism and reproductive strategies in *Chroodiscus* (*Ascomycota*, *Ostropales*). Stapfia 80, 267–292.
Lücking R, Hodkinson BP, Leavitt SD. 2017 – The 2016 classification of lichenized fungi in the *Ascomycota* and *Basidiomycota*–Approaching one thousand genera. The Bryologist 119(4), 361–416.
Lücking R, Huhndorf S, Pfister DH, Plata ER et al. 2009 – Fungi evolved right on track. Mycologia 101, 810–822.
Lücking R, Johnston MK, Aptroot A, Kraichak E et al. 2014 – One hundred and seventy-five new species of *Graphidaceae*: closing the gap or a drop in the bucket?. Phytotaxa 189(1), 7–38.
Lücking R, Lumbsch HT, Di Stefano JF, Lizano D et al. 2008 – *Eremithallus costaricensis* (*Ascomycota*: *Lichinomycetes*: *Eremithallales*), a new fungal lineage with a novel lichen symbiotic lifestyle discovered in an urban relict forest in Costa Rica. Symbiosis 46, 161–170.
Lücking R, Moncada B, Sipman HJ, Sobreira PNB et al. 2020 – *Saxiloba*, a new genus of placodioid lichens from the Caribbean and Hawaii shakes up the *Porinaceae* tree (lichenized *Ascomycota*, *Gyalectales*). Plant and Fungal Systematics 65(2), 577–585.
Lücking R, Rivas Plata E, Chaves J, Umana L et al. 2009 – How many tropical lichens are there really?. Bibliotheca Lichenologica 100, 399–418.

Lücking R, Sérusiaux E. 2013 – *Phyllobathelium nudum* Zahlbr. is a second species in the genus *Phyllocratera* (lichenized *Ascomycota*: *Strigulaceae*). The Lichenologist 45, 691–693.
Lücking R, Sipman HJM, Umaña L, Chaves JL et al. 2007 – *Aptrootia* (*Dothideomycetes*: *Trypetheliaceae*), a new genus of pyrenocarpous lichens for *Thelenella terricola*. The Lichenologist 39, 187–193
Lücking R, Stuart BL, Lumbsch HT. 2004 – Phylogenetic relationships of *Gomphillaceae* and *Asterothyriaceae*: evidence from a combined Bayesian analysis of nuclear and mitochondrial sequences. Mycologia 96 (2), 283–294.
Lücking R, Tehler A, Bungartz F, Rivas Plata E et al. 2013 – Journey from the West: did tropical *Graphidaceae* (lichenized *Ascomycota*: *Ostropales*) evolve from a saxicolous ancestor along the American Pacific coast?. American Journal of Botany 100(5), 844–856.
Lücking R. 1997 – The use of foliicolous lichens as bioindicators in the tropics, with special reference to the microclimate. Abstracta Botanica 21, 99–116.
Lücking R. 1998 – Foliicolous lichens and their lichenicolous fungi collected during the Smithsonian International Cryptogamic Expedition to Guyana 1996. Tropical Bryology 45–74.
Lücking R. 2008 – Foliicolous Lichenized fungi. flora neotropica monograph 103. Organization for Flora Neotropica and The New York Botanical Garden Press, Bronx, New York, 866.
Lücking R. 2019 – Stop the abuse of time! Strict temporal banding is not the future of rank-based classifications in fungi (including lichens) and other organisms. Critical Reviews in Plant Sciences 38(3), 199–253.
Lumbsch HT, Feige GB, Schmitz KE. 1994 – Systematic studies in the *Pertusariales* I. *Megasporaceae*, a new family of lichenized Ascomycetes. The Journal of the Hattori Botanical Laboratory *75*, 295–304.
Lumbsch HT, Guderley R, Feige GB. 1997 – Ascospore septation in *Diploschistes* (*Thelotremataceae*, lichenized *Ascomycota*) and the taxonomic significance of macro- and microcephalic ascospore types. Plant Systematics and Evolution 205, 179–184.
Lumbsch HT, Huhndorf SM (Eds.) 2007 – Outline of *Ascomycota* – 2007. Myconet 13, 1–58.
Lumbsch HT, Huhndorf SM. 2010 – "Outline of *Ascomycota*–2009". Myconet 14, 1–62.
Lumbsch HT, Lindemuth R. 2001 – Major lineages of *Dothideomycetes* (*Ascomycota*) inferred from SSU and LSU rDNA sequences. Mycological Research 105, 901–908.
Lumbsch HT, Lücking R, Tibell L. 2009a – Molecular data place *Tylophoron* as an additional calicioid genus in the *Arthoniales* (*Ascomycota*). Bibliotheca Botanica 99, 287–298.
Lumbsch HT, Lücking R. 2016 – Class *Lichinomycetes* Reeb, Lutzoni & Cl.Roux. In Engler's Syllabus of Plant Families, 13. Edition, Part 1/2 *Ascomycota*. Frey W (Ed)., Borntraeger, Stuttgart 205–206.
Lumbsch HT, Mangold A, Lücking R, García MA et al. 2004a – Phylogenetic position of the genera *Nadvornikia* and *Pyrgillus* (*Ascomycota*) based on molecular data. Symbolae Botanicae Upsalienses 34, 9–17.
Lumbsch HT, Prado R, Kantvilas G. 2005a – *Gregorella*, a new genus to accommodate Moelleropsis humida and a molecular phylogeny of *Arctomiaceae*. The Lichenologist 37, 291–302.
Lumbsch HT, Schmitt I, Barker D, Pagel M. 2006 – Evolution of micromorphological and chemical characters in the lichen-forming fungal family *Pertusariaceae*. Biological Journal of the Linnean Society 89(4), 615–626.
Lumbsch HT, Schmitt I, Lindemuth R, Miller A et al. 2005b – Performance of four ribosomal DNA regions to infer higher-level phylogenetic relationships of inoperculate *Euascomycetes* (*Leotiomyceta*). Molecular Phylogenetics and Evolution 34, 512–524.
Lumbsch HT, Schmitt I, Lücking R, Wiklund E et al. 2007a – The phylogenetic placement of *Ostropales* within *Lecanoromycetes* (*Ascomycota*) revisited. Mycological Research 111, 257–267.
Lumbsch HT, Schmitt I, Mangold A, Wedin M. 2007b – Ascus types are phylogenetically misleading in *Trapeliaceae* and *Agyriaceae* (*Ostropomycetidae*, *Ascomycota*). Mycological Research 111(9), 1133–1141.

Lumbsch HT, Schmitt I, Palice Z, Wiklund E et al. 2004b – Supraordinal phylogenetic relationships of *Lecanoromycetes* based on a Bayesian analysis of combined nuclear and mitochondrial sequences. Molecular Phylogenetics and Evolution 31, 822–832.
Lumbsch HT, Wirtz N, Lindemuth R, Schmitt I. 2002 – Higher level phylogenetic relationships of *Euascomycetes* (*Pezizomycotina*) inferred from a combined analysis of nuclear and mitochondrial data. Mycological Progress 1, 57–70.
Lumbsch HT, Zimmermann DG, Schmitt I. 2009b – Phylogenetic position of ephemeral lichens in *Thelocarpaceae* and *Vezdaeaceae* (*Ascomycota*). Bibliotheca Lichenologica 100, 389–398.
Lumbsch HT. 1994 – Calycin in *Lecanora fulvastra*. The Lichenologist 26 (1), 94–96.
Lumbsch HT. 1997 – Systematic studies in the suborder *Agyriineae* (*Lecanorales*). Journal of the Hattori Botanical Laboratory 83, 1–73.
Lumbsch T, Kantvilas G, Parnmen S. 2012 – Molecular data support placement of *Cameronia* in *Ostropomycetidae* (*Lecanoromycetes*, *Ascomycota*). MycoKeys 5, 31–44.
Lundqvist N. 1972 – Nordic *Sordariaceae* s. lat. Symbolae Botanicae Upsalienses 20, 1–374.
Lundqvist N. 1980 – On the genus *Pyxidiophora sensu lato* (*Pyrenomycetes*). Botaniska Notiser 133, 121–144.
Lunke T, Lumbsch HT, Feige GB. 1996 – Anatomical and ontogenetic studies on the lichen family *Schaereriaceae* (*Agyriineae*, *Lecanorales*). Bryologist 99, 53–63.
Luo J, Qiu H, Cai G, Wagner NE et al. 2015a – Phylogenomic analysis uncovers the evolutionary history of nutrition and infection mode in rice blast fungus and other *Magnaporthales*. Scientific Reports 5(1), 9448.
Luo J, Walsh E, Faulborn A, Gao K et al. 2024 – *Pinibarreniales*, a new order of *Sordariomycetes* from pine barrens ecosystem. Mycologia 116(5), 835–847.
Luo J, Walsh E, Zhang N. 2015b – Toward monophyletic generic concepts in *Magnaporthales*: species with *Harpophora* asexual states. Mycologia 107(3), 641–646.
Luo J, Yin J, Cai L, Zhang KQ et al. 2004 – Freshwater fungi in Lake Dianchi, a heavily polluted lake in Yunnan, China. Fungal Diversity 16, 93–112.
Luo J, Zhang N. 2022 – An E-monograph of the Fungal Order Magnaporthales: Taxonomy, Molecular Phylogeny, and Biogeography. https://magnaporthales.sebs.rutgers.edu.
Luo J, Zhang N. 2013 – *Magnaporthiopsis*, a new genus in *Magnaporthaceae* (*Ascomycota*). Mycologia 105(4), 1019–1029.
Luo X, Li Y, Zhong K, Luo D et al. 2023 – Discovering the effect of co-fermentation involving Saccharomyces cerevisiae and *Schizosaccharomyces pombe* on the sensory quality improvement of mandarin wine based on metabolites and transcriptomic profiles. Journal of the Science of Food and Agriculture 103(15), 7932–7940.
Luo Y, Lichtemberg PSF, Niederholzer FJA, Lightle DM et al. 2019a – Understanding the process of latent infection of canker-causing pathogens in stone fruit and nut crops in California. Plant Disease 103, 2374–2384.
Luo ZL, Bhat DJ, Jeewon R, Boonmee S et al. 2017 – Molecular phylogeny and morphological characterization of asexual fungi (*Tubeufiaceae*) from freshwater habitats in Yunnan, China. Cryptogamie, Mycologie 38, 27–53.
Luo ZL, Hyde KD, Liu JK, Bhat DJ et al. 2018 – Lignicolous freshwater fungi from China II: novel *Distoseptispora* (*Distoseptisporaceae*) species from northwestern Yunnan Province and a suggested unified method for studying lignicolous freshwater fungi. Mycosphere 9(3), 444–461.
Luo ZL, Hyde KD, Liu JK, Maharachchikumbura SS et al. 2019b – Freshwater *Sordariomycetes*. Fungal Diversity 99, 451–660.
Luo ZL, Maharachchikumbura SSN, Liu XY, Chen LJ et al. 2015c – *Annulatascus saprophyticus* sp. nov. and *Pseudoannulatascus* gen. nov. to accommodate *Annulatascus biatriisporus* (*Annulatascales*, *Sordariomycetes*) from Thailand. Phytotaxa 239, 174–182.

Luque J, Martos S, Garcia-Figueres F. 2010 – Effects of water stress and inoculation with *Eutypa lata* and *Neofusicoccum parvum* on young grapevine plants. Phytopathologia Mediterranea 49, 120.
Luttrell ES. 1951a – Taxonomy of the *Pyrenomycetes*. University of Missouri Studies 24, 1–120.
Luttrell ES. 1951b – The morphology of *Dothidea collecta*. American Journal of Botany 38, 460–471.
Luttrell ES. 1955 – The ascostromatic *Ascomycetes*. Mycologia 47(4), 511–532.
Luttrell ES. 1965 – Classification of the *Loculoascomycetes*. Mycologia 57, 828–833.
Luttrell ES. 1973 − *Loculoascomycetes*. In: Ainsworth GC, Sparrow FK, Sussman AS (eds) The fungi. An advanced treatise. Academic, New York, 135–219.
Lutzoni F, Kau VF, Cox CJ, McLaughlin D et al. 2004 – Where are we in assembling the fungal tree of life, classifying the fungi, and understanding the evolution of their subcellular traits. American Journal of Botany 91, 1446–1480.
Lutzoni F, Nowak MD, Alfaro ME, Reeb V et al. 2018 – Contemporaneous radiations of fungi and plants linked to symbiosis. Nature Communications 9, 5451.
Lutzoni F, Pagel M, Reeb V. 2001 – Major fungal lineages are derived from lichen symbiotic ancestors. Nature 411, 937–940.
Lv T, Hou CL, Johnston PR. 2019 – Three new species and a new combination of *Triblidium*. Mycokeys 60, 1–15.
Lysková P, Hubka V, Navrátilová P, Kolařík M et al. 2014 – Two cases of fungal infection of nails with participation of *Cryptendoxyla hypophloia*. Klin Mikrobiol Infekc Lek 20(1), 23–26.
M n TM. 1865 – Nya Skandinaviska Laf-arter. Botaniska Notiser 2, 38–40.
Ma HX, Yang ZE, Song ZK, Qu Z et al. 2023a – Taxonomic and phylogenetic contributions to *Diatrypaceae* from southeastern Tibet in China. Frontiers in Microbiology 14.
Ma J, Hyde KD, Tibpromma S, Gomdola D et al. 2024 – Taxonomy and systematics of lignicolous helicosporous *Hyphomycetes*. Fungal Diversity 129, 365–653.
Ma J, Xiao XJ, Liu NG, Boonmee S et al. 2023b – Morphological and Multi-gene phylogenetic analyses reveal *Pseudotubeufia* gen. nov. and two new species in *Tubeufiaceae* from China. Journal of Fungi 9, 742.
Ma J, Zhang LJ, Boonmee S, Xiao XJ et al. 2023c – Morphological and phylogenetic analyses reveal three new species and one new record of *Tubeufia* (*Tubeufiales*, *Tubeufiaceae*) from Southern China. MycoKeys 99, 87.
Ma JT, Ning JL, Wei FL, He J et al. 2022 – Chemical constituents from mushroom *Geoglossum fallax* and their bioactive activities. Fitoterapia 163, 105326.
Ma L, Chen Z, Huang DW, Kutty G et al. 2016 – Genome analysis of three *Pneumocystis* species reveals adaptation mechanisms to life exclusively in mammalian hosts. Nature Communications 7(1), 10740.
Ma L, Cissé OH, Kovacs JA. 2018 – A molecular window into the biology and epidemiology of *Pneumocystis* spp. Clinical Microbiology Reviews 31(3), 10–1128.
Machouart M, Samerpitak K, De Hoog GS, Gueidan C. 2014 – A multigene phylogeny reveals that *Ochroconis* belongs to the family *Sympoventuriaceae* (*Venturiales*, *Dothideomycetes*). Fungal Diversity 65, 77–88.
Magain N, Spribille T, DiMeglio J, Nelson PR et al. 2020 – Phylogenetic evidence for an expanded circumscription of *Gabura* (*Arctomiaceae*). The Lichenologist 52(1), 3–15.
Magain N. 2014 – Integrating photobiont phylogenetic and geographical data in macroevolutionary studies of lichens: case studies in *Peltigerales*. Doctoral Thesis. University of Liège, Liège, Belgium. 321.
Magnes M. 1997 – Weltmonographie der *Triblidiaceae*. Bibliotheca Mycologica 165, 1−177.
Magnus P. 1905 – Die Pilze (Fungi) von Tirol, Vorarlberg und Liechtenstein. In K.W. Dalla Torre von, L.G. Sarnthein von. (Eds.) Flora der Gefürsteten Grafschaft Tirol, des Landes Vorarlberg und des Fürstenthumes Liechtenstein Vol. 3. Innsbruck: Verlag der Wagner'-schen Universitäts-Buchhandlung

Magnusson AH. 1925 – Studies in the Rivulosa-group of the Genus *Lecidea*. Göteborgs Kungl. Vetensk.- Vitterh.-Samh. Handl. 22, 1–50.
Magnusson AH. 1929 – A monograph of the genus *Acarospora*. Kongliga Svenska Vetenskapsakademiens Handlingar 7, 1–400
Magnusson AH. 1934 – Die Flechtengattung Maronea Mass. Meddelelser fran Göteborgs Botaniska Trädgard 9, 41–66.
Magnusson AH. 1935 – *Acarosporaceae*, *Thelocarpaceae*. Rabenh Krypt-Fl 9, 5, 1–318.
Magnusson AH. 1936 – *Acarosporaceae* und *Thelocarpaceae*. In: Zahlbruckner, A. (Ed.) Dr. L. Rabenhorst's Kryptogamen Flora von Deutschland, Öesterreich und der Schweiz, 2nd, Band 9 (5/1). Akademische Verlagsgesellschaft M.B.H., Leipzig, pp. 1–318.
Magyar D, Vass M, Li DW. 2016 – Dispersal strategies of microfungi. In Biology of Microfungi; Li, D.W., Ed.; Springer International Publishing: Berlin/Heidelberg, Germany 315–371.
Mahabale TS. 1968 – On a fossil species of *Diplodia* from the Deccan Intertrappean series, MP, India. Journal of Palaeosciences 17, 295–297.
Maharachchikumbura SS, Chen Y, Ariyawansa HA, Hyde KD et al. 2021a – Integrative approaches for species delimitation in *Ascomycota*. Fungal Diversity 109(1), 155–179.
Maharachchikumbura SS, Wanasinghe DN, Cheewangkoon R, Al-Sadi AM. 2021b – Uncovering the hidden taxonomic diversity of fungi in Oman. Fungal Diversity 106, 229–268.
Maharachchikumbura SSN, Hyde KD, Jones EBG, McKenzie EHC et al. 2016 – Families of *Sordariomycetes*. Fungal Diversity 79, 1–317.
Maharachchikumbura SSN, Hyde KD, Jones EBG, McKenzie EHC et al. 2015 – Towards a natural classification and backbone tree for *Sordariomycetes*. Fungal diversity 72, 199–301.
Mains EB. 1954 – North American species of *Geoglossum* and *Trichoglossum*. Mycologia 46 (5), 586–631.
Mains EB. 1957 – Species of *Cordyceps* parasitic on *Elaphomyces*. Bulletin of the Torrey Botanical Club 84, 243–251.
Mains EB. 1958 – North American entomogenous species of *Cordyceps*. Mycologia 50, 169–222.
Maire MR. 1907 – Contribution à l'étude de la flore mycologique des Pyrénées. -Champignons récoltés à la Session de la Société botanique de France à Gavarnie et Cauterets en 1907. Bulletin de la Société botanique de France 54(9), CXLIV-CLXV.
Majewski T, Wiśniewski J. 1978 – New species of parasitic fungi occurring on mites (*Acarina*). Acta Mycologica 14(1/2), 3–12.
Makhija U, Adawadkar B. 2007 – Trans-septate species of *Acanthothecis* and *Fissurina* from India. The Lichenologist 39(2), 165–185.
Malavasi V, Klimešová M, Lukešová A, Škaloud P. 2022 – *Rindifilum ramosum* gen. nov. sp. nov. a new freshwater genus within the *Ulvales* (*Ulvophyceae*, *Chlorophyta*). Cryptogamie Algologie 43(8), 125–133.
Malençon G. 1979 – Nouvelles contributions a la flore mycologique du Maroc - II. Bulletin Trimestriel de la Société Mycologique de France 95(2), 119–137.
Malíček J, Berger F, Palice Z, Vondrák J. 2017 – Corticolous sorediate *Lecanora* species (*Lecanoraceae*, *Ascomycota*) containing atranorin in Europe. The Lichenologist 49, 431–455.
Malloch D, Blackwell M. 1993 – Dispersal biology of the ophiostomatoid fungi. In: *Ceratocystis* and *ophiostoma*: taxonomy, ecology, and pathogenicity, (Wingfield MJ, Seifert KA, Webber JF, ed.): 195–206. American Phytopathological Society Press., St. Paul, Minnesota.
Malloch D, Cain R.F. 1971a – New cleistothecial *Sordariaceae* and a new family, *Coniochaetaceae*. Canadian Journal of Botany 49, 869–880.
Malloch D, Cain RF, 1970a – The genus *Arachnomyces*. Canadian Journal of Botany 48, 839–845.
Malloch D, Cain RF. 1970b – Five new genera in the new family *Pseudeurotiaceae*. Canadian Journal of Botany 48, 1815–1825.
Malloch D, Cain RF. 1971b – Four new genera of cleistothecial *Ascomycetes* with hyaline ascospores. Canadian Journal of Botany 49, 847–854.

Malloch D, Cain RF. 1972 – New species and combinations in cleistothecial *Ascomycetes*. Canadian Journal of Botany 50, 61–72.
Malloch D, Sigler L, Hambleton S, Vanderwolf KJ et al. 2016 – Fungi associated with hibernating bats in New Brunswick caves: The genus *Leuconeurospora*. Botany 94, 1171–1181.
Malloch D, Sigler L. 1988 – The *Eremomycetaceae* (*Ascomycotina*). Canadian Journal of Botany 66, 1929–1932.
Malloch D. 1979 – Plectomycetes and their anamorphs. In: The whole fungus. Ed., B. Kendrick. National Museum of Canada, Ottawa, and The Kananaskis Foundation 1, 53–165.
Malloch D. 1985 – Taxonomy of *Trichocomaceae*. In: Arai T (ed.), Filamentous Microorganisms. Japan Scientific Society Press, Tokyo, 37–45.
Malloch D. 1986 – The *Trichocomaceae*: relationships with other *Ascomycetes*. In: Advances in *Penicillium* and *Aspergillus* systematics (Samson RA, Pitt JI, eds) Plenum Press, New York, 365–382.
Malloch D. 2022 – *Eurotiales*. Natural History of Fungi. New Brunswick Museum, Canada http://website.nbm-nb.ca/mycologywebpages/NaturalHistoryOfFungi/Eurotiales.html (Accessed on 16.10.2022)
Malme GO. 1928– Lichenes pyrenocarpi aliquot in Herbario Regnelliana asservati. Arkiv for Botanik 22A, 1–11.
Malme GOA. 1924 – Die Flechten der ersten Regnellschen Expedition. 2. *Astrotheliaceae*, *Paratheliaceae* und *Trypetheliaceae*. Arkiv för Botanik 19(1), 1–34.
Mamut R, Jiamahat A, Abbas A. 2022 – *Lecidea glacierensis* (*Lecideaceae*), a new lichen species from China revealed by morphology and molecular phylogenetics. The Lichenologist 54(6), 363–369.
Manamgoda DS, Rossman AY, Castlebury LA, Crous PW et al. 2014 – The genus *Bipolaris*. Studies in Mycology 79, 221–288.
Manawasinghe IS, Calabon M, Jones EBG, Senanayake IC et al. 2022 – Mycosphere notes 345–386. Mycosphere 13(1), 454–557.
Mangold A, Martín MP, Lücking R, Lumbsch TH. 2008 – Molecular phylogeny suggests synonymy of *Thelotremataceae* within *Graphidaceae* (*Ascomycota*: *Ostropales*). Taxon 57, 476–486.
Manimohan P, Amritha M, Sairabanu NK. 2011 – A comparison of diversity of marine fungi on three co-habiting mangrove plants. Mycosphere 2(5), 533–538.
Manojlovic NT, Vasiljevic PJ, Gritsanapan W, Supabphol R et al. 2010 – Phytochemical and antioxidant studies of *Laurera benguelensis* growing in Thailand. Biological Research 43, 169–176.
Manriquez V, Galdamez A, Veliz B, Rovirosa J et al. 2009 – N-methyl-1H-indole-2-carboxamide from the marine fungus *Cladosporium cladosporioides*. Journal of the Chilean Chemical Society 54(3), 314–316.
Mapook A, Hyde KD, Dai DQ, Li J et al. 2016a – *Muyocopronales*, ord. nov., (*Dothideomycetes*, *Ascomycota*) and a reappraisal of *Muyocopron* species from Northern Thailand. Phytotaxa 265(3), 225–37.
Mapook A, Hyde KD, Hongsanan S, Phukhamsakda C et al. 2016b − *Palawaniaceae* fam. nov., a new family *Dothideomycetes*, *Ascomycota* to accommodate *Palawania* species and their evolutionary time estimates. Mycosphere 7(11), 1732–1745.
Mapook A, Hyde KD, Huanraluek N, Boonmee S. 2023 – Addition to *Microascales* (*Sordariomycetes*, *Ascomycota*): *Synnematotriadelphiaceae* fam. nov., *Triadelphia mukdahanensis* sp. nov. (*Triadelphiaceae*) and the validation of *Graphiaceae*. Studies in Fungi 8, 10.
Mapook A, Hyde KD, McKenzie EH, Jones EG et al. 2020a – Taxonomic and phylogenetic contributions to fungi associated with the invasive weed *Chromolaena odorata* (Siam weed). Fungal Diversity 101, 1–175.

Mapook A, Macabeo AP, Thongbai B, Hyde KD et al. 2020b – Polyketide-derived secondary metabolites from a *Dothideomycetes* fungus, *Pseudopalawania siamensis* gen. et sp. nov., (*Muyocopronales*) with antimicrobial and cytotoxic activities. Biomolecules 10(4), 569.
Marais GJ, Wingfield MJ, Viljoen CD, Wingfield BD 1998 – A new Ophiostomatoid genus from *Protea infructescences*. Mycologia 90, 136–141.
Marasinghe DS, Boonmee S, Hyde KD, Xie N et al. 2020 – Morpho-molecular analysis reveals *Appendiculella viticis* sp. nov.(*Meliolaceae*). Phytotaxa 454(1), 45–54.
Marasinghe DS, Hongsanan S, Wanasinghe DN, Boonmee S et al. 2022a – Morpho-molecular characterization of *Brunneofissuraceae* fam. nov., *Cirsosia mangiferae* sp. nov., and *Asterina neomangiferae* nom. nov. Mycological Progress 21, 279–295.
Marasinghe DS, Hongsanan S, Zeng XY, Jones EBG et al. 2023 – Taxonomic monograph of epifoliar fungi. Fungal Diversity 121, 139–334.
Marasinghe DS, Hongsanan S, Zeng XY, Jones EGB et al. 2022b – Taxonomy and ecology of epifoliar fungi. Mycosphere 13(1), 558–601.
Marasinghe DS, Samarakoon MC, Hongsanan S, Boonmee S et al. 2019 − *Iodosphaeria honghense* sp. nov. (*Iodosphaeriaceae*, *Xylariales*) from Yunnan Province, China. Phytotaxa 420(4), 273−82.
Marchi G, Roberti S, D'Ovidio R, Mugnai L et al. 2001 – Pectic enzymes production by *Phaeomoniella chlamydospora*. Phytopathologia Mediterranea 40(3), 407–416.
Marcus DM, Hull DS, Rubin RM, Newman CL. 1999 – *Lecythophora mutabilis* endophthalmitis after long-term corneal cyanoacrylate. Retina 19, 351–353.
Mardones M, Trampe-Jaschik T, Hofmann T, Mangelsdorff RD et al. 2018a – New neotropical species of *Phyllachorales* based on molecular, morphological, and ecological data. Mycologia 110, 835–859.
Mardones M, Trampe-Jaschik T, Hofmann TA, Piepenbring M. 2018b – Contribution to the phylogeny and a new species of *Coccodiella* (*Phyllachorales*). Mycological Progress 17, 205–213.
Mardones M, Trampe-Jaschik T, Oster S, Elliott M et al. 2017 – Phylogeny of the order *Phyllachorales* (*Ascomycota*, *Sordariomycetes*): among and within order relationships based on five molecular loci. Persoonia 39, 74–90.
Mardones M, Trampe-Jaschik T, Piepenbring M, Romberg MK et al. 2022 – *Telimena* (*Telimenaceae*, *Phyllachorales*) species on Neotropical host plants: New species, combinations and key for species on *Polygonaceae*. Nova Hedwigia 114, 435–460.
Mardones M, Trampe-Jaschik T, Piepenbring M. 2020 – Phylogenetics and taxonomy of *Telimenaceae* (*Phyllachorales*) from Central America. Mycological Progress 19, 1587–1599.
Maria GL, Sridhar KR 2003 – Diversity of filamentous fungi on woody litter of five mangrove plant species from the southwest coast of India. Fungal Diversity 14, 109–126.
Maria GL, Sridhar KR 2004 – Fungal colonization of immersed wood in mangroves of the southwest coast of India. Canadian Journal of Botany 82, 1409–1418.
Maria GL, Sridhar KR. 2002 – Richness and diversity of filamentous fungi on woody litter of mangroves along the west coast of India. Current science 83 (12), 1573–1580.
Marincowitz S, Crous PW, Groenewald JZ, Wingfield MJ. 2008a – Microfungi occurring on the Proteaceae in the fynbos. CBS Diversity Series 60, 1–166.
Marincowitz S, Duong TA, Stephen SJ, de Beer ZW et al. 2020 – Fungal associates of an invasive pine-infesting bark beetle, *Dendroctonus valens* including seven new Ophiostomatalean fungi. Persoonia 45, 177–195.
Marincowitz S, Groenewald JZ, Wingfield MJ, Crous PW. 2008b – Species of *Botryosphaeriaceae* occurring on *Proteaceae*. Persoonia: Molecular Phylogeny and Evolution of Fungi 21, 111–118.
Marin-Felix Y, Groenewald JZ, Cai L, Chen Q et al. 2017 – Genera of phytopathogenic fungi: GOPHY 1. Studies in Mycology 86, 99–216.

Marin-Felix Y, Guarro J, Cano-Lira JF, García D et al. 2018 – *Melanospora* (*Sordariomycetes*, *Ascomycota*) and its relatives. MycoKeys 81–122.
Marin-Felix Y, Miller AN, Cano-Lira JF, Guarro J et al. 2020 – Re-evaluation of the order *Sordariales*: delimitation of *Lasiosphaeriaceae* s. str., and introduction of the new families *Diplogelasinosporaceae*, *Naviculisporaceae*, and *Schizotheciaceae*. Microorganisms 8(9), 1430.
Marin-Felix Y, Miller AN. 2022 – Corrections to recent changes in the taxonomy of the *Sordariales*. Mycological Progress 21, 69.
Marin-Felix Y, Stchigel AM, Miller AN, Guarro J et al. 2015 – A re-evaluation of the genus *Myceliophthora* (*Sordariales*, *Ascomycota*): its segregation into four genera and description of *Corynascus fumimontanus* sp. nov. Mycologia 107(3), 619–632.
Markovskaja S. 2003 – A new species of *Cordana* from *Lithuania*. Mycotaxon 87, 179–185.
Marmor L, Randlane T. 2007 – Effects of road traffic on bark pH and epiphytic lichens in Tallinn. Folia Cryptogamica Estonica 43, 23–37.
Marriott DJ, Wong KH, Aznar E, Harkness JL et al. 1997 – *Scytalidium Dimidiatum* and *Lecythophora Hoffmannii*: Unusual Causes of Fungal Infections in a Patient with AIDS. Journal of Clinical Microbiology 35(11), 294952.
Martin F, Kohler A, Murat C, Veneault-Fourrey C et al. 2016 – Unearthing the roots of ectomycorrhizal symbioses. Nature Reviews Microbiology 14, 760–773.
Martin GW. 1941 – Outline of the fungi. Studies in Natural History of Lowa University, 188 (suppl.), 1–64.
Martín MT, Cobos R, Martín L, López-Enríquez L. 2012 – Real-Time PCR Detection of *Phaeomoniella chlamydospora* and *Phaeoacremonium aleophilum*. Applied and Environmental Microbiology 78, 3985–3991.
Martin W. Koonin EV. 2006 – Introns and the origin of nucleus–cytosol compartmentalization. Nature 440(7080), 41–45.
Martínez I, Aragón G, Sarrión FJ, Escudero A et al. 2003 –Threatened lichens in central Spain (saxicolous species excluded). Cryptogamie, Mycologie 24(1), 73–97.
Masi M, Cimmino A, Boari A, Tuzi A et al. 2017 –Colletochlorins E and F, new phytotoxic tetrasubstituted pyran-2-one and dihydrobenzofuran, isolated from *Colletotrichum higginsianum* with potential herbicidal activity. Journal of Agricultural and Food Chemistry 65, 1124–1130.
Maslova NP, Tobias AV, Kodrul TM. 2021 – Recent studies of co-evolutionary relationships of fossil plants and fungi: success, problems, prospects. Paleontological Journal 55, 1–17.
Massalongo A. 1856a – *Sarcosagium*. Flora, Regensburg 39, 289.
Massalongo AB. 1854 – Geneacaena lichenum ab A. prof. Massalongo noviter proposita ac descripta. Tip. Antonellianis. Verona. 1–24.
Massalongo AB. 1856b – Genera lichenum aliquot nova proponit et describit A.B.D. Prof. Massalongo. Flora (Regensburg) 39, 281–286, 289–292.
Massalongo AB. 1860 – Esame comparativo di alcune genere di licheni. Atti del Reale Istituto Veneto di Scienze, Lettere ed Arti. ser. 3, 5: 247–276, 313–337.
Massalongo M. 1852 – Synopsis Lichenum Blasteniosporum. Flora 35, 561–576.
Massee G, Salmon ES. 1902 – Researches on coprophilous fungi. II. Annals of Botany 16, 57–97.
Mathey A, Hoder D. 1978 – Distribution of lichen substances by means of fluorescence microscopy, cathodoluminescence in scanning electron microscopy and X-ray microanalysis in *Lecanora*-, *Buellia*-, *Laurera*- and *Trypethelium*-species. Nova Hedwigia 30, 127–138.
Mathey A, Lukins PB. 2001 – Spatial distribution of perylenequinones in lichens and extended quinones in quincyte using confocal fluorescence microscopy. Micron 32, 107–113.
Mathey A, Van Roy W, Van Vaeck L, Eckhardt G. 1994 – In situ analysis of a new perylene quinone in lichens by Fourier-transform laser microprobe mass spectrometry with external source. Rapid Commun. Mass Spectrometry 8, 46–52.

Mathey A, Van Vaeck L, Steglich W. 1987 – Investigation of semi-thin cryosections of lichens by laser microprobe mass spectrometry. Analytica Chimica Acta 195, 89–96.
Matsuda Y, Yamakawa M, Inaba T, Obase K et al. 2017 – Intraspecific variation in mycelial growth of *Cenococcum geophilum* isolates in response to salinity gradients. Mycoscience 58, 369–377.
Matsumoto T, Padhye AA, Ajello L 1987 – Medical significance of the so-called black yeasts. European Journal of Epidemiology 3, 87–95.
Matsushima T. 1971 – Microfungi of the Solomon Islands and Papua-New Guinea. Publicado pelo autor, Kobe.
Matsushima T. 1975 – Icones microfungorum a Matsushima lectorum. Matsushima; Kobe, Japan.
Matsushima T. 1993 – Matsushima mycological memoirs No. 7. Matsushima; Kobe, Japan.
Matsushima T. 1995 – Matsushima Mycological Memoirs 8. Matsushima Mycological Memoirs 8, 1–44.
Matsushima T. 1996 – Matsushima mycological memoirs No. 9. Matsushima; Kobe, Japan.
Matwiejuk A. 2010 – Lichen secondary metabolites occurring in lichens of the genus *Rhizocarpon* Ramond ex DC. (*Rhizacarpaceae*, lichenized *Ascomcota*) in Poland. Roczniki Akademii Rolniczej w Poznaniu. Botanika-Steciana (14).
Mayer VE, De Hoog S, Cristescu SM, Vera L et al. 2021 – Volatile organic compounds in the Azteca/Cecropia ant-plant symbiosis and the role of Black Fungi. Journal of Fungi 7, 836.
Mayrhofer H, Poelt J. 1985 – Die Flechtengattung Microglaena *sensu* Zahlbruchner in Europa. - Herzogia 7, 13–79.
Mayrhofer H. 1982 – Ascosporen und Evolution der Flechtenfamilie *Physciaceae*. Journal of the Hattori Botanical Laboratory 52, 313–321.
Mayrhofer H. 1987 – Monographie der Flechtengattung Thelenella. Bibliotheca Lichenologica 26, 1-106 + Abb.
Mazars E, Guyot K, Fourmaintraux S, Renaud F et al. 1997 – Detection of *Pneumocystis* in European wild animals. Journal of Eukaryotic Microbiology 44, S39.
Mbenoun M, Wingfield MJ, Boyogueno AB, Amougou FN et al. 2016 – Diversity and pathogenicity of the *Ceratocystidaceae* associated with cacao agroforests in Cameroon. Plant Pathology 65, 64–78.
McCarthy M, Elix JA. 2017a – A new species of *Phlyctis* (lichenized *Ascomycota*, *Phlyctidaceae*) from Australia. Australasian Lichenology 81, 2–5.
McCarthy PM, Elix JA. 2014 – Two new lichens from Mount Canobolas, New South Wales. Telopea 16, 119–125.
McCarthy PM, Elix JA. 2017b – A new species and new record of *Candelariella* (lichenized *Ascomycota*, *Candelariaceae*) from Australia. Australasian Lichenology 81, 79–85.
McCarthy PM, Kantvilas G. 2013 – Two new species of *Sarcogyne* (lichenised *Ascomycota*: *Acarosporaceae*) from central and southern Australia. Journal of the Adelaide Botanic Garden 15–21.
McCarthy PM, Palice Z. 2003 – A new species of *Trichothelium* and new records of *Porinaceae* from Ecuador. The Lichenologist 35(3), 237–240.
McCarthy PM. 2008 – A new species of *Melanophloea* (*Thelocarpaceae*) from north-eastern Queensland. Australasian Lichenology 62, 26–28.
McCloskey S, Noppawan S, Mongkolthanaruk W, Suwannasai N et al. 2017 − A new cerebroside and the cytotoxic constituents isolated from *Xylaria allantoidea* SWUF76. Natural Product Research 31(12), 1422−30.
McCune B, Curtis MJ. 2012 – *Umbilicaria semitensis* (lichenized fungi: *Umbilicariaceae*) resurrected. The Bryologist 115, 255–264.
McCune B, Di Meglio J, Curtis MJ. 2014 – An unusual ascospore shape and a new species, *Umbilicaria nodulospora* (*Umbilicariaceae*), from California and Oregon. Bryologist 117, 170–178.

McCune B. 2017 – Microlichens of the Pacific Northwest, Volume 2: Keys to the species. - Wild Blueberry Media, Corvallis, Oregon 755 pp.
McDonald V, Lynch S, Eskalen A. 2009 – First report of *Neofusicoccum australe*, *N. luteum*, and *N. parvum* associated with avocado branch canker in California. Plant Disease 93, 967.
McGinnis MR, McKenzie RA, Connole MD. 1985a – *Phaeosclera dematioides*, a new etiologic agent of phaeohyphomycosis in cattle. Sabouraudia: Journal of Medical and Veterinary Mycology 23(2), 133–135.
McGinnis MR, Schell WA, Carson J. 1985b – *Phaeoannellomyces* and the *Phaeococcomycetaceae*, new dematiaceous blastomycete taxa. Sabouraudia: Journal of Medical and Veterinary Mycology 23(3), 179–188.
McHugh R, Mitchel D, Wright M, Anderson R. 2001 – The fungi of Irish grasslands and their value for nature conservation. In Biology and Environment: Proceedings of the Royal Irish Academy (225– 243). Royal Irish Academy.
McIlvaine C, Macadam RK. 1912 – Toadstools, Mushrooms, Fungi, Edible and Poisonous: One Thousand American Fungi; how to Select and Cook the Edible; how to Distinguish and Avoid the Poisonous, with Full Botanic Descriptions. Bobbs-Merrill Company.
McLoughlin S. 2001 – The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. Australian Journal of Botany 49, 271–300.
McMullin DR, Green BD, Miller JD. 2015 – Antifungal sesquiterpenoids and macrolides from an endophytic *Lophodermium* species of *Pinus strobus*. Phytochemistry Letters 14, 148–152.
McMullin DR, Green BD, Prince NC, Tanney JB et al. 2017 – Natural Products of *Picea* Endophytes from the Acadian Forest. Journal of Natural Products 80(5), 1475–1483.
McMullin DR, Tanney JB, McDonald KP, Miller JD. 2019 – Phthalides produced by *Coccomyces strobi* (*Rhytismataceae*, *Rhytismatales*) isolated from needles of *Pinus strobus*. Phytochemistry Letters 29, 17–24.
McNeill J, Barrie FR, Buck WR, Demoulin V et al. (eds.) 2012 – International Code of Nomenclature for Algae, Fungi, and Plants (Melbourne Code), adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. Regnum Vegetabile 154, Koeltz Scientific Books.
Mead ME, Steenwyk JL, Silva LP, de Castro PA et al. 2021 – An evolutionary genomic approach reveals both conserved and species-specific genetic elements related to human disease in closely related *Aspergillus* fungi. Genetics 218(2), iyab066.
Meade JC, Stringer JR. 1991 – PCR amplification of DNA sequences from the transcription factor IID and cation transporting ATPase genes in *Pneumocystis carinii*. Journal of Protozoology 38, S66–S68.
Medeiros ID, Fryday AM, Rajakaruna N. 2014 – Additional lichen records and mineralogical data from metal-contaminated sites in Maine. Rhodora 116(967), 323–347.
Medina RP, Araujo AR, Batista JM Jr, Cardoso CL et al. 2019 − Botryane terpenoids produced by *Nemania bipapillata*, an endophytic fungus isolated from red alga *Asparagopsis taxiformis* - *Falkenbergia stage*. Scientific Reports 9, 12318.
Mel'nik VA, Castaneda-Ruiz RF, Granados M. 2013 – A new species of *Heliocephala* from Vietnam. Mycotaxon 123, 281–284.
Melie T, Pirro S, Miller AN, Smith SD et al. 2023 – Comparative genomics and phylogenomic investigation of the class *Geoglossomycetes* provide insights into ecological specialization and the systematics of *Pezizomycotina*. Mycologia 115(4), 499–512.
Mendonça CO, Aptroot A, Cáceres MES. 2016 – Six new species of the lichen genus *Pyrenula* (*Pyrenulaceae*) from Northeast Brazil. Phytotaxa 286(3), 169–176.
Menezes AA, Cáceres MES, Bastos CJP, Lücking R. 2018 – The latitudinal diversity gradient of epiphytic lichens in the Brazilian Atlantic Forest: does Rapoport's rule apply? Bryologist 121, 480–497.
Menkis A, Urbina H, James TY, Rosling A. 2014 – *Archaeorhizomyces borealis* sp. nov. and a sequence-based classification of related soil fungal species. Fungal Biology 118, 943–955.

Merges D, Dal Grande F, Greve C, Otte J et al. 2021 – Virus diversity in metagenomes of a lichen symbiosis (*Umbilicaria phaea*): Complete viral genomes, putative hosts and elevational distributions. Environmental Microbiology 23(11), 6637-6650.
Merrill W, French DW, Wood FA. 1964 − Decay of wood by species of the *Xylariaceae*. Phytopathology 54, 56−58.
Messuti MI, Lorenzo LE. 1997 – A new species of *Hysterium* from *Patagonia*, *Argentina*. Mycological Research 101, 302–304.
Messuti MI, Lorenzo LE. 2003 – Notes on the genus *Hysterographium* (*Ascomycota*, *Hysteriaceae*) in southern South America. Nova Hedwigia 76, 451–458.
Meyers SP, Reynolds ES. 1959a – Growth and cellulolytic activity of lignicolous *Deuteromycetes* from marine localities. Canadian Journal of Microbiology 5, 493–455.
Meyers SP, Reynolds ES. 1959b – Cellulolytic activity in lignicolous marine *Ascomycetes*. Bulletin of Marine Science 9, 441–455.
Meyers SP. 1953 – Marine fungi of Biscayne Bay, Florida. Bull Mar Sci Gulf Caribbean 2, 590–601.
Meyers SP. 1954 – Marine fungi of Biscayne Bay, Florida II. Further studies of occurrence and distribution. Bulletin of Marine Science 3, 307–327.
Meyers SP. 1957 – Taxonomy of marine *Pyrenomycetes*. Mycologia 49, 475–528.
Mhmoud NA, Ahmed SA, Fahal AH, de Hoog GS et al. 2012 – *Pleurostomophora ochracea*, a novel agent of human eumycetoma with yellow grains. Journal of Clinical Microbiology 50, 2987–2994.
Miadlikowska J, Kauff F, Hofstetter V, Fraker E et al. 2006 – New insights into classification and evolution of the *Lecanoromycetes* (*Pezizomycotina*, *Ascomycota*) from phylogenetic analyses of three ribosomal RNA- and two protein-coding genes. Mycologia 98, 1088–1103.
Miadlikowska J, Kauff F, Högnabba F, Oliver CJ et al. 2014 – A multigene phylogenetic synthesis for the class *Lecanoromycetes* (*Ascomycota*): 1307 fungi representing 1139 infrageneric taxa, 317 genera and 66 families. Molecular Phylogenetics and Evolution 79, 132–168.
Miadlikowska J, Lutzoni F. 2004 – Phylogenetic classification of peltigeralean fungi (*Peltigerales*, *Ascomycota*) based on ribosomal RNA small and large subunits. American Journal of Botany 91(3), 449–464.
Mibey RK, Hawksworth DL. 1997 – *Meliolaceae* and *Asterinaceae* of the Shimba Hills. Kenya Mycological Papers 174, 1–108.
Michailides TJ. 1991 – Pathogenicity, distribution, sources of inoculum, and infection courts of *Botryosphaeria dothidea* on pistachio. Phytopathology 81, 566–573.
Middelborg J, Mattsson J. 1987 – Crustaceous lichenized species of the *Caliciales* in Norway. Sommerfeltia 5(1), 1–1.
Millardet A. 1870 – De la germination des zygospores des genres Closterium et Staurastrum et sur un genre nouveau d'algues chlorospores. Memoires de la Societe de Sciences Naturelles de Strasbourg 6, 37–50.
Millarini V, Ignesti S, Cappelli S, Ferraro G et al. 2020 – Protection of wine from protein haze using *Schizosaccharomyces japonicus* polysaccharides. Foods 9(10), 1407.
Miller AN, Huhndorf SM. 2001 – Neotropical *Ascomycetes* 10. New and interesting *Cercophora* species. Sydowia 53, 211–226.
Miller AN, Huhndorf SM. 2004 – A natural classification of *Lasiosphaeria* based on nuclear LSU rDNA sequences. Mycological Research 108(1), 26–34.
Miller AN, Huhndorf SM. 2005 – Multi-gene phylogenies indicate ascomatal wall morphology is a better predictor of phylogenetic relationships than ascospore morphology in the *Sordariales* (*Ascomycota*, Fungi). Molecular Phylogenetics and Evolution 35(1), 60–75.
Miller JH. 1938 – Studies in the development of two *Myriangium* species and the systematic position of the order *Myriangiales*. Mycologia 30, 158–181.
Miller JH. 1949 – A revision of the classification of the *Ascomycetes* with special emphasis on the *Pyrenomycetes*. Mycologia 41, 99–127.

Minet M, Nurse P, Thuriaux P, Mitchison JM. 1979 – Uncontrolled septation in a cell division cycle mutant of the fission yeast *Schizosaccharomyces pombe*. Journal of Bacteriology 137(1), 440–446.
Minks A. 1900 – Analysis der Flechtengattung Umbilicaria. Zugleich ein lichenologischer Beitrag zur Kenntniss der Entstehung und des Begriffes der naturwissenschaftlichen Art // Mémoires de l'Herbier Boissier № 22, 77 pp.
Minnis AM, Kennedy AH, Grenier DB, Palm ME et al. 2012 – Phylogeny and taxonomic revision of the *Planistromellaceae* including its coelomycetous anamorphs: Contributions towards a monograph of the genus *Kellermania*. Persoonia: Molecular Phylogeny and Evolution of Fungi 29, 11–28.
Minnis AM, Lindner DL. 2013 – Phylogenetic evaluation of *Geomyces* and allies reveals no close relatives of *Pseudogymnoascus destructans*, comb. nov., in bat hibernacula of Eastern North America. Fungal Biology 117(9), 638–649.
Minter DW, Holubová-Jechová V. 1981 – New or interesting *Hyphomycetes* on decaying pine litter from Czechoslovakia. Folia Geobotanica et Phytotaxonomica 16, 195–217.
Minter DW, Millar CS. 1993 – *Lophodermella arculata*, *Lophodermella cerina*. IMI Descriptions of Fungi and Bacteria. nos. 1144–1145.
Minter DW, Peredo HL, Watson AT. 2007 − *Acrospermum chilense* sp. nov. from Chile and the *Acrospermales* ord. nov. Boletín de la Sociedad Argentina de Botánica 42(1–2), 107–12.
Minter DW, Rodríguez-Hernández M, Mena-Portales J. 2001 – Check- list of the Caribbean Fungi. In Minter DW, Rodríguez-Hernández M, Mena-Portales J (eds) Fungi of the Caribbean: An annotated checklist. PMDS Publisher 718–743.
Minter DW, Staley JM, Millar CS. 1978 – Four species of *Lophodermium* on *Pinus sylvestris*. Transactions of the British. Mycological Society 71, 295–301.
Minter DW. 1981 – *Lophodermium* on pines. Mycological Papers 147, 1−54.
Minter DW. 2003 – *Propolis* and *Marthamyces* gen. nov. (*Rhytismatales*). Mycotaxon 87, 43–52.
Minter DW. 2006 – IMI Descriptions of Fungi and Bacteria No. 1667. *Corynelia uberata*. UK, Egham: CABI.
Miranda-González R, Bungartz F, Lücking R, Gaya E et al. 2022 – Phylogeny of the *Pyrenula ochraceoflava* group (*Pyrenulaceae*) reveals near-cryptic diversification and the inclusion of the *Mazaediothecium album* aggregate. The Bryologist 125(4), 541–557.
Miranda-González R, Lücking R, Barcenas-Peña A, de los Ángeles Herrera-Campos M. 2020 – The new genus *Jocatoa* (*Lecanoromycetes*: *Graphidaceae*) and new insights into subfamily *Redonographoideae*. The Bryologist 123(2), 127–143.
Misas-Villamil JC, Van der Hoorn RA. 2008 – Enzyme inhibitor interactions at the plant pathogen interface. Current Opinion in Plant Biology 11, 380e388.
Mitchell J, Garrido-Benavent I, Quijada L, Pfister, DH. 2021 – *Sareomycetes*: more diverse than meets the eye. International Mycological Association Fungus12(1), 1–36.
Mitchell JK, Quijada L, Johnston PR, Pfister DH. 2022 – Species of the common discomycete genus *Bisporella* reassigned to at least four genera. Mycologia 114(4), 713–731.
Mitchell JK. 2021 – Investigations into resinicolous fungi (Doctoral dissertation, Harvard University).
Mitchison-Field LMY, Vargas-Muñiz JM, Stormo BM, Vogt DJE et al. 2019 – Unconventional cell division cycles from marine-derived yeasts. Current Biology 29, 3439–3456.
Mittal J, Szymczak WA, Pirofski LA, Galen BT. 2018 – Fungemia caused by *Aureobasidium pullulans* in a patient with advanced AIDS: a case report and review of the medical literature. JMM Case Reports 5(4), e005144.
Mix AJ. 1949 – A monograph of the genus *Taphrina*. University of Kansas Science Bulletin 33(1), 1–167.
Mo M, Huang X, Zhou W, Huang Y et al. 2005 – *Arthrobotrys yunnanensis* sp. nov., the fourth anamorph of *Orbilia auricolor*. Fungal Diversity 18, 107–115.
Moberg R. 1986 – Lichenes Selecti Exsiccati Upsaliensis. Fasc. 1 (Nos 1–25). Thunbergia 2, 1–10.

Mohali SR, Slippers B, Wingfield MJ. 2007 – Identification of *Botryosphaeriaceae* from *Eucalyptus, Acacia* and *Pinus* in Venezuela. Fungal Diversity 25, 103–125.
Mohr F, Ekman S, Heegaard E. 2004 – Evolution and taxonomy of the marine *Collemopsidium* species (lichenized *Ascomycota*) in north-west Europe. Mycological Research 108(5), 515–532.
Mojsov KD. 2016 – *Aspergillus* Enzymes for Food Industries. In (Eds. Vijai Kumar Gupta) New and Future Developments in Microbial Biotechnology and Bioengineering, Elsevier publishers 215–222.
Molins A, Chiva S, Calatayud Á, Marco F et al. 2020 – Multidisciplinary approach to describe *Trebouxia* diversity within lichenized fungi *Buellia zoharyi* from the Canary Islands. Symbiosis 82(1), 19–34.
Möller A. 1901 – Phycomyceten und Ascomyceten. Untersuchungen aus Brasilien. Botanische Mittheilungen aus den Tropen 9. Gustav Fischer, Jena, Germany.
Möller EJ. 2021 – Molecular phylogenetics and genus delimitation in the *Rhizocarpaceae* (lichenized *Ascomycetes*) with focus on the *Rhizocarpon* hochstetteri-complex (Master's thesis).
Momota K, Nakaoka M. 2017 – Influence of different types of sessile epibionts on the community structure of mobile invertebrates in an eelgrass bed. PeerJ 5, e2952.
Monkai J, Jayawardena RS, Maharachchikumbura SS, Hyde KD. 2020 – Sexual morph of *Furcasterigmium furcatum* (*Plectosphaerellaceae*) from *magnolia liliifera* collected in Northern Thailand. Phyton 89(3), 765.
Monkai J, Liu JK, Boonmee S, Chomnunti P et al. 2013 – *Planistromellaceae* (*Botryosphaeriales*). Cryptogamie, Mycologie 34(1), 45–77.
Monod M. 1983 – Monographie taxonomique des *Gnomoniaceae* (*Ascomycetes* de l'ordre des *Diaporthales*) I Beih. Sydowia 9, 1–315.
Montagne C. 1851 – Cryptogamia Guyanensis seu plantarum cellularium in Guyana gallica annis 1835–1849 a cl. Leprieur collectarum enumeratio universalis. suite. Annales des Sciences Naturelles, Botanique 16, 47–81.
Montagne C. 1856 – Sylloge Generum Specierumque Cryptogamarum. Paris: J.-B. Baillire.
Montagne JPFC. 1842 – Botanique. Plantes cellulaires. In: de la Sagra R (ed) Histoire Physique Politique et Naturelle de l'Ile de Cuba 2, 1–549.
Moore MJ, Bell CD, Soltis PS, Soltis DE. 2007 – Using plastid genome-scale data to resolve enigmatic relationships among basal angiosperms. Proceedings of the National Academy of Sciences, U.S.A. 104, 19363–19368.
Moore RT, Meyers SP. 1962 – *Thalassiomycetes*: III. The genus Zalerion. Canadian Journal of Microbiology 8, 407–416.
Moore RT. 1958 – *Deuteromycetes* I: the S*poridesmium* complex. Mycologia 50(5), 681–692.
Moore RT. 1990 – The genus *Lalaria* gen. nov.: *Taphrinales* anamorphosum. Mycotaxon 38, 315–330.
Morales-Cruz A, Amrine KCH, Blanco-Ulate B, Lawrence DP et al. 2015 – Distinctive expansion of gene families associated with plant cell wall degradation, secondary metabolism, and nutrient uptake in the genomes of grapevine trunk pathogens. BMC Genomics 16, 469.
Morath SU, Hung R, Bennett JW. 2012 – Fungal volatile organic compounds: a review with emphasis on their biotechnological potential. Fungal biology reviews 26, 73–83.
Moreno LF, Feng P, Weiss VA, Vicente VA et al. 2017 – Phylogenomic analyses reveal the diversity of laccase-coding genes in Fonsecaea genomes. PLoS ONE 12, e0171291.
Morgan-Jones G, Gintis BO, Rodriguez-Kabana R. 1984 – New species of *Chalara* and *Scytalidium* isolated from cysts of *Heterodera glycines*. Mycologia 76(2), 211–217.
Morse CA. 2016 – Two new species of *Thelenella* and new reports from the Great Plains of central North America, with a worldwide key to the genus. Opuscula Philolichenum 15, 22–36.
Mortimer PE, Jeewon R, Xu JC, Lumyong S et al. 2021 – Morpho-phylo taxonomy of novel dothideomycetous fungi associated with dead woody twigs in Yunnan Province, China. Frontiers in Microbiology 12, 654683.

Mosbach K. 1967 – On the biosynthesis of lichen substances. Part 4. The formation of pulvic acid derivatives by isolated lichen fungi. Acta Chemica Scandinavica 21, 2331–2334.
Mostert L, Crous PW, Ewald Groenewald JZ, Gams W et al. 2003 – *Togninia* (*Calosphaeriales*) is confirmed as teleomorph of *Phaeoacremonium* by means of morphology, sexual compatibility and DNA phylogeny. Mycologia 95, 646–659
Mostert L, Groenewald JZ, Summerbell RC, Gams W et al. 2006 – Taxonomy and pathology of *Togninia* (*Diaporthales*) and its *Phaeoacremonium* anamorphs. Studies in Mycology 54, 1–113.
Mosunova OV, Navarro-Muñoz JC, Haksar D, van Neer J et al. 2022 – Evolution-informed discovery of the naphthalenone biosynthetic pathway in fungi. MBio 13, e0022322.
Motoyama T, Yun CS, Osada H. 2021 – Biosynthesis and biological function of secondary metabolites of the rice blast fungus *Pyricularia oryzae*. Journal of Industrial Microbiology and Biotechnology 48(9–10), kuab058.
Moulíková Š, Kolařík M, Lorch JM, Kolarczyková D et al. 2023 – Wild rodents harbour high diversity of *Arthroderma*. Persoonia 50, 27–47.
Moussa TA, Gerrits van den Ende BH, Al Zahrani HS, Kadasa NM et al. 2017 – The genus *Anthopsis* and its phylogenetic position in *Chaetothyriales*. Mycoses 60(4), 254–259.
Mouzouras R. 1986 – Decay of wood by microorganisms in marine environments. In British Wood Preserving and Damp Proofing Association; Annual Convention (pp. 1–18).
Mouzouras R. 1989a – Decay of mangrove wood by marine fungi. Botanica Marina 32, 65–69.
Mouzouras R. 1989b – Soft rot decay of wood by marine microfungi. Journal Institute Wood Science 11, 193–201.
Moya P, Chiva S, Molins A, Garrido-Benavent I et al. 2021 – Unravelling the symbiotic microalgal diversity in *Buellia zoharyi* (lichenized *Ascomycota*) from the Iberian Peninsula and Balearic Islands using DNA metabarcoding. Diversity 13(6), 220.
Muchnik EE, Konoreva LA, Kazakova MV, Sobolev NA. 2018 – The lichen biota of the Meshchera National Park (Vladimir Region, Russia) and Meshchersky National Park (Ryazan Region, Russia). Nature Conservation Research 4(1), 64–82.
Mugambi GK, Huhndorf SM. 2009 – Molecular phylogenetics of *Pleosporales*: *Melanommataceae* and *Lophiostomataceae* recircumscribed (*Pleosporomycetidae*, *Dothideomycetes*, *Ascomycota*). Studies in Mycology 64, 103–121.
Mugambi GK, Huhndorf SM. 2010 – Multigene phylogeny of the *Coronophorales*: morphology and new species in the order. Mycologia 102(1), 185–210.
Muggia L, Coleine C, De Carolis R, Cometto A et al. 2021a – *Antarctolichenia onofrii* gen. nov. sp. nov. from Antarctic endolithic communities untangles the evolution of rock-inhabiting and lichenized fungi in *Arthoniomycetes*. Journal of Fungi 7, 935.
Muggia L, Grube M. 2018 – Fungal diversity in lichens: from extremotolerance to interactions with algae. Life 8, 15.
Muggia L, Gueidan C, Grube M. 2010 – Phylogenetic placement of some morphologically unusual members of *Verrucariales*. Mycologia 102(4), 835–846.
Muggia L, Gueidan C, Knudsen K, Perlmutter G et al. 2012 – The lichen connections of Black fungi. Mycopathologia 175, 523–535.
Muggia L, Hafellner J, Wirtz N, Hawksworth DL et al. 2008 – The sterile microflamentous lichenized fungi *Cystocoleus ebeneus* and *Racodium rupestre* are relatives of plant pathogens and clinically important dothidealean fungi. Mycological Research 112, 50–56.
Muggia L, Kocourková J, Knudsen K. 2015 – Disentangling the complex of *Lichenothelia* species from rock communities in the desert. Mycologia 107(6), 1233–1253.
Muggia L, Quan Y, Gueidan C, Al-Hatmi AM et al. 2021b – Sequence data from isolated lichen-associated melanized fungi enhance delimitation of two new lineages within *Chaetothyriomycetidae*. Mycological Progress 20, 911–927.
Muller E, Loeffler W. 1976 – Mycology: Mycology: an outline for science and medical students. G. Stuttgart, Germany: Thieme Publishers.

Müller E, Samuels GJ. 1982 – Anamorphs of pyrenomycetous *Ascomycetes* I. *Rhamphoria* Niessl and *Trichosphaerella* Bommer, Rousseau & Saccardo. Sydowia 35, 143–149.
Müller E, Von Arx J. 1962 – Die Gattungen der didymosporen Pyrenomyceten. Beiträge zur Kryptogamenflora der Schweiz 11, 1–922.
Müller E, von Arx JA. 1950 – Einige Aspekte zur Systematik pseudosphärialer Ascomyceten. Berichte der Schweizerischen Botanischen Gesellschaft 60, 329–397.
Müller E, von Arx JA. 1973 – *Pyrenomycetes*: *Meliolales*, *Coronophorales*, *Sphaeriales*. Ainsworth GC, Sparrow FK, Sussman AS, eds Fungi 4A, 87–132.
Müller E. 1973 – *Pyrenomycetes*: *meliolales*, *coronophorales*, *sphaeriales*. The fungi, an advanced treatise. Academic Press, New York.4A., 87–132.
Müller J. 1884 – Revisio lichenum eschweilerianorum. Flora 67, 667–672 + 686–691.
Müller J. 1885 – Pyrenocarpae Cubenses a cl. C. Wright lectae. Botanische Jahrbücher für Systematik 6, 375–421.
Müller J. 1894 – Conspectus systematicus lichenum Novae Zelandiae, quem elaboravit. Bull. Herb. Boissier 2(app. 1), 1–114.
Munk A. 1948 – Pyrenomycetes collected in the peninsula Mols, Jutland. Dansk Botanisk Arkiv 12, 1–19.
Munk A. 1953 – The system of the *Pyrenomycetes*. Dansk Botanisk Arkiv 15(2), 1–163.
Munk A. 1957 – Danish *Pyrenomycetes*. A preliminary flora. Dansk Botanisk Arkiv 17, 1–491.
Murat C, Payen T, Noel B, Kuo A et al. 2018 – *Pezizomycetes* genomes reveal the molecular basis of ectomycorrhizal truffle lifestyle. Nature ecology and Evolution 2(12), 1956–1965.
Muscavitch ZM, Lendemer JC, Harris RC. 2017 – A review of the lichen genus *Phlyctis* in North America (*Phlyctidaceae*) including the description of a new widespread saxicolous species from eastern North America. The Bryologist 120(4), 388–417.
Musvuugwa T, De Beer ZW, Duong TA, Dreyer LL et al. 2015 – New species of *Ophiostomatales* from *Scolytinae* and *Platypodinae* beetles in the Cape Floristic Region, including the discovery of the sexual state of *Raffaelea*. Antonie van Leeuwenhoek 108, 933–950.
Musvuugwa T, De Beer ZW, Duong TA, Dreyer LL et al. 2016 – Wounds on *Rapanea melanophloeos* provide habitat for a large diversity of *Ophiostomatales* including four new species. Antonie van Leeuwenhoek 109, 877–894.
MycoBank. 2023 – MycoBank Database: Fungal Databases, Nomenclature & Species Banks. Available at: https://www.mycobank.org/
MycoBank. 2025 – MycoBank Database: Fungal Databases, Nomenclature & Species Banks. Available at: https://www.mycobank.org/
Mycological teaching diagrams by Meike Piepenbring. 2023 –. https://species-id.net/openmedia/Mycological_teaching_diagrams_by_Meike_Piepenbring#Ascomycota(Accessed on 29 August 2023).
Myllys L, Källersjö M, Tehler A. 1998 – A comparison of SSU rDNA data and morphological data in *Arthoniales* (*Euascomycetes*) phylogeny. Bryologist 101, 70–85.
Myllys L, Lohtander K, Källersjö M, Tehler A. 1999 – Applicability of ITS data in *Roccellaceae* (*Arthoniales*, *Euascomycetes*) phylogeny. The Lichenologist 31, 461–476.
Nag Raj TR. 1993 – Coelomycetous anamorphs with appendage bearing conidia. Mycologue publications, Waterloo 1–1101.
Nagarajan K, Tong WY, Leong CR, Tan WN. 2021 – Potential of Endophytic *Diaporthe* sp. as a New Source of Bioactive Compounds. Journal of Microbiology and Biotechnology 31(4), 493–500.
Nagel JH, Wingfield MJ, Slippers B. 2021 – Increased abundance of secreted hydrolytic enzymes and secondary metabolite gene clusters define the genomes of latent plant pathogens in the *Botryosphaeriaceae*. BMC Genomics 22, 589.
Nakagiri A, Ito T. 1997 – *Retrostium amphiroae* gen. et sp. nov. inhabiting a marine red alga, *Amphiroa zonata*. Mycologia 89(3), 484–493.

Nakagiri A. 1993 – A new marine ascomycete in *Spathulosporales*, *Hispidicarpomyces galaxauricola* gen. et sp. nov. (*Hispidicarpomycetaceae* fam. nov.), inhabiting a red alga, *Galaxaura falcata*. Mycologia 85(4), 638–652.
Nakai H, Nagashima K, Itazaki H. 1991 – Structure of a new cyclotetrapeptide trapoxin A. Acta Crystallographica Section C: Crystal Structure Communications 47, 1496–1499.
Nakamura H, Tateyama M, Tasato D, Haranaga S et al. 2009 – Clinical utility of serum β-D-glucan and KL-6 levels in *Pneumocystis jirovecii* pneumonia. Internal Medicine 48(4), 195–202.
Nambiar G, Raveendran K. 2009 – Marine mycoflora in backwater ecosystem of Kerala, India. Journal of Environmental Biology 30(5), 647–649.
Nambiar R, Raveendran K. 2015 – Identification of marine mycoflora in Amini Dweep of Lakshadweep islands. BIOINFOLET-A Quarterly Journal of Life Sciences 12, 518–520.
Nannfeldt J. 1932 – Studien über die Morphologie und Systematik der nichtlichenisierten inoperculaten Discomyceten. Nova Acta Regiae Societatis Scientiarum Upsaliensis 8, 1–368.
Nannfeldt JA. 1934 – Repert. mic. uomo. 498.
Nannfeldt JA. 1972 – *Camarops* Karst (*Sphaeriales–Boliniaceae*). Svensk Bot Tidskr 66, 335–376.
Nannfeldt JA. 1975 – Stray studies in the *Coronophorales* (*Pyrenomycetes*) 4-8. Svensk Botanisk Tidskrift 69, 289–335.
Nannizzi A. 1934 – Repertorio sistematico dei miceti dell'uomo e degli animali. SA Poligrafica Meini.
Napitupulu TP, Ramadhani I, Kanti A, Sudiana IM. 2021 – Diversity, phosphate solubilizing, and IAA production of culturable fungi associated with healthy and wilt banana. Archives of Phytopathology and Plant Protection 54 (19-20), 2306–2332.
Naranjo-Ortiz MA, Gabaldón T. 2019 – Fungal evolution: major ecological adaptations and evolutionary transitions. Biological Reviews of the Cambridge Philosophical Society 94(4), 1443–1476.
Narui T, Culberson CF, Culberson WL, Johnson A et al. 1996a – A contribution to the chemistry of the lichen family *Umbilicariaceae* (*Ascomycotina*). The Bryologist 99, 199–211.
Narui T, Takatsuki S, Sawada K, Okuyama T et al. 1996b – Lasallic acid, a tridepside from the lichen, *Lasallia asiae-orientalis*. - Phytochemistry 42(3), 839–842.
Nascimbene J, Nimis PL, Ravera S. 2013 – Evaluating the conservation status of epiphytic lichens of Italy: A red list. Plant Biosystems 147(4), 898–904.
Nash III TH. 2008 – Nitrogen, its metabolism and potential contribution to ecosystems. In Lichen Biology, Nash III TH (ed). Cambridge University Press. Cambridge 216–233.
Nash TH, Ryan BD, Diederich P, Gries C et al. (eds.). 2004 – Lichen Flora of the Greater Sonoran Desert Region. Lichens Unlimited, Arizona State University, Tempe, Arizona, U.S.A.
Nasr S, Bien S, Soudi MR, Alimadadi N et al. 2018 – Novel *Collophorina* and *Coniochaeta* species from *Euphorbia polycaulis*, an endemic plant in Iran. Mycological Progress 17, 755–771.
Navarro-Rosinés PRC, Bricaud O. 1998 – *Sarcopyrenia acutispora* Nav. Ros. et Cl. Roux sp. nov. nelikeniginta fungo likenloga (*Ascomycetes*, *Verrucariales*, *Sarcopyreniaceae* Nav.-Ros. et Cl. Roux fam. nov.). Bulletin de la Société linnéenne de Provence 49, 125–135.
Nawawi A, Kuthubutheen AJ. 1989 – *Canalisporium*, a new genus of lignicolous hyphomycetes from Malaysia. Mycotaxon 34(2), 475–487.
Nawawi A, Webster J. 1982 – *Phalangispora constricta* gen. et sp. nov., a sporodochial Hyphomycete with branched conidia. Transactions of the British Mycological Society 79(1), 65–68.
Nawrot-Chorabik K, Sułkowska M, Gumulak N. 2022 – Secondary metabolites produced by trees and fungi: achievements so far and challenges remaining. Forests 13, 1338.
Nayaka S, Upreti DK, Ingle KK. 2012 – Mangroves of India: Potential habitat for unique lichen flora. International Day for Biological Diversity – Marine Biodiversity (68–74). Lucknow, India: Uttar Pradesh State Biodiversity Board.
Nechet KL, Barreto RW, Mizubuti ESG. 2004 – *Sphaceloma poinsettiae* as a potential biological control agent for wild poinsettia (*Euphorbia heterophylla*). Biological Control 30, 556–565.

Nees von Esenbeck CGD. 1817 – Das System der Pilze und Schwämme. Ein Versuch von Dr. C.G. Nees von Esenbeck. Würzburg: Stahelschen Buchhandlung, 334.
Negash L. 1995 – Indigenous Trees of Ethiopia: Biology, Uses and Propagation Techniques. Umea, Sweden: SLU Reprocentralen.
Nel WJ, Duong TA, Wingfield BD, Wingfield MJ et al. 2018 – A new genus and species for the globally important, multihost root pathogen *Thielaviopsis basicola*. Plant Pathology 67, 871–882.

Nela WJ, Duongb TA, Wingfieldb BD, Wingfielda MJ et al. 2018 – A new genus and species for the globally important, multihost root pathogen *Thielaviopsis basicola*. Plant Pathology 67, 871–882.
Nelsen MP, Lücking R, Andrew CJ, Aptroot A et al. 2014a – Molecular phylogeny reveals the true colors of *Myeloconidaceae* (*Ascomycota*: *Ostropales*). Australian Systematic Botany 27(1), 38–47.
Nelsen MP, Lücking R, Aptroot A, Andrew CJ et al. 2014b – Elucidating phylogenetic relationships and genus-level classification within the fungal family *Trypetheliaceae* (*Ascomycota*: *Dothideomycetes*). Taxon 63(5), 974–992.
Nelsen MP, Lücking R, Grube M, Mbatchou JS et al. 2009 – Unravelling the phylogenetic relationships of lichenised fungi in *Dothideomyceta*. Studies in Mycology 64, 135–144.
Nelsen MP, Lücking R, Mbatchou JS, Andrew CJ et al. 2011a – New insights into relationships of lichen– forming *Dothideomycetes*. Fungal Diversity 51, 155–162.
Nelsen MP, Lücking R. Cáceres MES. Aptroot A et al. 2017 – Assessing the phylogenetic placement and redundancy of *Aspidotheliaceae* (*Ascomycota*), an orphaned family of lichen-forming fungi. Systematics and Biodiversity 15(1), 63–73.
Nelsen MP, Rivas Plata E, Andrew CJ, Lücking R et al. 2011b – Phylogenetic diversity of trentepohlialean algae associated with lichen–forming fungi. Journal of Phycology 47, 282–290.
Nelson S. 2008. – Sooty molds. Plant Disease 52, 1–6.
Németh C, Eckstein J. 2018 – *Vezdaea retigera* (*Vezdaeaceae*), a facultatively epibryophytic lichenized fungus new to Hungary. Studia botanica hungarica 49, 41–46.
Netherer S, Kandasamy D, Jirosová A, Kalinová B et al. 2021 – Interactions among Norway spruce, the bark beetle *Ips typographus* and its fungal symbionts in times of drought. Journal of Pest Science 94, 591–614.
Neuwirth G. 2014 – Revision of the lichen genus *Candelaria* (*Ascomycota*, *Candelariales*) in Upper Austria. Stapfia 101, 39–46.
Newcombe G. 2003 – Native *Venturia inopina* sp. nov., specific to *Populus trichocarpa* and its hybrids. Mycological Research 107, 108–116.
Nguyen HT, Kim S, Yu NH, Park AR et al. 2019 − Antimicrobial activities of an oxygenated cyclohexanone derivative isolated from *Amphirosellinia nigrospora* JS-1675 against various plant pathogenic bacteria and fungi. Journal of Applied Microbiology 126(3), 894−904.
Nguyen KH, Chollet-Krugler M, Gouault N, Tomasi S. 2013 – UV-protectant metabolities from lichen and their symbiotic partners. Natural Product Reports 30 (2013), 1490–1508.
Nguyen TTT, Kang KH, Kim DH, Kim SJ et al. 2023 – Additions to the knowledge of the fungal order *Eurotiales* in Korea: eight undescribed species. Mycobiology 51, 417–435.
Niego AG, Rapior S, Thongklang N, Raspé O et al 2023a – Reviewing the contributions of macrofungi to forest ecosystem processes and services. Fungal Biology Reviews 44, 100294.
Niego AGT, Lambert C, Mortimer P, Thongklang N et al. 2023b – The contribution of fungi to the global economy. Fungal Diversity 121, 95–137.
Nielsen JC, Grijseels S, Prigent S, Ji B et al. 2017 – Global analysis of biosynthetic gene clusters reveals vast potential of secondary metabolite production in *Penicillium* species. Nature Microbiology 2, 17044.

Niessl G. 1876 – Notizen über neue und kritische Pyrenomyceten. Verhandlungen des Naturforschenden Vereines in Brünn 14, 165–218.
Nilsson RH, Sánchez-García M, Ryberg MK, Abarenkov K et al. 2017 – Read quality based trimming of the distal ends of public fungal DNA sequences is nowhere near satisfactory. MycoKeys 26, 13–24.
Nimis PL, Hafellner J, Roux C, Clerc P et al. 2018 – The lichens of the Alps – an annotated checklist. MycoKeys 31, 1–634.
Nimis PL, Poelt J, Puntillo D. 1989 – *Candelariella faginea* spec. nov. (Lichenes, *Candelariaceae*) eine bemerkenswerte neue Art einer schwierigen Gattung aus Sudeuropa. Nova Hedwigia 49(3–4), 274–280.
Nimis PL. 1998 – A critical appraisal of modern generic con-cepts in lichenology. Lichenologist 30, 427–438.
Nimis PL. 2016 – The lichens of Italy. A second annotated catalogue. EUT Edizioni Università di Trieste.
Nishi M, Okano I, Sawada T, Hara Y et al. 2018 – Chronic *Kirschsteiniothelia* infection superimposed on a pre-existing non-infectious bursitis of the ankle: the first case report of human infection. BMC Infectious Diseases 18(1), 1–5.
Nishida H, Ando K, Ando Y, Hirata A et al. 1995 – *Mixia osmundae*: transfer from the *Ascomycota* to the *Basidiomycota* based on evidence from molecules and morphology. Canadian Journal of Botany 73, S660–S666.
Nishida H, Blanz PA, Sugiyama J. 1993 – The higher fungus *Protomyces inouyei* has two group I introns in the 18S rRNA Gene. Journal of Molecular Evolution 37(1), 25–28.
Nishida H, Sugiyama J. 1994 – *Archiascomycetes*: detection of a major new lineage within the *Ascomycota*. Mycoscience 35(4), 361–366.
Nitare J. 1982 – *Geoglossum arenarium*, sandjordtunga – ekologi och utbredning I Sverige. Svensk Botanisk Tidskrift 76, 349–357.
Nitare J. 1988 – Jordtungor, en svampgrupp pa tillbakagang i naturliga fodermarker. Svensk botanisk tidskrift 5(82), 341–368.
Nitschke TH. 1867 – *Pyrenomycetes* Germanici. Breslau.
Niu DL, Wang LS, Zhang YJ, Yang CR. 2008 – *Acroscyphus sphaerophoroides* (lichenized *Ascomycota*, *Caliciaceae*) in Hengduanshan Mountains. Biochemical Systematics and Ecology 36(5–6), 423–429.
Niu S, Si L, Liu D, Zhou A et al. 2016 – Spiromastilactones: A new class of influenza virus inhibitors from deep-sea fungus. European Journal of Medicinal Chemistry 108, 229–244.
Niu X, Al-Hatmi AM, Vitale RG, Lackner M et al. 2024 – Evolutionary trends in antifungal resistance: a meta-analysis. Microbiology Spectrum 12, e02127–02123.
Niu Y, Wei JC. 1993 – Variations in ITS2 sequences of nuclear rDNA from two *Lasallia* species and their systematic significance. Mycosystema 6, 25–29.
Noda H, Kodama K. 1996 – Phylogenetic position of yeastlike endosymbionts of anobiid beetles. Applied and Environmental Microbiology 62, 162–167.
Nokes LF, Haelewaters D, Pfister DH. 2022 – Exploration of marine lichenized fungi as bioindicators of coastal ocean pollution in the Boston Harbor Islands National Recreation Area. Rhodora 122(992), 251–273.
Noppawan S, Mongkolthanaruk W, Suwannasai N, Senawong T et al. 2020 − Chemical constituents and cytotoxic activity from the wood-decaying fungus *Xylaria* sp. SWUF08-37. Natural Product Research 34, 464–73.
Nordén B, Sunhede S, Larsson E. 2005 – New species of *Moristroma* (*Ascomycetes*) and phylogenetic position of the genus. Mycological Progress 4, 325–332.
Norphanphoun C, Gentekaki E, Hongsanan S, Jayawardena R et al. 2022 – *Diaporthe*: formalizing the species-group concept. Mycosphere 13(1), 752–819.
Norphanphoun C, Hongsanan S, Doilom M, Bhat DJ et al. 2016 – *Lamproconiaceae* fam. nov. to accommodate *Lamproconium desmazieri*. Phytotaxa 270, 89–102.

Norphanphoun C, Jeewon R, Mckenzie EHC, Wen TC et al. 2017 – Taxonomic position of *Melomastia italica* sp. nov. and phylogenetic reappraisal of *Dyfrolomycetales*. Cryptogamie, Mycologie 38, 507–525.
Norros V, Rannik Ü, Hussein T, Petäjä T et al. 2014 – Do small spores disperse further than large spores? Ecology 95, 1612–1621.
Nosanchuk JD, Casadevall A. 2006 – Impact of Melanin on Microbial Virulence and Clinical Resistance to Antimicrobial Compounds. Antimicrob Agents Chemother 50(11), 351928.
Nouri MT, Lawrence DP, Holland LA, Doll DA et al. 2019 – Identification and pathogenicity of fungal species associated with canker diseases of pistachio in California. Plant Disease 103, 2397–2411.
Nouri MT, Lawrence DP, Yaghmour MA, Michailides TJ et al. 2018 – *Neoscytalidium dimidiatum* causing canker, shoot blight and fruit rot of almond in California. Plant Disease 102, 1638–1647.
Nugent LK, Sihanonth P, Thienhirun S, Whalley AJ. 2005 – *Biscogniauxia*: a genus of latent invaders. Mycologist 19(1), 40–43.
Nukina M. 1987 – Pyrichalasin H, a new phytotoxic metabolite belonging to the cytochalasans from *Pyricularia grisea* (Cooke) Saccardo. Agricultural and Biological Chemistry 51(9), 2625–2628.
Nukina M. 1988 – Terrestric acid as a phytotoxic metabolite from *Pyricularia oryzae* Cavara. Agricultural and Biological Chemistry 52(9), 2357–2358.
Nurse P, Thuriaux P, Nasmyth K. 1976 – Genetic control of the cell division cycle in the fission yeast *Schizosaccharomyces pombe*. Molecular and General Genetics MGG 146, 167–178.
Nurse P. 1994 – Ordering S phase and M phase in the cell cycle. Cell 79(4), 547–550.
Nutaratat P, Boontham W, Khunnamwong P. 2022 – A novel yeast genus and two novel species isolated from pineapple leaves in Thailand: *Savitreella phatthalungensis* gen. nov., sp. nov. and *Goffeauzyma siamensis* sp. nov. Journal of Fungi 8(2).
Nylander W. 1853 – Lichenes algerienses novi. Annales des Sciences Naturelles. Botanique. sér. 3, 20, 315–320.
Nylander W. 1854 – Essai d'une nouvelle classification des Lichens. Mémoires de la Société Impériale des Sciences Naturelles de Cherbourg 2, 5–16.
Nylander W. 1855 – Essai d'une nouvelle classification des lichens. 2. Mémoire. - Mém. Soc. Sci. Nat. Cherbourg 3, 161–194.
Nylander W. 1862 – *Tylophoron* et *Parathelium* genera Lichenum nova. Bot. Zeitung (Berlin) 20, 278–279.
Nylander W. 1862–1863 – Lichenographiae Novo-Granatensis Prodro- mus. Acta Soc. Sci. Fenn. 7, 417–504.
Nylander W. 1869 – De reactionibus in genere Umbilicaria. Flora (Regensburg) 52: 387–389.
Nylander W. 1874 – Addenda nova ad Lichenographiam europaeam. Continuatio septima decima. Flora (Regensburg) 57, 6–16.
Nylander W. 1876 – Collemacei, Caliciei, Cladoniei et Thelo- tremei Cubani novi. Flora 59, 558–562.
O'Brien HE, Miadlikowska J, Lutzoni F. 2013 – Assessing population structure and host specialization in lichenized cyanobacteria. New Phytologist 198(2), 557–566.
O'Connell RJ, Thon MR, Hacquard S, Amyotte SG et al. 2012 – Lifestyle transitions in plant pathogenic *Colletotrichum* fungi deciphered by genome and transcriptome analyses. Nature Reviews Microbiology 10(7), 478–494.
Ogaki MB, Vieira R, Muniz MC, Zani CL et al. 2020 – Diversity, ecology, and bioprospecting of culturable fungi in lakes impacted by anthropogenic activities in Maritime Antarctica. Extremophiles 24, 637–655.
Ogórek R, Kurczaba K, Cal M, Apoznański G et al. 2020 – Culture-based ID of *Micromycetes* on the Wing Membranes of Greater Mouse-Eared Bats (Myotis myotis) from the "Nietoperek" Site (Poland). Animals 10(8), 1337.

Oh DC, Scott JJ, Poulsen M, Currie CR et al. 2008 – Discovery of new secondary metabolites mediating insect-microorganism symbioses. Planta Medica 74, SL2.
Oh SY, Woo JJ, Hur JS. 2019 – Distribution of foliicolous lichen *Strigula* and genetic structure of *S. multiformis* on Jeju Island, South Korea. Microorganisms 7, 430.
Oh SY, Yang JH, Woo JJ, Oh SO et al. 2020 − Diversity and distribution patterns of endolichenic fungi in Jeju Island, South Korea. Sustainability 12(9), 3769.
Ohenoja E. 1995 – Occurrence of *Geoglossum*, *Trichoglossum* and *Microglossum* (*Ascomycota*, *Leotiales*) in Finland. Documents Mycologiques 25(98–100), 285–294.
Ohmura Y, Sugimoto M, Yakovchenko L, Davydov EA. 2022 – Additional Species and ITS rDNA data for the lichen mycota of the Imperial Palace Grounds, Tokyo, Japan. Bulletin of the National Museum of Nature and Science, Series B, Botany 48(1), 1–16.
Ohnuki T, Yano T, Furukawa Y, Takatsu T. 2009 – Haplofungins, novel inositol phosphorylceramide synthase inhibitors, from *Lauriomyces bellulus* SANK 26899 III. Absolute structure of haplofungin A. The Journal of Antibiotics 62(10), 559–563.
Okane I, Nakagiri A, Ito T. 2003 – Endophytic fungal diversity in Japanese deciduous forests. Mycoscience 44(5), 369–378.
Okeke BC, Obi SK. 1992 – Preliminary studies on a xylanase from an *Arthrographis* species. FEMS Microbiology Letters 96(1), 43–47.
Olariaga I, Teres J, Martín J, Prieto M et al. 2019 – *Pseudosclerococcum golindoi* gen. et sp. nov., a new taxon with apothecial ascomata and a *Chalara*-like anamorph within the *Sclerococcales* (*Eurotiomycetes*). Mycological Progress 18, 895–905.
Old KM, Wingfield MJ, Yuan ZQ. 2003 – A manual of diseases of eucalyptus in South-East Asia, 106.
Olech M, Słaby A. 2016 – Changes in the lichen biota of the Lions Rump area, King George Island, Antarctica, over the last 20 years. Polar Biology 39, 1499–1503.
Oono R, Lutzoni F, Arnold AE, Kaye L et al. 2014 – Genetic variation in horizontally transmitted fungal endophytes of pine needles reveals population structure in cryptic species. American Journal of Botany 101(8), 1362–1374.
Orange A. 1991 – *Thelidium pluvium* (*Verrucariaceae*), a new lichenized species from north-west Europe. The Lichenologist 23, 99–106.
Orpurt PA, Meyers SP, Boral LL, Sims J. 1964 – *Thalassiomycetes* V. A new species of Lindra from turtle grass, *Thalassia testudinum* König. Bulletin of Marine Science 14, 405–417.
Ortiz-García S, Gernandt DS, Stone JK, Johnston PR et al. 2003 – Phylogenetics of *Lophodermium* from pine. Mycologia 95, 846−859.
Orton CR. 1924 – Studies in the morphology of the *Ascomycetes* I. The stroma and the compound fructification of the *Dothideaceae* and other groups. Mycologia 16, 49–95.
Osorio M. 1985 – *Ceratocystis pilifera*, hongo causante de mancha azul en madera de Pinus radiata. Bosque (Valdivia) 6(2), 116–119.
Ostry ME, Anderson NA. 2009 − Genetics and ecology of the *Entoleuca mammata-Populus pathosystem*: Implications for aspen improvement and management. Forest Ecology and Management 257, 390−400.
Otálora MA, Aragón G, Martínez I, Wedin M. 2013 – Cardinal characters on a slippery slope–a re-evaluation of phylogeny, character evolution, and evolutionary rates in the jelly lichens (*Collemataceae* s. str). Molecular Phylogenetics and Evolution 68(2), 185–198.
Otálora MA, Martínez I, O'Brien H, Molina MC et al. 2010 – Multiple origins of high reciprocal symbiotic specificity at an intercontinental spatial scale among gelatinous lichens (*Collemataceae*, *Lecanoromycetes*). Molecular Phylogenetics and Evolution 56(3): 1089–1095.
Otašević B, Krmar J, Đajić N, Ignjatović J et al. 2020 – Chemometric window to antimicrobial activity of biomolecules isolated from endophytic fungi. Archives of Pharmacy, 70(Notebook 3), 142–156.

Ott S, Brinkmann M, Wirtz N, Lumbsch HT. 2004 – Mitochondrial and nuclear ribosomal DNA data do not support the separation of the Antarctic lichens *Umbilicaria kappeni* and *Umbilicaria antarctica* as distinct species. The Lichenologist 36, 227–234.
Ott S, Lumbsch HT. 2001 – Morphology and phylogeny of acomycete lichens. In The Mycota. Vol. IX. Fungal Associations (B. Hock, ed.), 189–210. Springer-Verlag, Berlin.
Otte V, Yakovchenko L, Clerc P, Westberg M. 2013 – *Candelariella commutata* sp. nov. for *C. unilocularis* auct. medioeur. – an arctic-alpine lichen on calcareous substrata from the Caucasus and Europe. Herzogia 26, 217–222.
Ouellette GB. 1966 – On Thyriopsis halepensis and its conidial stage. Mycologia 58(2), 322–325.
Ouoba LII, Kando C, Parkouda C, Sawadogo-Lingani H et al. 2012 – The microbiology of Bandji, palm wine of *Borassus akeassii* from Burkina Faso: identification and genotypic diversity of yeasts, lactic acid and acetic acid bacteria. Journal of Applied Microbiology 113(6), 1428–1441.
Øvstedal DO, Lewis Smith RI. 2009 – Further additions to the lichen flora of Antarctica and South Georgia. Nova Hedwigia 88(1–2), 157–168.
Ozenda P, Clauzade G. 1970 – Les Lichens. Etude Biologique et Flore Illustree. Masson & Cie, Belgique.
Padaruth OD. 2023 – *Jobellisiaceae* - Facesoffungi number: FoF 01906. Faces Of Fungi. Retrieved 1 July 2023.
Paden JW. 1967 – The conidial state of *Peziza brunneoatra*. Mycologia 59, 932–934.
Palencarova E, Jesenska Z, Plank L, Traka SS et al. 1995 – *Phaeohyphomycosis* caused by *Alternaria* species and *Phaeosclera dematioides* Sigler, Tsuneda and Carmichael. Clinical and experimental dermatology 20(5), 419–422.
Palmer ME, Covich AP, Finlay BJ, Gilbert J et al. 1997 – Biodiversity and ecosystem processes in freshwater sediments. Ambio 26, 571–577.
Pan L. 1994 – The symptoms of five grape disease and main control methods. Bulletin of Agricultural Science and Technology 1, 27–28.
Pang KL, Abdel-Wahab MA, Sivichai S, El-Sharouney HM et al. 2002 – *Jahnulales* (*Dothideomycetes*, *Ascomycota*): A new order of lignicolous freshwater *Ascomycetes*. Mycological Research 106.
Pang KL, Guo SY, Aisyah Alias S, Hafellner J et al. 2014 – A new species of marine *Dactylospora* and its phylogenetic affinities within the *Eurotiomycetes*, *Ascomycota*. Botanica Marina 57(4), 315–321.
Pang KL, Guo SY, Shaumi A, Suetrong S et al. 2023 – *Lanspora dorisauae*, a new marine fungus from rocky shores in Taiwan. PeerJ, 11, e15958.
Pang KL, Hassett BT, Shaumia A, Guo SY et al. 2021 – Pathogenic fungi of marine animals: A taxonomic perspective. Fungal Biology Reviews 38, 92–106.
Pang KL, Hyde KD, Alias SA, Suetrong S et al. 2013 – *Dyfrolomycetaceae*, a new family in the *Dothideomycetes*, *Ascomycota*. Cryptogamie, Mycologie 34, 223–232.
Parbery DG, Langdon RFN. 1964 – Studies on graminicolous species of *Phyllachora* FCKL. IV. Evaluation of the criteria of species. Australian Journal of Botany 12, 265–281.
Parbery DG. 1963a – Studies on graminicolous species of *Phyllachora* Fckl. I. Ascospores--their liberation and germination. Australian Journal of Botany 11, 117–130.
Parbery DG. 1963b – Studies on graminicolous species of *Phyllachora* Fckl. II. Invasion of the host and development of the fungus. Australian Journal of Botany 11, 131–140.
Parbery DG. 1964 – Studies on graminicolous species of *Phyllachora* Fckl. IV. Evaluation of the criteria of species. Australian Journal of Botany 12, 265–281.
Parbery DG. 1978 – *Phyllachora*, *Linochora* and hyperparasites. Taxonomy of Fungi 1, 263–277.
Parbery DG. 1996 – Spermatial states of fungi are andromorphs. Mycological Research 100, 1400.
Park H, Lee S, Park N. 2021 – Phylogenetic Analysis on Wild *Cordyceps* Collected from Miryang Region of South Korea. Korean Journal of Plant Resources 34(1), 1–16.

Parmasto E. 2009 – Red data list of Estonian fungi 2008. Official Estonian Red List authorized by Minister of the Environment of the Estonian Republic.
Pärtel K, Baral HO, Tamm H, Põldmaa K. 2017 – Evidence for the polyphyly of *Encoelia* and *Encoelioideae* with reconsideration of respective families in *Leotiomycetes*. Fungal Diversity 82, 183–219.
Paruya DK, Ghosh R, Bismas O, Bera M et al. 2017 – Dispersed fungal remains from the Neogene Siwalik forest of sub Himalayan Arunachal Pradesh, India and their palaeoenvironmental indicative values. Journal of Mycopathological Research 55, 303–307.
Pascoe IG, Smith IW, Dinh SQ, Edwards J. 2018 – *Caliciopsis pleomorpha* sp. nov. (*Ascomycota*: *Coryneliales*) causing a severe canker disease of *Eucalyptus cladocalyx* and other eucalypt species in Australia. Fungal Systematics and Evolution 2(1), 45–56.
Patjana T, Jantaharn P, Katrun P, Mongkolthanaruk W et al. 2021 – Anti-inflammatory and cytotoxic agents from *Xylaria* sp. SWUF09-62 fungus. Natural Product Research 35(12), 2010–9.
Patouillard NT, De Lagerheim G. 1895a – Champignons de l'Équateur (Pugillus IV). Bulletin de l'Herbier Boissier 3, 1, 53–74.
Patouillard NT, Lagerheim Gd. 1895b – Champignons de l'Équateur (Pugillus V). Bulletin de la Société Mycologique de France 11, 205–234.
Pautasso M, Döring TF, Garbelotto M, Pellis L et al. 2012 – Impacts of climate change on plant diseases–opinions and trends. European Journal of Plant Pathology 133, 295–313.
Pawłowska J, Istel Ł, Gorczak M, Galera H et al. 2017 – *Psychronectria hyperantarctica*, gen. nov., comb. nov., epitypification and phylogenetic position of an Antarctic bryophilous ascomycete. Mycologia 109(4), 601–607.
Payen T, Murat C, Bonito G. 2014 – Truffle phylogenomics: new insights into truffle evolution and truffle life cycle. In Advances in Botanical Research 70, 211–234.
Paz-Bermúdez G, Calvino-Cancela M, López de Silanes ME, Prieto B. 2021 – Lichen saxicolous communities on granite churches in Galicia (NW Spain) as affected by the conditions of north and south orientations. The Bryologist 124(3), 414–428.
Pažoutová S, Follert S, Bitzer J, Keck M et al. 2013 – A new endophytic insect-associated *Daldinia* species, recognised from a comparison of secondary metabolite profiles and molecular phylogeny. Fungal Diversity 60, 107–23.
Pearce CA, Hyde KD. 2006 – *Phyllachoraceae* of Australia. Fungal Diversity Press, Hong Kong.
Pedra NS, Canuto KM, de Queiroz Souza AS, Ribeiro PR et al. 2023 – Endophytic fungus of *Achyrocline satureioides*: molecular identification, chemical characterization, and cytotoxic evaluation of its metabolites in human melanoma cell line. Applied Biochemistry and Biotechnology 18, 1–25.
Peinter U, Knapp M, Fleischer V, Walch G et al. 2016 – *Myrmecridium hiemale* sp. nov. from snow-covered alpine soil is the first eurypsychrophile in this genus of anamorphic fungi. The International Journal of Systematic and Evolutionary Microbiology 66, 2592–2598.
Pem D, Gafforov Y, Jeewon R, Hongsanan S et al. 2018 – Multigene phylogeny coupled with morphological characterization reveal two new species of *Holmiella* and taxonomic insights within *Patellariaceae*. Cryptogamie, Mycologie 39(2), 193–209.
Pem D, Hyde KD, Doilom M, Camporesi E. 2019a – Multigene phylogenetic analyses to establish new *Valsaria* species and taxonomic significance of spore ornamentation. PLoS ONE 14(6), e0217982.
Pem D, Hyde KD, McKenzie EHC, Hongsanan S et al. 2024 – A comprehensive overview of genera in *Dothideomycetes*. Mycosphere 15(1), 2175–4568.
Pem D, Jeewon R, Bhat DJ, Doilom M et al. 2019b – Mycosphere Notes 275-324: A morphotaxonomic revision and typification of obscure *Dothideomycetes* genera (*incertae sedis*). Mycosphere 10(1), 1115–1246.
Pem D, Jeewon R, Chethana KWT, Hongsanan S et al. 2021 – Species concepts of *Dothideomycetes*: classification, phylogenetic inconsistencies and taxonomic standardization. Fungal Diversity 109, 283–319.

Peng J, Chang D, Huang Y, Yu ZF. 2016 – *Nawawia oviformis* sp. nov. from China. Mycotaxon 131, 735–738.
Peng J, Lin T, Wang W, Xin Z et al. 2013 – Antiviral alkaloids produced by the mangrove derived fungus *Cladosporium* species. PJX – 41, Journal of Natural Products 76(6), 1133–1140.
Peng T, Lu YZ, Bai S, Zhang JY et al. 2025 – Novel *Helicosporium* and *Neohelicomyces* (*Tubeufiaceae*, *Tubeufiales*) species from terrestrial habitats in China and Thailand. MycoKeys 112, 81.
Peng XJ, Wang QC, Zhang SK, Guo K, Zhou XD 2023 – *Colletotrichum* species associated with Camellia anthracnose in China. Mycosphere 14(2), 130–157.
Penzig AJO, Saccardo PA. 1902 – Diagnoses fungorum novorum in insula Java collectorum. Series Tertia. Malpighia 15, 201–260.
Perdomo H, García D, Gené J, Cano J et al. 2013 – *Phialemoniopsis*, a new genus of *Sordariomycetes*, and new species of *Phialemonium* and *Lecythophora*. Mycologia 105(2), 398–421.
Perdomo H, Sutton DA, García D, Fothergill AW et al. 2011 – Molecular and phenotypic characterization of *Phialemonium* and *Lecythophora* isolates from clinical samples. Journal of Clinical Microbiology 49(4), 1209–1216.
Perera RH, Maharachchikumbura S, Jones EBG, Bahkali AH et al. 2017 – *Delonicicola siamense* gen. & sp. nov. (*Delonicicolaceae* fam. nov., *Delonicicolales* ord. nov.), a saprobic species from *Delonix regia* seed pods. Cryptogamie, Mycologie 38, 321–340.
Perera RH, Maharachchikumbura SS, Bhat JD, Al-Sadi AM et al. 2016a– New species of *Thozetella* and *Chaetosphaeria* and new records of *Chaetosphaeria* and *Tainosphaeria* from Thailand. Mycosphere 7(9), 1301–1321.
Perera RH, Maharachchikumbura SSN, Ariyawansa HA, Bahkali AH et al. 2016b – Two new *Pseudohalonectria* species on beech cupules (*Fagus sylvatica*) and a new genus to accommodate *P. suthepensis*. Phytotaxa 278, 115–131.
Pérez LI, Gundel PE, Ghersa CM, Omacini M. 2013 – Family issues: fungal endophyte protects host grass from the closely related pathogen *Claviceps purpurea*. Fungal Ecology 6(5), 379–386.
Pérez-Ortega S, Etayo J, Elix JA, Crespo A 2011a – A new species of *Zwackhiomyces* (*Xanthopyreniaceae*, *Ascomycota*) growing on *Austroparmelina* from Australia. Nova Hedwigia 93(3), 395–400.
Perez-Ortega S, Etayo J. 2010 – *Labrocarpon* gen. nov. for *Melaspilea canariensis*, with the description of *Buelliella protoparmeliopsis* sp. nov. from South America. The Lichenologist 42(3), 271–276.
Pérez-Ortega S, Garrido-Benavent I, Grube M, Olmo R et al. 2016 – Hidden diversity of marine borderline lichens and a new order of fungi: *Collemopsidiales* (*Dothideomyceta*). Fungal Diversity 80, 285–300.
Pérez-Ortega S, Suija A, Crespo A, de los Ríos A. 2014 – Lichenicolous fungi of the genus *Abrothallus* (*Dothideomycetes*: *Abrothallales* ordo nov.) are sister to the predominantly aquatic *Janhulales*. Fungal Diversity 64, 295–304.
Pérez-Ortega S, Suija A, de los Ríos A. 2011b – The connection between *Abrothallus* and its anamorph state Vouauxiomyces established by Denaturing Gradient Gel Electrophoresis (DGGE). The Lichenologist 43, 277–279.
Pérez-Victoria I, Martin J, Gonzalez-Menendez V, de Pedro N et al. 2012 – Isolation and structural elucidation of cyclic tetrapeptides from *Onychocola sclerotica*. Journal of natural products 75(6), 1210–1214.
Perlmutter G. 2009 – Measuring the effects of air quality with lichens. Newsletter of the North Carolina Native Plant Society 7(1), 1.
Perreau M, Haelewaters D, Tafforeau P. 2021 – A parasitic coevolution since the Miocene revealed by phase-contrast synchrotron X-ray microtomography and the study of natural history collections. Scientific Reports 11(1), 2672.

Perrone G, Susca A. 2017 – *Penicillium* Species and Their Associated Mycotoxins. Mycotoxigenic Fungi: Methods and Protocols 1542, 107–119.
Peršoh D, Beck A, Rambold G. 2004 – The distribution of ascus types and photobiontal selection in *Lecanoromycetes* (*Ascomycota*) against the background of a revised SSU nrDNA phylogeny. Mycological Progress 3(2), 103–121.
Peršoh D, Rambold G. 2012 – Lichen-associated fungi of the *Letharietum vulpinae*. Mycological Progress 11, 753–760.
Persoon CH. 1794a – Einige Bemerkungen u¨ ber die Flechten: Nebst Beschreibungen einiger neue Arten aus dieser Familie der Aftermoose. Uster's Annalen der Botanick 7, 1–36.
Persoon CH. 1794b – Neuer Veersuch einer systematischen Eintheilung der Schwamme (Dispositio methodica fungorum). Romer's News Mag. Bot. 1, 63–128.
Persoon CH. 1797 – Tentamen dispositionis methodicae fungorum. - P. P. Wolf, Lipsiae, 76 pp.
Persoon CH. 1801 – Synopsis methodica fungorum. Sistens enumerationem omnium huc usque detectarum specierum, cum brevibus descriptionibus nec non. Pars secunda. – Gottingae: Henricum Dieterich, 241–706.
Persoon CH. 1822–1828 – Mycologia europea seu completa omnium fungorum in variis europaeae regionibus detectorium enumeratio, methodo naturali disposita; descriptione succincta, synonymia selecta et observationibus criticus additis. Sectio prima [-tertia]. – Erlangae: Joann Jacob Palm.
Petersen C, Sørensen T, Nielsen MR, Sondergaard TE et al. 2023 – Comparative genomic study of the *Penicillium* genus elucidates a diverse pangenome and 15 lateral gene transfer events. IMA Fungus 14, 3.
Petrak F. 1914 – Beiträge zur Pilzflora von Mähren und Österr. Schlesien: éditeur non identifié.
Petrak F. 1921 – Mykologische Beitr€age I. Hedwigia 62, 282–319.
Petrak F. 1924 – MykologischeNotizen. VII. Annales Mycologici 22, 1–182.
Petrak F. 1927 – MykologischeNotizen. IX. Annales Mycologici 25, 193–343.
Petrak F. 1928 – Über *Bagnisiopsis* und verwandte Gattungen. Hedwigia 68, 251–290.
Petrak F. 1947 – ÜberGibbera Fr. und verwandteGattungen. Sydowia 1, 169–201.
Petrak F. 1950 – Index of fungi 1936–1939. Commonwealth Mycological Institute, Kew.
Petrini O, Carroll G. 1981 – Endophytic fungi in foliage of some *Cupressaceae* in Oregon. Canadian Journal of Botany 59, 629–636.
Petrini O, Hake U, Dreyfuss M. 1990 – An analysis of fungal communities isolated from fruticose lichens. Mycologia 82, 444–451.
Petrini O, Samuels GJ, Müller E. 1979 – *Holmiella sabina* (de Not.) comb. nov. (syn. *Eutryblidiella sabina*) and its *Cornicularia*-like anamorph, an endophyte of *Juniperus* species. Bericht der Schweizerischen Botanischen Gesellleschaft 89, 80–90.
Pfister D, Kimbrough JW. 2000 – "*Discomycetes*". In Mclaughlin DJ, McLaughlin EG, Lemke PA (eds.). The Mycota VII Part A. Systematics and Evolution. Berlin: Springer, 257–81.
Pfister DH, Healy R. 2021 – *Pezizomycetes*. In: Zaragoza, O. (ed) Encyclopedia of Mycology. Oxford: Elsevier 1, 295–309.
Pfister DH. 1984 – Two new localities for *Medeolaria farlowii* in New England. Rhodora 86, 235–236.
Pfister DH. 1994 – *Orbilia fimicola*, a nematophagous discomycete and its *Arthrobotrys* anamorph. Mycologia 86, 451–453.
Pfister DH. 1997 – Castor, pollux and life histories of fungi. Mycologia 89, 1–23.
Pfister DH. 2015 – *Pezizomycotina*: *Pezizomycetes*, *Orbiliomycetes*. Systematics and Evolution: Part B 35–55.
Pfliegler WP, Bathori F, Wang TW, Tartally A et al. 2018 – *Herpomyces* ectoparasitic fungi (*Ascomycota*, *Laboulbeniales*) are globally distributed by their invasive cockroach hosts and through the pet trade industry. Mycologia 110, 39–46.
Phadtare NR. 1989 – Palaeoecologic significance of some fungi from the Miocene of Tanakpur (U.P.) India. Review of Palaeobotany and Palynology 59, 127–131.

Phillips AJ, Hyde KD, Alves A, Liu JK. 2019 – Families in *Botryosphaeriales*: a phylogenetic, morphological and evolutionary perspective. Fungal Diversity 94(1), 1–22.
Phillips AJL, Alves A, Abdollahzadeh J, Slippers B et al. 2013a – The *Botryosphaeriaceae*: genera and species known from culture. Studies in Mycology 76, 51–167.
Phillips AJL, Lopes J, Abdollahzadeh J, Bobev S et al. 2012 – Resolving the *Diplodia* complex on apple and other *Rosaceae* hosts. Persoonia 29, 29–38.
Phillips AJL, Slippers B, Groenewald JZ, Crous PW. 2013b – Plant pathogenic and endophytic *Botryosphaeriales* known from culture. Studies in Mycology 76, 1–167.
Phillips AJL. 1994 – A comparison of methods for inoculating bean plants with *Elsinoë phaseoli* and some factors affecting infection. Annals of Applied Biology 125, 97–104.
Phillips CJ, Rember WC. 2004 – Epiphyllous fungi from the Miocene of Clarkia, Idaho: reproductive structures. Review of Palaeobotany and Palynology 129, 67–79.
Phookamsak R, Hyde KD, Jeewon R, Bhat DJ et al. 2019 – Fungal diversity notes 929–1035: taxonomic and phylogenetic contributions on genera and species of fungi. Fungal Diversity 95, 1–273.
Phookamsak R, Li WJ, Dai DQ, Singtripop C et al. 2015 – *Poaceascoma* gen et sp. nov., a new genus with scolecospores in *Lentitheciaceae*. Cryptogamie, Mycologie 36, 225–236.
Phukhamsakda C, Hongsanan S, Ryberg M, Ariyawansa HA et al. 2016 – The evolution of *Massarineae* with *Longipedicellataceae* fam. nov. Mycosphere 7, 1713–1731.
Phukhamsakda C, Mckenzie EH, Phillips AJ, Gareth Jones E et al. 2020 – Microfungi associated with *Clematis* (*Ranunculaceae*) with an integrated approach to delimiting species boundaries. Fungal Diversity 102, 1–203.
Phukhamsakda C, Nilsson RH, Bhunjun CS, de Farias AR et al. 2022 – The numbers of fungi: Contributions from traditional taxonomic studies and challenges of metabarcoding. Fungal Diversity 114(1), 327–86.
Piątek M, Stryjak-Bogacka M, Czachura P. 2024 – *Arthrocatenales*, a new order of extremophilic fungi in the *Dothideomycetes*. MycoKeys108, 47.
Pichova K, Pažoutova S, Kostovčik M, Chudičkova M et al. 2018 – Evolutionary history of ergot with a new infrageneric classification (*Hypocreales*: *Clavicipitaceae*: *Claviceps*). Molecular Biology and Evolution 123, 73–87.
Piepenbring M, Hofmann T, Kirschner R, Mangelsdorff R et al. 2011 – Diversity patterns of neotropical plant parasitic microfungi. Ecotropica 17, 27–40.
Piepenbring M, Maciá Vicente J, Evans Codija J, Glatthorn C et al. 2020 – Mapping mycological ignorance – checklists and diversity patterns of fungi known for West Africa. IMA Fungus 11, 13.
Piepenbring M. 2015 – Introduction to mycology in the tropics / Introducción a la micología en los trópicos. APS Press St. Paul.
Pihlgren A, Hallingbäck T, Aronsson M, Dahlberg A et al. 2010 – The new Swedish Red List 2010. Svensk Botanisk Tidskrift 104(4), 210–226.
Pinnoi A, Lumyong S, Hyde KD, Jones EBG. 2006 – Biodiversity of fungi on the palm *Eleiodoxa conferta* in Sirindhorn peat swamp forest, Narathiwat, Thailand. Fungal Diversity 22, 205–218.
Pino-Bodas R, Zhurbenko MP, Stenroos S. 2017 – Phylogenetic placement within *Lecanoromycetes* of lichenicolous fungi associated with *Cladonia* and some other genera. Persoonia-Molecular Phylogeny and Evolution of Fungi 39(1), 91–117.
Pinruan U, Sakayaroj J, Hyde KD, Jones EB. 2008 – *Thailandiomyces bisetulosus* gen. et sp. nov. (*Diaporthales*, *Sordariomycetidae*, *Sordariomycetes*) and its anamorph *Craspedodidymum*, is described based on nuclear SSU and LSU rDNA sequences. Fungal Diversity 29, 89–98.
Pinto-Figueroa EA, Seddon E, Yashiro E, Buri A et al. 2019 – *Archaeorhizomycetes* spatial distribution in soils along wide elevational and environmental gradients reveal co-abundance patterns with other fungal saprobes and potential weathering capacities. Frontiers in Microbiology 10, 656.

Pirozynski K. 1972 – Microfungi of Tanzania. I. Miscellaneous fungi on oil palm. II. New *Hyphomycetes*. Mycological Papers 129, 1–29.
Pirozynski KA, Reid J. 1966 – Studies on the *Patellariaceae*: i. *Eutryblidiella sabina* (de not.) höhn. Canadian Journal of Botany 44, 655–662.
Pitt JI, Hocking AD. 2009 – Fungi and food spoilage. Springer, Dordrecht Heidelberg London New York.
Pitt JI. 1980 – The genus *Penicillium* and its teleomorphic states *Eupenicillium* and *Talaromyces*. Academic Press, London.
Pixley FJ, Wakefield AE, Banerji S, Hopkin JM. 1991 – Mitochondrial gene sequences show fungal homology for *Pneumocystis carinii*. Molecular Microbiology 5, 1347–1351.
Plata ER, Lumbsch HT. 2011 – Parallel evolution and phenotypic divergence in lichenized fungi: a case study in the lichen-forming fungal family *Graphidaceae* (*Ascomycota*: *Lecanoromycetes*: *Ostropales*). Molecular Phylogenetics and Evolution 61(1), 45–63.
Poch GK, Gloer JB, Shearer CA. 1992 – New bioactive metabolites from a freshwater isolate of the fungus *Kirschsteiniothelia* sp. Journal of Natural Products 55(8), 1093–9.
Poelt J, Hafellner J. 1975 – Schlauchpforten bei der Flechtengattung Thelocarpon. Phyton (Austria), 17(1-2), 66–77.
Poelt J, Hinteregger E. 1993 – Beiträge zur Kenntnis der Flechtenflora des Himalaya, vol. 7, Die Gattungen Ca-loplaca, Fulgensia und Ioplaca (mit englischem Bestim-mungsschlüssel). Bibliotheca Lichenologica 50. J. Cramer, Berlin, Stuttgart.
Poelt J, Nash TH. 1993 – Studies in the *Umbilicaria vellea* group (*Umbilicariaceae*) in North America. The Bryologist 96, 422–430.
Poelt J, Obermayer W. 1990 – Über Thallosporen bei einigen Krustenflechten. Herzogia 8, 273–288.
Poelt J, Reddi BV. 1969 – *Candelaria* und *Candelariella*. Lichenes, *Candelariaceae*. (Flechten des Himalaya 4). Khumbu Himal [Universitatsverlag Wagner, Innsbruck-München] 6(1), 1–16.
Poelt J, Vezda A. 1976 – *Candelariella plumbea* und *C. rhodax* sp. novae, zwei neue Arten der europaischen Flechten-Flora. Folia geobotanica & phytotaxonomica 11, 87–92.
Poelt J, Vězda A. 1977 – Bestimmungsschlüssel europäischer Flechten. Ergänzungsheft I. Bibliotheca Lichenologica 9. Cramer, Vaduz.
Poelt J, Vezda A. 1981 – Bestimmungsschlüssel europäischer Flechten. Erganzungsheft II. Bibl Lichenol 16, J. Cramer, Vaduz. 390
Poelt J. 1958 – Die lobaten Arten der Flechtengattung *Lecanora* Ach. *sensu* ampl. in der Holarktis. Mitt. der Bot. Staatssammlung München 2(19–20), 411–573.
Poelt J. 1962 – Bestimmungsschlüssel der Höheren Flechten von Europa // Mitt. Bot. Staatssammlung München 4, 301–571.
Poelt J. 1965 – Zur Systematik der Flechtenfamilie *Physciaceae*. Nova Hedwigia 9, 21–32.
Poelt J. 1973 – Classification. In: V. Ahmadjian & M. E. Hale (eds.): The Lichens. Academic Press, New York and London, pp. 599–632.
Poelt J. 1974a – Classification. In: V. Ahmadjian, & M. E. Hale (Eds.), The lichens. London: Academic Press.
Poelt J. 1974b – Zur Kenntnis der Flechtenfamilie *Candelariaceae*. Ein Beitrag mit besonderer Berücksichtigung einiger südamerikanischer Arten. Phyton [Austria] 16, 189–210.
Poelt J. 1990 – Parasitische Arten der Flechtengattung Rhizocarpon: eine weitere Übersicht. Mitteilungen der Botanische Staatssammlung München 29, 515–538.
Pointing SB, Buswell JA, Jones EBG, Vrijmoed LLP. 1999 – Extracellular cellulolytic enzyme profiles of five lignicolous mangrove fungi. Mycological Research 103(6), 696–700.
Põldmaa K. 2011 – Tropical species of *Cladobotryum* and *Hypomyces* producing red pigments. Studies in Mycology 68, 1–34.
Poli A, Bovio E, Ranieri L, Varese GC et al. 2020 – Fungal Diversity in the Neptune Forest: Comparison of the Mycobiota of *Posidonia oceanica*, *Flabellia* petiolata, and *Padina pavonica*. Frontiers in Microbiology 11, 933.

Poli A, Bovio E, Verkley G, Prigione V et al. 2019 – *Elbamycella rosea* gen. et sp. nov. (*Juncigenaceae*, *Torpedosporales*) isolated from the Mediterranean Sea. MycoKeys 55, 15–28.
Poli A, Prigione V, Bovio E, Perugini I et al. 2021 – Insights on *Lulworthiales* inhabiting the Mediterranean Sea and description of three novel species of the genus *Paralulworthia*. Journal of Fungi, 7(11), 940.
Poli A, Varese GC, Garzoli L, Prigione V. 2022 – Seagrasses, seaweeds and plant debris: An extraordinary reservoir of fungal diversity in the Mediterranean Sea. Fungal Ecology 60, 101156.
Pomerleau R. 1980 – Flore des champignons au Québec et régions limitrophes. Les éditions la presse, Ottawa, Ontario, Canada.
Poncet R, Voglmayr H, Kervran L. 2022 – A new species of *Stigmatodiscus* (*Ascomycota*, *Dothideomycetes*, *Stigmatodiscaceae*) from Juan de Nova (Mozambique Channel, Scattered Islands, French Southern and Antarctic Lands). Plant and Fungal Systematics 67, 55–62.
Poon MH, Hyde KD. 1998 – Biodiversity of intertidal estuarine fungi on Phragmites at Mai Po marshes, Hong Kong. Botanica Marina 41, 141–155.
Popov ES. 2007 – Fungi and Slime Molds: *Discomycetes*. In: Environment and Biological Diversity of Berezovye Islands Archipelago, the Gulf of Finland (Tsvelev NN, ed). Boston-spektr, Russia 238–245.
Porollo A, Meller J, Joshi Y, Jaiswal V et al. 2012 – Analysis of current antifungal agents and their targets within the *Pneumocystis carinii* genome. Current drug targets 13(12), 1575–1585.
Poumarat S, Roux C, Daval G. 2022 – *Zwackhiomyces fuscatus* Poumarat, Daval et Cl. Roux sp. Nov. champignon lichénicole (*Ascomycota*, *Xanthopyreniaceae*) parasite d'*Acarospora fuscata*. Le Bulletin de la Société Linnéenne de Provence 73, 73–50.
Pourmoghaddam MJ, Ekiz G, Lambert C, Surup F et al. 2022 – Studies on the secondary metabolism of *Rosellinia* and *Dematophora* strains (*Xylariaceae*) from Iran. Mycological Progress 21(8), 65.
Poveda J, Abril-Urias P, Escobar C. 2020 – Biological control of plant-parasitic nematodes by filamentous fungi inducers of resistance: *Trichoderma*, mycorrhizal and endophytic fungi. Frontiers in Microbiology 11, 992.
Powell PE. 1974 – Taxonomic studies in the genus *Hypoderma* (*Rhytismataceae*). PhD Dissertation, Cornell University. 1–117.
Prabhugaonkar A, Pratibha J. 2017 – New record of *Trichoglossum rasum* from Asia. Mycosphere 8, 583–591.
Prasher IB, Verma RK. 2015 – Two new species of *Acroconidiella* from India. Journal on New Biological Reports 4, 111–114.
Prasongsuk S, Lotrakul P, Ali I, Bankeeree W et al. 2018 – The current status of *Aureobasidium pullulans* in biotechnology. Folia Microbiologica 63, 129–140.
Pratibha J, Prabhugaonkar A, Hyde KD, Bhat DJ. 2014 – Phylogenetic placement of *Bahusandhika*, *Cancellidium* and *Pseudoepicoccum* (asexual *Ascomycota*). Phytotaxa 176(1), 68–80.
Prenafeta-Boldú FX, Andrea K, Luykx DM, Heidrun A et al. 2001 – Isolation and characterisation of fungi growing on volatile aromatic hydrocarbons as their sole carbon and energy source. Mycological Research 105, 477–484.
Pressel S, Duckett J. 2011 – The parasitic ascomycete *Mniaecia jungermanniae* induces the formation of giant perichaetia and apogamous sporophytes in leafy liverworts. Canadian Journal of Botany 84, 384–392.
Prieto M, Baloch E, Tehler A, Wedin M. 2013 – Mazaedium evolution in the *Ascomycota* (Fungi) and the classification of mazaediate groups of formerly unclear relationship. Cladistics 29(3), 296–308.
Prieto M, Etayo J, Olariaga I. 2021 – A new lineage of mazaediate fungi in the *Eurotiomycetes*: *Cryptocaliciomycetidae* subclass. nov., based on the new species *Cryptocalicium blascoi* and the revision of the ascoma evolution. Mycological Progress 20(7), 889–904.

Prieto M, Olariaga I, Pérez-Ortega S, Wedin M. 2020 – The identity of *Calicium corynellum* (Ach.) Ach. The Lichenologist 52(4), 333–335.
Prieto M, Schultz M, Olariaga I, Wedin M. 2019 – *Lichinodium* is a new lichenized lineage in the *Leotiomycetes*. Fungal Diversity 94(1), 23–39.
Prieto M, Wedin M, Schultz M. 2024 – Phylogeny, evolution and a re-classification of the *Lichinomycetes*. Studies in Mycology 109, 595.
Prieto M, Wedin M. 2013 – Dating the diversification of the major lineages of *Ascomycota* (fungi). PLoS ONE 8(6), e65576.
Prieto M, Wedin M. 2017 – Phylogeny, taxonomy and diversification events in the *Caliciaceae*. Fungal Diversity 82(1), 221–238.
Prihatini R, Boonyuen N, Sivichai S. 2008 – Phylogenetic evidence that two submerged-habitat fungal species, *Speiropsis pedatospora* and *Xylomyces chlamydosporus*, belong to the order Jahnulales *insertae sedis Dothideomycetes*. Microbiology Indonesia 2, 136–140.
Prillinger H, Dörfler C, Laaser G, Eckerlein B et al. 1990 – Ein Beitrag zur Systematik und Entwicklungsbiologie Höherer Pilze: Hefe-Typen der Basidiomyceten. Teil I: *Schizosaccharomycetales*, *Protomyces*-Typ. Zeitschrift für Mykologie 56, 219–250.
Printzen C. 2010 – Lichen systematics: the role of morphological and molecular data to reconstruct phylogenetic relationships. In Progress in Botany 71, 233–275.
Promputtha I, Lumyong S, Dhanasekaran V, McKenzie EHC et al. 2007 − A phylogenetic evaluation of whether endophytes become saprotrophs at host senescence. Microbial Ecology 53, 579–590.
Promputtha I, Miller AN. 2010 − Three new species of *Acanthostigma* (*Tubeufiaceae*, *Dothideomycetes*) from Great Smoky Mountains National Park. Mycologia 102(3), 574–587.
Ptach-Styn Ł, Guzow-Krzemińska B, Lendemer JC, Tønsberg T et al. 2024 – Phylogeny of the genus *Loxospora* sl (*Sarrameanales*, *Lecanoromycetes*, *Ascomycota*), with *Chicitaea* gen. nov. and five new combinations in *Chicitaea* and *Loxospora*. MycoKeys 102, 155.
Punithalingam E, Spooner BM. 1997 – A new species of *Hainesia* from Southern England. Mycological Research 101(10), 1228–1232.
Punithalingam E. 2003 – Nuclei, micronuclei and appendages in tri-and tetraradiate conidia of Cornutispora and four other coelomycete genera. Mycological Research 107(8), 917–948.
Puntillo D, Puntillo M. 2009 – Calicioid lichens and fungi of Italy: A state of the art. Flora Mediterranea 19, 251–260.
Purahong W, Hyde KD. 2011 – Effects of fungal endophytes on grass and non-grass litter decomposition rates. Fungal Diversity 47, 1–7.
Purvis OP, Coppins BJ, Hawksworth D, James PW et al. 1992 – The liehen flora of Great Britain and Ireland. - 710 p, Brit. Lichen Soc. Natural Hist. Mus. Publ., London. Sa
Qian S, Zeng X, Qian Y, Lu Y et al. 2023 – A saprophytic fungus *Tubeufia rubra* produces novel rubracin D and E reversing multidrug resistance in cancer cells. Journal of Fungi 9, 309.
Qiao M, Tian W, Castañeda-Ruiz RF, Xu J et al. 2019 – Two new species of *Verruconis* from Hainan, China. MycoKeys 48, 41.
Qiao M, Zhang Y, Li SF, Baral HO et al. 2012 – *Orbilia blumenaviensis* and its *Arthrobotrys* anamorph. Mycological Progress 11, 255–262.
Qiao M, Zheng H, Lv R, Yu Z. 2020 – *Neodactylariales*, *Neodactylariaceae* (*Dothideomycetes*, *Ascomycota*): new order and family, with a new species from China. MycoKeys 73, 69.
Qin XD, Dong ZJ, Liu JK, Yang LM et al. 2006 – Concentricolide, an anti-HIV agent from the ascomycete *Daldinia concentrica*. Helvetica Chimica Acta 89(1), 127–33.
Quaedvlieg W, Binder M, Groenewald JZ, Summerell BA et al. 2014 – Introducing the consolidated species concept to resolve species in the *Teratosphaeriaceae*. Persoonia 33, 1–40.
Quaedvlieg W, Verkley GJM, Shin HD, Barreto RW et al. 2013 – Sizing up *Septoria*. Studies in Mycology 75, 307–390.

Quan Y, Ahmed SA, da Silva NM, Al-Hatmi AM et al. 2021 – Novel black yeast-like species in *Chaetothyriales* with ant-associated life styles. Fungal biology 125, 276–284.
Quan Y, Deng S, Prenafeta-Boldů FX, Mayer VE et al. 2023 – The origin of human pathogenicity and biological interactions in *Chaetothyriales*. Fungal Diversity 1–22.
Quan Y, Muggia L, Moreno LF, Wang M et al. 2020 – A re-evaluation of the *Chaetothyriales* using criteria of comparative biology. Fungal Diversity 103, 47–85.
Quan Y, van den Ende BG, Shi D, Prenafeta-Boldú FX et al. 2019 – A comparison of isolation methods for black fungi degrading aromatic toxins. Mycopathologia 184, 653–660.
Quandt CA, Haelewaters D. 2021 – Phylogenetic advances in *Leotiomycetes*, an understudied clade of taxonomically and ecologically diverse fungi. Encyclopedia of Mycology 1, 284–294.
Quijada L, Johnston PR, Cooper JA, Pfister DH. 2018 – Overview of *Phacidiales*, including *Aotearoamyces* gen. nov. on Nothofagus. IMA fungus 9, 371–382.
Quijada L, Matočec N, Kušan I, Tanney JB. 2022 – Apothecial ancestry, evolution, and re-evolution in *Thelebolales* (*Leotiomycetes*, Fungi). Biology 11(4), 583.
Quijada L, Tanney JB, Popov E, Johnston PR et al. 2020 – Cones, needles and wood: *Micraspis* (*Micraspidaceae, Micraspidales* fam. et ord. nov.) speciation segregates by host plant tissues. Fungal Systematics and Evolution 5, 99–111.
Raggio J, Green TGA, Sancho LG. 2016 – In situ monitoring of microclimate and metabolic activity in lichens from Antarctic extremes: a comparison between South Shetland Islands and the McMurdo Dry Valleys. Polar Biology 39(1), 113–122.
Rai MK. 1989 – Mycosis in man due to *Arthrinium phaeospermum* var. *indicum*. First case report: mykose durch *Arthrinium phaeospermum* var. *indicum* beim Menschen. Erstbericht. Mycoses 32, 472–475.
Raillo A. 1929 – Beiträge zur Kenntnis der Bodenpilze. Zentbl. Bakl. ParasilKde (Abt. 2) 78, 515–524.
Raimondo ML, Carlucci A. 2018 – Characterization and pathogenicity assessment of *Plectosphaerella* species associated with stunting disease on tomato and pepper crops in Italy. Plant pathology 67(3), 626–641.
Raitviir A, Spooner BM. 1994 – *Cyttariales, Lahmiales, Leotiales, Medeolariales, Ostropales, Patellariales, Rhytismatales*, and *Triblidiales*. In: Hawksworth, D.L. (eds) Ascomycete Systematics. NATO ASI Series, vol 269. Springer, Boston, MA.
Raja H, Schoch CL, Hustad V, Shearer C et al. 2011 – Testing the phylogenetic utility of MCM7 in the *Ascomycota*. MycoKeys 1, 63–94.
Raja HA, Campbell J, Shearer CA. 2003 – Freshwater *Ascomycetes*: *Cyanoannulus petersenii*, a new genus and species from submerged wood. Mycotaxon 88, 1–17.
Raja HA, El-Elimat T, Oberlies NH, Shearer CA et al. 2015a – *Minutisphaerales* (*Dothideomycetes*, *Ascomycota*): a new order of freshwater *Ascomycetes* including a new family, *Minutisphaeraceae*, and two new species from North Carolina, USA. Mycologia 107, 845–862.
Raja HA, Kaur A, El-Elimat T, Figueroa M et al. 2015b – Phylogenetic and chemical diversity of fungal endophytes isolated from *Silybum arianum* (L) Gaertn. Mycology 6(1), 8–27.
Raja HA, Miller AN, Shearer CA. 2012 – Freshwater *Ascomycetes*: *Natipusillaceae*, a new family of tropical fungi, including *Natipusilla bellaspora* sp. nov. from the Peruvian Amazon. Mycologia 104, 569–573.
Raja HA, Oberlies NH, Figueroa M, Tanaka K et al. 2013 – Freshwater *Ascomycetes*: *Minutisphaera* (*Dothideomycetes*) revisited, including one new species from Japan. Mycologia 105, 959–976.
Raja HA, Shearer CA. 2008 – Freshwater *Ascomycetes*: new and noteworthy species from aquatic habitats in Florida. Mycologia 100(3), 467–489.
Rajeshkumar KC, Sharma R. 2013 – *Tamhinispora* a new genus belongs to family *Tubeufiaceae* from the Western Ghats, India based on morphology and phylogenetic analysis. Mycosphere 4(2), 165–174.

Rajkowska K, Otlewska A, Koziróg A, Piotrowska M et al. 2014 – Assessment of biological colonization of historic buildings in the former Auschwitz II-Birkenau concentration camp. Annals of Microbiology 64(2), 799–808.
Raju J, Nagaraju DK, Priti S, Kalleshwaraswamy CM et al. 2022 – Invasion of wood degraders through wood import and need to strengthen the plant quarantine measures in India. Science of Wood Degradation and its Protection 709–744.
Ramaley AW. 1996 – *Comminutispora* gen. nov. and its *Hyphospora* gen. nov. anamorph. Mycologia 88, 132–136.
Rambold G, Davydov E, Elix JA, Haiduk, E et al. 2001 onwards [last visited: 2023-07-16] – LIAS light – A Database for Rapid Identification of Lichens. liaslight.lias.net/; https://divnavikey.snsb.info/static/index.html.
Rambold G, Triebel D, Hertel H. 1993 – *Icmadophilaceae*, a new family in the *Helotiales*. Bibliotheca Lichenologica 53, 217–240.
Rambold G, Triebel D. 1992 – The inter-lecanoralean associations. Bibliotheca Lichenologica 48, 1–201.
Rambold G. 1989 – A monograph of the saxicolous lecideoid lichens of Australia (excl. Tasmania). Bibliotheca Lichenologica 34, 345 J. Cramer, Berlin-Stuttgart.
Ramstad S, Hestmark G. 2001. Population structure and size-dependent reproductive effort in *Umbilicaria spodochroa*. Mycologia 93(3), 453-458.
Randlane T, Jüriado I, Degtjarenko P, Saag A. 2021 – New assessment of least concern lichens in the Red List of Estonia: are common species still common? Folia Cryptogamica Estonica 58, 199–212.
Ranft H, Moncada B, de Lange PJ, Lumbsch HT et al. 2018 – The *Sticta filix* morphodeme (*Ascomycota*: *Lobariaceae*) in New Zealand with the newly recognized species *S. dendroides* and *S. menziesii*: indicators of forest health in a threatened island biota? The Lichenologist 50, 185–210.
Ranghoo VM, Hyde KD, Liew ECY, Spatafora JW. 1999 – Family placement of *Ascotaiwania* and *Ascolacicola* based on DNA sequences from the large subunit rRNA gene. Fungal Diversity 2, 159–168.
Ranghoo VM, Hyde KD. 2000 – *Ascominuta lignicola*, a new loculoascomycete from submerged wood in Hong Kong. Mycoscience 41, 1–5.
Ranghoo VM. 1998 – Phylogeny of freshwater *Ascomycetes*. Dissertation, University of Hong Kong.
Rao V, De Hoog GS. 1986 – New or critical *Hyphomycetes* from India. Studies in Mycology 28: 1–84.
Rao V, Reddy KA, Hoog GSD. 1984 – *Heliocephala*, a new genus of dematiaceous *Hyphomycetes*. Persoonia 12, 239–242.
Rappaz F. 1992 – *Phomatospora berkeleyi*, *P. arenaria* and their Sporothrix anamorphs. Mycotaxon 45, 323–330.
Rappaz F. 1995 – *Anthostomella* and related Xylariaceous fungi on hardwood from Europe and North America. Mycologia Helvetica 7, 99–167.
Räsänen V. 1943 – Das System der Flechten. Acta Botanica Fennici 33, 1–82.
Räsänen V. 1944 – Lichenes Novi I. Annales Botanici Societatis Zoologicae-Botanicae Fennicae "Vanamo". Ann. Bot. Soc. Zool.-Bot. Fenn. ‘Vanamo’ 20, 1–34.
Raspé O, Sloover J. 1998 – Morphology, ecology and chorology of *Mniaecia jungermanniae* (*Ascomycota*) in Belgium and the significance of its association to leafy liverworts (*Jungermanniales*). Belgian Journal of Botany 131, 251–259.
Rateb ME, Ebel R. 2011 – Secondary metabolites of fungi from marine habitats. Natural Product Reports 28(2), 290–344.
Rathnayaka AR, Chethana KWT, Phillips AJL, Liu JK et al. 2023 – Re-evaluating *Botryosphaeriales*: Ancestral state reconstructions of selected characters and evolution of nutritional modes. Journal of Fungi 2, e184.

Ravera S, Puglisi M, Vizzini A, Totti C et al. 2019 – Notulae to the Italian flora of algae, bryophytes, fungi and lichens: 7. Italian Botanist 7, 69–91.
Raymundo T, Martínez YAG, Pineda MM, Garza RV. 2022 – *Marthamyces manglicola*, una especie nueva (*Ascomycota*, *Marthamycetaceae*) sobre mangle negro de la Isla de Cozumel, México. Acta Botánica Mexicana 8.
Raymundo T, Valenzuela R, Esqueda M. 2016 – *Marthamyces coronadoae* sp. nov. in a *Fagus grandifolia* subsp. mexicana forest from Hidalgo State, México. Mycotaxon 131, 521–526.
Read SJ, Jones EBG, Moss ST. 1993 – Taxonomic studies of marine *Ascomycotina*: ultrastructure of the asci, ascospores and appendages of *Savoryella* species. Canadian Journal of Botany 71, 273–283.
Reátegui RF, Wicklow DT, Gloer JB. 2006 – Phaeofurans and sorbicillin analogues from a fungicolous *Phaeoacremonium* species (NRRL 32148). Journal of Natural Products 69, 113–117.
Réblová M, Gams W, Seifert KA. 2011 – *Monilochaetes* and allied genera of the *Glomerellales*, and a reconsideration of families in the *Microascales*. Studies in Mycology 68(1), 163–191.
Réblová M, Barr ME, Samuels GJ. 1999 – *Chaetosphaeriaceae*, a new family for *Chaetosphaeria* and its relatives. Sydowia 51, 49–70.
Réblová M, Fourneir J, Štěpánek V. 2016a – Two new lineages of aquatic *Ascomycetes*: *Atractospora* gen. nov. and *Rubellisphaeria* gen. et sp. nov. and a sexual morph of *Myrmecridium montsequrinum* sp. nov. Mycological Progress 15, 1–39.
Réblová M, Fournier J, Hyde KD. 2010 – *Achroceratosphaeria*, a new ascomycete genus in the *Sordariomycetes*, and re-evaluation of *Ceratosphaeria incolorata*. Fungal Diversity 43, 75–84.
Réblová M, Fournier J, Štěpánek V. 2015a – *Pisorisporiales*, a new order of aquatic and terrestrial fungi for *Achroceratosphaeria* and *Pisorisporium* gen. nov. in the *Sordariomycetes*. Persoonia 34, 40–49.
Réblová M, Hernandez-Restrepo M, Fournier J, Nekvindová J. 2020a – New insights into the systematics of *Bactrodesmium* and its allies and introducing new genera, species and morphological patterns in the *Pleurotheciales* and *Savoryellales* (*Sordariomycetes*). Studies in Mycology 95, 415–466.
Réblová M, Jaklitsch W, Réblová K, Štěpánek V. 2015b – Phylogenetic reconstruction of the *Calosphaeriales* and *Togniniales* using five genes and predicted RNA secondary structures of ITS, and *Flabellascus tenuirostris* gen. et sp. nov. PLoS ONE 10, e0144616.
Réblová M, Kolařik M, Nekvindová J, Miller AN et al. 2021a – Phylogeny, global biogrography and pleomorphism of *Zanclospora*. Microorganism 9, 706.
Réblová M, Kolařík M, Nekvindová J, Réblová J et al. 2021b – Phylogenetic reassessment, taxonomy, and biogeography of *Codinaea* and similar fungi. Journal of Fungi 7(12), 1097.
Réblová M, Miller AN, Réblová K, Štěpánek V. 2018 – Phylogenetic classification and generic delineation of *Calyptosphaeria* gen. nov., *Lentomitella*, *Spadicoides* and *Torrentispora* (*Sordariomycetes*). Studies in Mycology 89, 1–62.
Réblová M, Miller AN, Rossman AY, Seifert KA et al. 2016b – Recommendations for competing sexual-asexually typified generic names in *Sordariomycetes* (except *Diaporthales*, *Hypocreales*, and *Magnaporthales*). IMA Fungus 7, 131–153.
Réblová M, Mostert L, Gams W, Crous PW. 2004 – New genera in the *Calosphaeriales*: *Togniniella* and its anamorph *Phaeocrella*, and *Calosphaeriophora* as anamorph of *Calosphaeria*. Studies in Mycology 50, 533–550.
Réblová M, Mostert L. 2007 – *Romellia* is congeneric with *Togninia*, and description of *Conidiotheca* gen. nov. for one species of this genus with polysporous asci. Mycological Research 111(3), 299–307.
Réblová M, Nekvindová J, Fournier J, Miller AN. 2020b – Delimitation, new species and teleomorph-anamorph relationships in *Codinaea*, *Dendrophoma*, *Paragaeumannomyces* and *Striatosphaeria* (*Chaetosphaeriaceae*). MycoKeys 74, 17–74.

Réblová M, Nekvindová J, Hernández-Restrepo M. 2021c – Reflections on *Menisporopsis*, *Multiguttulispora* and *Tainosphaeria* using molecular and morphological data. Journal of Fungi 7(6, no 438), 1–36.
Réblová M, Nekvindová J, Kolařík M, Hernández-Restrepo M. 2021d – Delimitation and phylogeny of *Dictyochaeta*, and introduction of *Achrochaeta* and *Tubulicolla*, genera nova. Mycologia 113(2), 390–433.
Réblová M, Nekvindová J. 2023 – New genera and species with chloridium-like morphotype in the *Chaetosphaeriales* and *Vermiculariopsiellales*. Studies in Mycology. 106, 199–258.
Réblová M, Réblová K, Štěpánek V. 2015 – Molecular systematics of *Barbatosphaeria* (*Sordariomycetes*): multigene phylogeny and secondary ITS structure. Persoonia-Molecular Phylogeny and Evolution of Fungi 35(1), 21–38.
Réblová M, Seifert KA, Fournier J, Štěpánek V. 2012 – Phylogenetic classification of *Pleurothecium* and *Pleurotheciella* gen. nov. and its dactylaria-like anamorph (*Sordariomycetes*) based on nuclear ribosomal and protein-coding genes. Mycologia 104, 1299–1314.
Réblová M, Seifert KA, Fournier J, Štěpánek V. 2016c – Newly recognised lineages of perithecial *Ascomycetes*: the new orders *Conioscyphales* and *Pleurotheciales*. Persoonia: Molecular Phylogeny and Evolution of Fungi 37, 57–81.
Réblová M, Seifert KA. 2004 – *Conioscyphascus*, a new ascomycetous genus for holomorphs with *Conioscypha* anamorphs. Studies in Mycology 50, 95e108.
Réblová M, Seifert KA. 2008 –Molecular data re-assess the taxonomic concept of *Reticulascus* (*Glomerellales*) and its phylogenetic position. Mycological Research 112(6), 722–736.
Réblová M, Seifert KA. 2011 – Discovery of the teleomorph of the hyphomycete, *Sterigmatobotrys macrocarpa*, and epitypification of the genus to holomorphic status. Studies in Mycology 68, 193–202.
Réblová M, Seifert KA. 2012 – *Cirrosporium novae-zelandiae*, an enigmatic coelomycete with meristem arthroconidia, with ancestors in the *Eurotiomycetes*. Mycologia 104, 1315–1324.
Réblová M, Štěpánek V. 2009 – New fungal genera, *Tectonidula* gen. nov. for *Calosphaeria*-like fungi with holoblastic-denticulate conidiogenesis and *Natantiella* gen. nov. for three species segregated from *Ceratostomella*. Mycological Research 113, 991–1002.
Réblová M, Štěpánek V. 2018 – Introducing the *Rhamphoriaceae*, fam. nov.(*Sordariomycetes*), two new genera, and new life histories for taxa with *Phaeoisaria*-and *Idriella*-like anamorphs. Mycologia 110(4), 750–770.
Réblová M, Untereiner WA, Réblová K. 2013 – Novel evolutionary lineages revealed in the *Chaetothyriales* (Fungi) based on multigene phylogenetic analyses and comparison of ITS secondary structure. PLoS ONE 8, e63547.
Réblová M, Untereiner WA, Štěpánek V, Gams W. 2017 – Disentangling *Phialophora* section *Catenulatae*: disposition of taxa with pigmented conidiophores and recognition of a new subclass, *Sclerococcomycetidae* (*Eurotiomycetes*). Mycological Progress 16, 27–46.
Réblová M. 1998 – Fungal diversity in the Czech Republic. New species of *Apiorhynchostoma*, *Capronia*, *Ceratosphaeria* and *Lasiosphaeria*. Sydowia 50(2), 229–251.
Réblová M. 1999a – Studies in *Chaetosphaeria sensu lato* I. The genera *Chaetosphaerella* and *Tengiomyces* gen. nov. of the *Helminthosphaeriaceae*. Mycotaxon 70, 387–420.
Réblová M. 1999b – Studies in *Chaetosphaeria sensu lato* IV. *Crassochaeta* gen. nov., a new lignicolous genus of the *Trichosphaeriaceae*. Mycotaxon 71, 45–67.
Réblová M. 1999c – Teleomorph-anamorph connections in Ascomycetes 2. Three new lignicolous species of *Helminthosphaeria*. Sydowia 51, 210–222.
Réblová M. 1999d – Teleomorph-anamorph connections in *Ascomycetes* 3: Three new lignicolous species of *Helminthosphaeria*. Sydowia 51(2), 223–244.
Réblová M. 2006 – Molecular systematics of *Ceratostomella sensu* lato and morphologically similar fungi. Mycologia 98(1), 68–93.
Réblová M. 2007 – *Barbatosphaeria* gen. et comb. nov., a new genus for *Calosphaeria barbirostris*. Mycologia 99(5), 723–732.

Réblová M. 2008 – *Bellojisia*, a new sordariaceous genus for *Jobellisia rhynchostoma* and a description of *Jobellisiaceae* fam. nov. Mycologia 100, 893–901.
Réblová M. 2009 – Teleomorph of *Rhodoveronaea* (*Sordariomycetidae*) discovered and re-evolution of *Pleurophragmium*. Fungal Diversity 36, 129.
Réblová M. 2011 – New insights into the systematics and phylogeny of the genus *Jattaea* and similar fungi of the *Calosphaeriales*. Fungal Diversity 49, 167–198.
Réblová M. 2013 – Two taxonomic novelties in the *Sordariomycetidae*: *Ceratolenta caudata* gen. et sp. nov. and *Platytrachelon abietis* gen. et comb. nov. for *Ceratosphaeria abietis*. Mycologia 105(2), 462–475.
Reddy MS, Kramer CL. 1975 – A taxonomic revision of the *Protomycetales*. Mycotaxon 3, 1–50.
Redhead SA. 1977 – The genus *Neolecta* (*Neolectaceae* fam. nov., *Lecanorales, Ascomycetes*) in Canada. Canadian Journal of Botany 55(3), 301–306.
Reeb V, Lutzoni F, Roux C. 2004 – Contribution of RPB2 to multilocus phylogenetic studies of the *Euascomycetes* (*Pezizomycotina*, Fungi) with special emphasis on the lichen-forming *Acarosporaceae* and evolution of polyspory. Molecular phylogenetics and evolution 32(3), 1036–1060.
Reed CF, Farr DF. 1993 – Index to Saccardo's Sylloge Fungorum Volumes I-XXVI in XXIX 1882–1972. Rose Printing Company, Inc., Talahassee, Florida.
Rees HJ, Drakulic J, Cromey MG, Bailey AM et al. 2022 – Endophytic *Trichoderma* spp. can protect strawberry and privet plants from infection by the fungus *Armillaria mellea*. PLoS ONE 17(8), e0271622.
Rehm H. 1887 − Rabenhorst's Kryptogamen-Flora. Pilze – Ascomyceten 1, 1–64.
Rehm H. 1887-1896 – Die Pilze Deutschlands, Oesterreichs und der Schweiz. III. Abtheilung: Ascomyceten: Hysteriaceen und Discomyceten. In: Rab Krypt Fl 1, 1–1272.
Rehm H. 1891 − Die Discomyceten-Gattung Ahlesia Fuckel und die Pyrenomyceten-Gattung *Thelocarpon* Nyl. - Hedwigia 30(1), 1–12.
Rehm H. 1896 – Die Pilze. Ascomycoten: Hysteriaceen und Discomyceten. In Rabenhorst , L. Kryptogflora Deutschl. Österr. und Schweiz 1, 1–1275.
Rehm H. 1900 – Ascomyceten aus Neufoundland. Hedwigia 39, 321–324.
Rehner SA, Samuels GJ. 1995 – Molecular systematics of the *Hypocreales*: a teleomorph gene phylogeny and the status of their anamorphs. Canadian Journal of Botany 73, 816–823.
Řehulka J, Kubátová A, Hubka V. 2016 – *Cephalotheca sulfurea* (*Ascomycota*, *Sordariomycetes*), a new fungal pathogen of the farmed rainbow trout Oncorhynchus mykiss. Journal of Fish Diseases 39(12), 1413–1419.
Reichenbach HTL. 1841 – Der deutsche Botaniker. Erster Band. Das Herbarienbuch. Dresden und Leipzig: Arnoldischen Buchhandlung.
Reichenbach L. 1837 – Handbuch des Natürlichen Pflanzensystems. Dresden.
Reid J, Booth C. 1966 – The Genus *Flageoletia* (Sacc.) Höhn. Canadian Journal of Botany 44, 445–451.
Reinke J. 1895 – Abhandlungen über Flechten, III & IV. Jahrbücher für Wissenschaftliche Botanik 28, 39–150.
Ren GC, Wanasinghe DN, Jeewon R, Monkai J et al. 2022 – Taxonomy and phylogeny of the novel *Rhytidhysteron*-like collections in the Greater Mekong Subregion. Mycokeys 86, 65.
Renobales G, Aguirre B. 1990 – The nomenclature and systematic position of the genus *Encephalographa*. Systema Ascomycetum 8(2), 87–92.
Rep M, Dekker HL, Vossen JH, de Boer AD et al. 2005 – A tomato xylem sap – and apoplast-predominant chitinase with a basic thaumatin-like domain from *Cladosporium fulvum*: a virulence factor disguised as a hydrolytic enzyme. The Plant Journal 41(5), 793–804.
Resl P, Schneider K, Westberg M, Printzen C et al. 2015 – Diagnostics for a troubled backbone: testing topological hypotheses of trapelioid lichenized fungi in a large-scale phylogeny of *Ostropomycetidae* (*Lecanoromycetes*). Fungal Diversity 73, 239–258.

Reynolds DR, Gilbert GS. 2005 – Epifoliar fungi from Queensland, Australia. Australian Systematic Botany 18:265–289
Reynolds DR, Gilbert GS. 2006 – Epifoliar fungi from Panama. Cryptogamie, Mycologie 27, 249–270
Reynolds DR. 1991 – A phylogeny of fissitunicate ascostromatic fungi. Mycotaxon 42, 99–123.
Richards AG, Smith MN. 1955a – Infection of cockroaches with *Herpomyces* (*Laboulbeniales*). I. Life history studies. The Biological Bulletin 108(2), 206–218.
Richards AG, Smith MN. 1955b – Infection of cockroaches with *Herpomyces* (*Laboulbeniales*). IV. Development of *H. stylopygae* Spegazzini. The Biological Bulletin 109(2), 306–315.
Richards AG. 1954 – Similarities in histochemical differentiation of insect cuticle and the walls of parasitic fungi. Science 120(3123), 761–762.
Richardson DHS, Cameron RP. 2004 – Cyanolichens: their response to pollution and possible management strategies for their conservation in northeastern North America. Northeast Nat 11, 1– 22
Rick JE. 1931 – Monographia Boliniarum Riograndensium. Brotéria Série Botânica 25, 65–71.
Riddick EW, Schaefer PW. 2005 – Occurrence, density, and distribution of parasitic fungus *Hesperomyces virescens* (*Laboulbeniales*: *Laboulbeniaceae*) on multicolored Asian lady beetle (*Coleoptera*: *Coccinellidae*). Annals of the Entomological Society of America 98(4), 615–624.
Riddle LW. 1920 − Observations on the genus *Acrospermum*. Mycologia 12,175–181.
Riebold D, Lubig J, Wolf P, Wolf C et al. 2020 – First molecular detection of *Pneumocystis* spp. in red foxes (*Vulpes vulpes* Linnaeus, 1758) and raccoon dogs (*Nyctereutes procyonoides* Gray, 1834). Comparative Immunology, Microbiology and Infectious Diseases 73, 101531.
Riebold D, Mohr E, Sombetzki M, Fritzsche C et al. 2012 – *Pneumocystis* species in Brown Leghorn laying hens—A hint for an extra-mammalian reservoir. Poultry Science 91, 1813–1818.
Riffle JW. 1986 – Diseases of trees in the Great Plains (Vol. 129). US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.
Rigling D, Prospero S. 2018 – *Cryphonectria parasitica*, the causal agent of chestnut blight: invasion history, population biology and disease control. Molecular Plant Pathology 19, 7–20.
Rikkinen J, Meinke K, Grabenhorst H, Gröhn C et al. 2018 – Calicioid lichens and fungi in amber: Tracing extant lineages back to the Paleogene. Geobios 51(5), 469–479.
Rikkinen J. 2003a – Calicioid lichens and fungi in the forests and woodlands of western Oregon. Acta Botanica Fennica 175, 1–41.
Rikkinen J. 2003b – Calicioid lichens from European Tertiary amber. Mycologia Nov 1 95(6), 1032–6.
Rivas Plata E, Lücking R, Aptroot A, Sipman HJM et al. 2006 – A first assessment of the Ticolichen biodiversity inventory in Costa Rica: the genus *Coenogonium* (*Ostropales*: *Coenogoniaceae*), with a world-wide key and checklist and a phenotype-based cladistic analysis. Fungal Diversity 23, 255–321.
Rivas Plata E, Lücking R, Lumbsch HT. 2008 – When family matters: an analysis of *Thelotremataceae* (lichenized *Ascomycota*: *Ostropales*) as bioindicators of ecological continuity in tropical forests. Biodiversity and Conservation 17, 1319–1351.
Rivero M, Hidalgo A, Alastruey-Izquierdo A, Cía M et al. 2009 – Infections due to *Phialemonium* species, case report and review. Medical Mycology 47(7), 766–774.
Rizzo L, Sutton DA, Wiederhold NP, Thompson EH et al. 2014 – Isolation and characterisation of the fungus *Spiromastix asexualis* sp. nov. from discospondylitis in a German Shepherd dog, and review of *Spiromastix* with the proposal of the new order *Spiromastixales* (*Ascomycota*). Mycoses 57(7), 419–428.
Roberts DT. 1992 – Prevalence of dermatophyte onychomycosis in the United Kingdom: results of an omnibus survey. British Journal of Dermatology 126 (Suppl 39), S23–S27.

Rocha PS, Paula VMB, Olinto SCF, Santos EL et al. 2020 – Diversity, Chemical Constituents and Biological Activities of Endophytic Fungi Isolated from *Schinus terebinthifolius* Raddi. Microorganisms 8, 859.
Rodrigues FÁ, Rios JA, Debona D, Aucique-Pérez CE 2017 – *Pyricularia oryzae*-wheat interaction: physiological changes and disease management using mineral nutrition and fungicides. Tropical Plant Pathology 42, 223–229.
Rodrigues KF, Leuchtmann L, Petrini O. 1993 – Endophytic species of *Xylaria*: cultural and isozymic studies. Sydowia 45, 116–138.
Rodrigues MG, Fonseca Á. 2003 – Molecular systematics of the dimorphic ascomycete genus *Taphrina*. International Journal of Systematic and Evolutionary Microbiology 53, 607–616.
Rodriguez Justavino D, Kirschner R, Piepenbring M. 2015 – New species and new records of *Meliolaceae* from Panama. Fungal Diversity 70, 73–84.
Rodriguez RJ, White Jr JF, Arnold AE, Redman RS. 2009 – Fungal endophytes: diversity and functional roles. New Phytologist 182, 314e330.
Rodríguez-Andrade E, Cano-Lira JF, Wiederhold N, Pérez-Cantero A et al. 2021 – A revision of malbranchea-like fungi from clinical specimens in the United States of America reveals unexpected novelty. IMA Fungus 12(1), 25.
Rodríguez-Andrade E, Stchigel AM, Guarro J, Cano-Lira JF. 2020 – Fungal diversity of deteriorated sparkling wine and cork stoppers in Catalonia, Spain. Microorganisms 8(1), 12.
Rogers JD, Fournier J, Lechat C, Courtecuisse R. 2006 – *Camarops antillana* sp. nov. and *Camarops biporosa* var. *tetraspora* var. nov. from French West Indies. Sydowia 58, 105–109.
Rogers JD, Ju YM, Laessøe T. 1994 – *Neohypodiscus* nom. nov. for *Hypodiscus*. Mycologia 86, 684–690.
Rogers JD. 1979 – The *Xylariaceae* Fungi: systematic, biological and evolutionary aspects. Mycologia 71, 1–42.
Rogers JD. 2000 – Thoughts and musings on tropical *Xylariaceae*. Mycological Research 104, 1412–1420.
Rogers R.W. 1982 – The nomenclature of some Australian lichens described as *Lecanora* and *Placodium* by Müller-Argoviensis. Muelleria 5(1), 31–34.
Rogers RW, Hafellner J. 1988 – *Haematomma* and *Ophioparma*: two superficially similar genera of lichenized fungi. The Lichenologist 20(2), 167-174.
Rogerson CT, Harris RC, Samuels GJ. 1990 – Fungi collected by Bassett Maguire and collaborators in the Guyana Highland, 1944–1983. Memoirs of the New York Botanical Garden 64, 130–164.
Rogerson CT. 1970 – The hypocrealean fungi (*Ascomycetes*, *Hypocreales*). Mycologia 62, 865–910.
Rola K, Osyczka P, Kafel A. 2016[2015] – Different heavy metal accumulation strategies of epilithic lichens colonising artificial post-smelting wastes. Archives of Environmental Contamination and Toxicology 70(2), 418–428.
Rolshausen G, Dal Grande F, Sadowska-Deś AD, Otto J et al. 2017 – Quantifying the climatic niche of symbiont partners in a lichen symbiosis indicates mutualist-mediated niche expansions. Ecography 10.1111/ecog.03457.
Roman H. 2013 – *Elaphomyces muricatus* (*Ascomycota*), a new record for hypogeous fungi in Armenia. An International Journal of Mycology 22, 7–14.
Romao-Dumaresq AS, Dourado MN, de Lima Favaro LC, Mendes R. 2016 – Diversity of cultivated fungi associated with conventional and transgenic sugarcane and the interaction between endophytic *Trichoderma virens* and host plant. PLoS ONE 11, e0158974.
Romero A. Samuels GJ. 1991 – Studies on xylophilous fungi from Argentina VI. *Ascomycotina* on *Eucalyptus viminalis* (*Myrtaceae*). Sydowia 43, 228–248.
Romon P, De Beer ZW, Fernández M, Diez J et al. 2014 – Ophiostomatoid fungi including two new fungal species associated with pine root-feeding beetles in northern Spain. Antonie van Leeuwenhoek 106, 1167–1184.

Romon P, Zhou X, Iturrondobeitia JC, Wingfield MJ et al. 2007 – *Ophiostoma* species (*Ascomycetes*: *Ophiostomatales*) associated with bark beetles (*Coleoptera*: *Scolytinae*) colonizing *Pinus radiata* in northern Spain. Canadian Journal of Microbiology 53, 756–67.
Rondon Y. 1966 – Une espece nouvelle de lichen: *Candelariella oleaginescens* nov. spec. Revue Bryologique et Lichenologique 34, 831–832.
Rooney-Latham S, Escalen A, Gubler WD. 2005a – Teleomorph formation of *Phaeoacremonium aleophilum*, cause of esca and grapevine decline in California. Plant Disease 89, 177–184.
Rooney-Latham S, Eskalen A, Gubler WD 2004 – Ascospore discharge and occurrence of *Togninia minima* (anamorph = *Phaeoacremonium aleophilum*) in California vineyards. (Abstr.) Phytopathology 94, S57.
Rooney-Latham S, Eskalen A, Gubler WD 2005b – Ascospore release of *Togninia minima*, cause of esca and grapevine decline in California. Online. Plant Health Progress.
Rose F. 1976 – Lichenological indicators of age and environmental continuity in wood- lands. In Lichenology: Progress and Problems (Braun DH, Hawksworth DL, Bailey RH eds.), 279–307.
Rosling A, Cox F, Cruz-Martinez K, Ihrmark K et al. 2011 – *Archaeorhizomycetes*: Unearthing an Ancient Class of Ubiquitous Soil Fungi. Science 333, 876–79.
Ross AJ, Yasutake T, Leek S. 1975 – *Phoma herbarum*, a fungal plant saprophyte, as a fish pathogen. Journal of the Fisheries Research Board of Canada 32, 1648–1652.
Rossi W, Kotrba M, Triebel D. 2005 – A new species of *Stigmatomyces* from Baltic amber, the first fossil record of *Laboulbeniomycetes*. Mycological Research 109(3), 271–274.
Rossman AY, Adams GC, Cannon PF, Castlerbury LA et al. 2015a – Recommendations of generic names in *Diaporthales* competing for protection or use. IMA Fungus 6, 145–154.
Rossman AY, Allen WC, Braun U, Castlebury LA et al. 2016 – Overlooked competing asexual and sexually typified generic names of *Ascomycota* with recommendations for their use or protection. IMA Fungus 7(2), 289–308.
Rossman AY, Cathie Aime M, Farr DF, Castlebury LA et al. 2004 – The coelomycetous genera *Chaetomella* and *Pilidium* represent a newly discovered lineage of inoperculate *Discomycetes*. Mycological Progress 3, 275–290.
Rossman AY, Crous PW, Hyde KD, Hawksworth DL et al. 2015b – Recommended names for pleomorphic genera in *Dothideomycetes*. IMA Fungus 6, 507–523.
Rossman AY, Farr DF, Castlebury LA. 2007 – A review of the phylogeny and biology of the *Diaporthales*. Mycoscience 48, 135–144.
Rossman AY, Farr DF, Schoch CL, Nishijima K et al. 2010 – *Dolabra nepheliae* on rambutan and lychee represents a novel lineage of phytopathogenic *Eurotiomycetes*. Mycoscience 51, 300–309.
Rossman AY, Samuels GJ, Rogerson CT, Lowen R. 1999 – Genera of *Bionectriaceae*, *Hypocreaceae* and *Nectriaceae* (*Hypocreales*, *Ascomycetes*). Studies in mycology 42, 1–248.
Rossman AY, Seifert KA, Samuels GJ, Minnis AM et al. 2013 – Genera in *Bionectriaceae*, *Hypocreaceae*, and *Nectriaceae* (*Hypocreales*) proposed for acceptance or rejection. IMA Fungus 4, 41–51.
Rossman AY. 1976 – *Xylobotryum andinum*, a tropical *Pyrenomycete* from Northern California. Myxotaxon 4(1), 179–183.
Rossman AY. 1996 – Morphological and molecular perspectives on systematics of the *Hypocreales*. Mycologia 88(1), 1–19.
Rossman AY. 2000 – Towards monophyletic genera in the holomorphic *Hypocreales*. Studies in Mycology 45, 27–34.
Roux C. 2021 – *Lichenostigma cupreogriseae* P. Pinault et Cl. Roux sp. nov. et *L. spermatomanis* P. Pinault et Cl. Roux sp. nov., champignons lichénicoles non lichénisés (*Ascomycota*). Le Bulletin de la Société Linnéenne de Provence 72, 63.
Roux J, Van Wyk M, Hatting H, Wingfield MJ. 2004 – *Ceratocystis* species infecting stem wounds on *Eucalyptus grandis* in South Africa. Plant Pathology 53, 414–421.

Roux J, Wingfield MJ, Bouillet JP, Wingfield BD et al. 2000 – A serious new wilt disease of *Eucalyptus* caused by *Ceratocystis fimbriata* in Central Africa. Forest Pathology 30, 175–184.
Ruibal C, Gueidan C, Selbmann L, Gorbushina AA et al. 2009 – Phylogeny of rock-inhabiting fungi related to *Dothideomycetes*. Studies in Mycology 64(1), 123–133.
Ruibal C, Platas G, Bills G. 2008 – High diversity and morphological convergence among melanised fungi from rock formations in the central mountain system of Spain. Persoonia: Molecular Phylogeny and Evolution of Fungi 21, 93–110.
Ruinen J. 1956 – Occurrence of *Beijerinckia* species in the 'Phyllosphere'. Nature 177, 220–221.
Rundong L, Shuhua J, Baosong C, Augusto PJ et al. 2022 – Diversity of secondary metabolites from the lichen-forming fungus *Endocarpon pusillum* (*Verrucariaceae, Ascomycota*). Mycosystema 41(12).
Ruprecht U, Lumbsch HT, Brunauer G, Green TGA et al. 2010 – Diversity of *Lecidea* (*Lecideaceae*, *Ascomycota*) species revealed by molecular data and morphological characters. Antarctic Science 22, 721 – 726.
Russell JJ, Theriot JA, Sood P, Marshall WF et al. 2017 – Non-model model organisms. BMC Biology 15(1), 1–31.
Rustamova N, Bozorov K, Efferth T, Yili A. 2020 – Novel secondary metabolites from endophytic fungi: synthesis and biological properties. Phytochemistry Reviews 19 (2), 425–448.
Ryan BD, Nimis PL. 2004 – *Melaspilea*. In Lichen Flora of the Greater Sonoran Desert Region, Vol. 2 (T. H. Nash III, B. D. Ryan, P. Diederich, C. Gries & F. Bungartz, eds), 358–359. Tempe: Lichens Unlimited.
Ryder G, Fastovsky DE, Gartner S. 1996 – The Cretaceous-Tertiary event and other catastrophes in earth history. Geological Society of America 307, 1–550.
Saccardo PA, Saccardo D. 1906 – *Supplementum universale*. Pars VII. *Discomycetae-Deuteromycetae*. Sylloge Fungorum 18, 1–838
Saccardo PA, Sydow P. 1899 – Supplementum Universale, Pars IV. Sylloge Fungorum 14, 1–1316.
Saccardo PA. 1876 – Fungi Veneti novi vel critici. Series V. Nuovo Giornale Botanico Italiano 8, 162–211.
Saccardo PA. 1878 – Fungi Veneti novi vel critici vel mycologiae Venetae addendi. Series IX. Michelia 1(4), 361–445.
Saccardo PA. 1882a – Sylloge fungorum omnium hucusque cognitorum. Vol. 2. Published by author, Padova, Italy. pp. 1–768.
Saccardo PA. 1882b – Sylloge Pyrenomycetum, Vol. I. Sylloge Fungorum 1, 1–768.
Saccardo PA. 1883a – Sylloge fungorum omnium hucusque cognitorum. Vol. 3. Published by author, Padova, Italy. pp. 1–959.
Saccardo PA. 1883b – Sylloge Pyrenomycetum, Vol. II. Sylloge Fungorum 2, 1–813.
Saccardo PA. 1883c − Sylloge Fungorum, vol II. Patavii, Italy.
Saccardo PA. 1884 – Conspectus generum Discomycetum hucuscue cognitorum. *Bot. Centralbl 18*, 247–256.
Saccardo PA. 1886 – *Corynelieae*. In AN Berlese, P Voglino, Sylloge Fungorum Omnium hucusque Cognitorum Digessit P.A. Saccardo. Additamenta ad Volumina I-IV, 193–194.
Saccardo PA. 1889a – Sylloge Discomycetum et Phymatosphaeriacearum. In: Saccardo PA (ed) Sylloge Fungorum Omnium Hucusque Cognitorum. Typis Seminarii, Padua, 1–859.
Saccardo PA. 1889b – Sylloge Fungorum VIII: 75.
Saccardo PA. 1891 – Family 7. Coryneliaceae Sacc. Sylloge Fungorum 9, 1073–1074.
Saccardo PA. 1895a – Supplementum Universale, Pars. III. Sylloge Fungorum 11, 1–753.
Saccardo PA. 1895b – Sylloge Fungorum 11, 1–754. Padua
Saccardo PA. 1928 – Sylloge fungorum XXIV, sect. II. Abellini. Sylloge Fungorum 24, 705–1438.
Sadowska-Des AD, Dal Grande F, Lumbsch HT, Beck A et al. 2014 – Integrating coalescent and phylogenetic approaches to delimit species in the lichen photobiont Trebouxia. Molecular Phylogenetics and Evolution 76(1), 202–210.

Sadowski EM, Beimforde C, Gube M, Rikkinen J. 2012 – The anamorphic genus *Monotosporella* (*Ascomycota*) from Eocene amber and from modern Agathis resin. Fungal Biology 116, 1099–1110.
Sahfiee M, Sohrabi M. 2021 – Antibacterial activity of *Candelariella rhodax* and *Protoparmeliopsis muralis*. Iranian Journal of Biology 34(1), 1–17.
Saini KC, Bast F, Nayaka S, Gautam AK. 2021 – Morpho-molecular characterization of rock-inhabiting lichen *Dermatocarpon miniatum* (*Verrucariaceae*, *Ascomycota*) and its symbiont in Indian Himalayas. The Nucleus 64(2), 193–202.
Sais G, Jucgla A, Peyri J. 1995 – Prevalence of dermatophyte onychomycosis in Spain: a cross-sectional study. British Journal of Dermatology 132, 758–761.
Sakaeyama S, Sano A, Murata Y, Kamei K et al. 2007 – Lecythophora Hoffmannii Isolated from a Case of Canine Osteomyelitis in Japan. Medical Mycology 45(3), 26772.
Sakayaroj J, Pang KL, Jones EBG, Vrijmoed LLP et al. 2005a – A systematic reassessment of marine ascomycetes *Swampomyces* and *Torpedospora*. Botanica Marina 48, 395–406.
Sakayaroj J, Pang KL, Phongpaichit S, Jones EBG. 2005b – A phylogenetic study of the genus *Haligena* (*Halosphaeriales*, *Ascomycota*). Mycologia 97, 804–811.
Salas-Lizana R, Oono R. 2018 – A comparative analysis of *Lophodermium fissuratum*, sp. nov. found in haploxylon pine needles in the pacific northwest, and other *Lophodermium* endophytes. Mycologia 110(5), 1–14.
Salisbury G. 1953 – The genus *Thelocarpon* in Britain. — Northwestern Naturalist (N. S.) 1, 66–76.
Salisbury G. 1966 – A monograph of the lichen genus *Thelocarpon* Nyl. Lichenologist 3, 175–196.
Salvatore MM, Alves A, Andolfi A. 2020a – Secondary metabolites of *Lasiodiplodia theobromae*: distribution, chemical diversity, bioactivity, and implications of their occurrence. Toxins 12, 457.
Salvatore MM, Alves A, Andolfi A. 2021a – Secondary Metabolites Produced by *Neofusicoccum* Species Associated with Plants: A Review. Agriculture 11.
Salvatore MM, Andolfi A, Nicoletti R. 2021b – The genus *Cladosporium*: A rich source of diverse and bioactive natural compounds. Molecules 26(13), 3959.
Salvatore MM, DellaGreca M, Andolfi A et al. 2022 – New insights into chemical and biological properties of funicone-like compounds. Toxins 14, 466.
Salvatore MM, Félix C, Lima F, Ferreira V et al. 2020b – Secondary metabolites produced by *Macrophomina phaseolina* isolated from *Eucalyptus globulus*. Agriculture 10, 72.
Salvatore MM, Masi M, Andolfi A. 2024b – The current status on secondary metabolites produced by fungi of the genus *Diplodia* associated with plants. Phytochemical Reviews.
Salvatore MM, Nicoletti R, Russo MT, Mahamedi AE et al. 2024a – First report of 6-methylpyridione analogues from *Dothiorella sarmentorum*, a botryosphaeriaceous fungus associated with grapevine trunk diseases. Natural Product Research 38, 2748–2755.
Samarakoon MC, Gafforov Y, Liu N, Maharachchikumbura SS et al. 2018 – Combined multi-gene backbone tree for the genus *Coniochaeta* with two new species from Uzbekistan. Phytotaxa 336(1), 43–58.
Samarakoon MC, Hyde KD, Hongsanan S, McKenzie EH et al. 2019 – Divergence time calibrations for ancient lineages of *Ascomycota* classification based on a modern review of estimations. Fungal Diversity 96, 285–346.
Samarakoon MC, Hyde KD, Maharachchikumbura SS, Stadler M et al. 2022 – Taxonomy, phylogeny, molecular dating and ancestral state reconstruction of *Xylariomycetidae* (*Sordariomycetes*). Fungal Diversity 112(1), 1–88.
Samarakoon MC, Hyde KD, Promputtha I, Hongsanan S et al. 2016 – Evolution of *Xylariomycetidae* (*Ascomycota*: *Sordariomycetes*). Mycosphere 7, 1746–1761.
Sambo MC. 1940 – Licheni del Brasile. Annali di Botanica 22, 19–41.
Samerpitak K, Alfjorden A, Seyedmousavi S, Rijs AJ et al. 2019 – *Ochroconisglobalis* infecting Atlantic salmon (Salmo salar), with a review of *Ochroconis* species in cold-blooded animals. Journal of Fish Diseases 42, 947–957.

Samerpitak K, Linde EVD, Choi HJ, Gerrits van den Ende AHG et al. 2014 – Taxonomy of *Ochroconis*, genus including opportunistic pathogens on humans and animals. Fungal Diversity 65, 89–126.
Samson RA, Hong S, Peterson SW, Frisvad JC et al. 2007 – Polyphasic taxonomy of *Aspergillus* section Fumigati and its teleomorph *Neosartorya*. Studies in Mycology 59, 147–203.
Samson RA, Houbraken J, Thrane U, Frisvad JC et al. 2010 – Food and Indoor Fungi, CBS laboratory manual series 2, CBS-Fungal Biodiversity Centre, Utrecht.
Samson RA, Varga J, Meijer M, Frisvad JC et al. 2011 – New taxa in *Aspergillus* section Usti. Studies in Mycology 69, 81–97.
Samson RA. 1972 – Notes on *Pseudogymnoascus*, *Gymnoascus* and related genera. Acta Botanica Neerlandica 21(5), 517–527.
Samuels GJ, Candoussau F, Magni JF. 1997 – Fungicolous pyrenomycetes 1. *Helminthosphaeria* and the new family *Helminthosphaeriaceae*. Mycologia 89, 141–155.
Samuels GJ, Muller E, Petrini O. 1987 – Studies in the *Amphisphaeriaceae* (*sensu lato*). 3. New species of *Monographella* and *Pestalosphaeria*, and two new genera. Mycotaxon 28, 473–499.
Samuels GJ, Muller E. 1978 − Life history studies of Brazilian Ascomycetes 2. Sydowia 31, 137–141.
Sánchez S, Gómez E, Martín M, De Miguel AM et al. 2014 – Experiments on the life cycle and factors affecting reproduction of *Sphaerosporella brunnea* provide evidence for rapid asexual propagation by conidiospores and for homothallism in an ectomycorrhizal competitor of cultivated truffle species. Fungal Ecology 8, 59–65.
Sancho LG, Pintado A, Green TGA, Pannewitz S et al. 2003 – Photosynthetic and morphological variation within and among populations of the Antarctic lichen *Umbilicaria aprina*: implications of the thallus size. In: Jensen, M (ed.): Lichenological Contributions in Honour of G.B. Feige. Bibliotheca Lichenologica, J. Cramer, Berlin, Stuttgart 299–311.
Sancho LG, Schroeter B, Valladares F 1997 – Photosynthetic performance of two closely related *Umbilicaria* species in central Spain: temperature as a key factor. The Lichenologist 29(1): 67–82.
Sanders WB, Masumoto H. 2021 – Lichen algae: The photosynthetic partners in lichen symbioses. The Lichenologist 53, 347–393.
Sanderson N A, Hawksworth DL, Aptroot A. 2009 – *Melaspilea* Nyl. (1857). In: Smith, C.W., Aptroot, A., Coppins, B.J., Fletcher, A., Gilbert, O.L., James, P.W. & Wolseley, P.A. (eds), The Lichens of Great Britain and Ireland. British Lichen Society, London 576–579.
Sandnes ACS. 2006 – Phylogenetic relationshipsamong species and genera of *Geoglossaceae* (*Helotiales*) based on ITS and LSU nrDNAsequences. Cand. Scient. Thesis. University of Oslo, Dep. of biology.
Sandoval-Denis M, Gene J, Sutton DA, Cano-Lira JF et al. 2016a – Redefining *Microascus*, *Scopulariopsis* and allied genera. Persoonia 36, 1–36.
Sandoval-Denis M, Gené J, Sutton DA, Wiederhold NP et al. 2016b – New species of *Cladosporium* associated with human and animal infections. Persoonia 36, 281–298.
Sandoval-Denis M, Guarro J, Cano-Lira JF, Sutton DA et al. 2016c – Phylogeny and taxonomic revision of *Microascaceae* with emphasis on synnematous fungi. Studies in Mycology 83(1), 193–233.
Sandoval-Denis M, Sutton DA, Fothergill AW, Cano-Lira J et al. 2013 – *Scopulariopsis*, a poorly known opportunistic fungus: spectrum of species in clinical samples and *in vitro* responses to antifungal drugs. Journal Clinical Microbiology 51, 3937–3943.
Sandoval-Denis M, Sutton DA, Martin-Vicente A, Cano-Lira JF et al. 2015 – *Cladosporium* species recovered from clinical samples in the United States. Journal of Clinical Microbiology 53, 2990–3000.
Sanmartín P, Fuentes E, Montojo C, Barreiro P et al. 2019 – Tertiary bioreceptivity of schists from prehistoric rock art sites in the Côa Valley (Portugal) and Siega Verde (Spain) archaeological

parks: Effects of cleaning treatments. International Biodeterioration and Biodegradation 142, 151–159.
Santamaria S, Espadaler X. 2015 – *Rickia lenoirii*, a new ectoparasitic species, with comments on world *Laboulbeniales* associated with ants. Mycoscience 56(2), 224–229.
Santesson J. 1967 – Chemical studies on lichens—III. The pigments of *Thelocarpon epibolum*, *T. laureri* and *Ahlesia lichenicola*. Phytochemistry 6(5), 685–686.
Santesson R, Moberg R, Nordin A, Tønsberg T et al. 2004 – Lichen-forming and lichenicolous fungi of Fennoscandia. Museum of Evolution, Uppsala University.
Santesson R. 1945 – Notes on the *Cryptotheciaceae*, the most primitive lichens. Svensk Botanisk Tidskrift 39, 1–8.
Santesson R. 1949 – *Dolichocarpus* and *Xanthopeltis*, two new lichen genera from Chile. Svensk Botanisk Tidskrift 43, 547–567.
Santesson R. 1952 – Foliicolous lichens. I. A revision of the taxonomy of the obligately foliicolous, lichenized fungi. Symbolae Botanicae Upsalienses 12, 1–590.
Santini A, Ghelardini L, De Pace C, Desprez-Loustau ML et al. 2013 – Biogeographical patterns and determinants of invasion by forest pathogens in Europe. New Phytologist 197, 238–50.
Sanz M, Oujja M, Ascaso C, Pérez-Ortega S et al. 2017 – Influence of wavelength on the laser removal of lichens colonizing heritage stone. Applied Surface Science 399, 758–768.
Sarhy-Bagnon V, Lozano P, Pioch D, Roussos S. 1997 – Coconut like aroma production by *Trichoderma harzianum* in solid state fermentation. Kluwer Academic.
Sarrión FJ, Hafellner J, Burgaz AR. 2002 – Three new species of the genus *Dactylospora* in Spain. The Lichenologist 34(5), 361–368.
Sassa T, Togashi M, Kitaguchi T. 1975 – The structures of cotylenins A, B, C, D and E. Agricultural and Biological Chemistry 39, 1735–1744.
Sassa T. 1971 – Cotylenins, leaf growth substances produced by a fungus. Agricultural and Biological Chemistry 35, 1415–1418.
Sati S, Pathak R. 2017 – New root endophytic water borne conidial fungi from Kumaun Himalaya. Current Botany 8, 12–16.
Satyanarayana T, Deshmukh SK, Deshpande MV. 2019 – Advancing frontiers in mycology & mycotechnology: basic and applied aspects of fungi. Springer. 701.
Savić S, Tibell L, Gueidan C, Lutzoni F. 2008 – Molecular phylogeny and systematics of *Polyblastia* (*Verrucariaceae*, *Eurotiomycetes*) and allied genera. Mycological Research 112(11), 1307–1318.
Savicz VP. 1950 – Conspectus lichenum ad flora Umbilicariacearum in URSS // Notulae System. e Sect. Cryptogamica Inst. Bot. nomine V. L. Komarovii Acad. Sci. URSS, 6(7–12), 97–108.
Savory JG. 1954a – Breakdown of timber by *Ascomycetes* and Fungi Imperfecti. Annals of Applied Biology 41, 336–347.
Savory JG. 1954b – Damage to wood caused by micro-organisms. Journal of Applied Bacteriology 17, 213–218.
Saxena P, Kumar A, Shrivastava JN. 2005 – Keratinophilic fungi: a microbial way to manage poultry waste feathers. Indian Journal of Microbiology 45, 151–154.
Saxena RK, Wijayawardene NN, Dai DQ, Hyde KD et al. 2021– Diversity in fossil fungal spores. Mycosphere 12, 670–874.
Sbaraini N, Andreis FC, Thompson CE, Guedes RL et al. 2017 – Genome-wide analysis of secondary metabolite gene clusters in *Ophiostoma ulmi* and *Ophiostoma novo-ulmi* reveals a Fujikurin-like gene cluster with a putative role in infection. Frontiers in Microbiology 8, 1063.
Scardaci SC, Webster RK, Greer CA et al. 2003 – "Rice Blast: A New Disease in California". Agronomy Fact Sheet Series. University of California-Davis (UCD). Archived from the original on 2006–09–11. Retrieved 2014–02–25.
Scarlett KA, Shuttleworth LA, Collins D, Rothwell CT. 2018 – *Botryosphaeriales* associated with stem blight and dieback of blueberry (*Vaccinium* spp.) in New South Wales and Western Australia. Australasian Plant Pathology 48, 45–57.

Schadt CW, Martin AP, Lipson DA, Schmidt SK. 2003 – Seasonal dynamics of previously unknown fungal lineages in tundra soils. Science 301(5638), 1359–1361.
Schaerer LE. 1833 – *Lichenum Helveticorum Spicilegium* (Vol. 2).
Schaumann K, Mulach W, Molitoris HP. 1986 – Comparative studies on growth and exoenzyme production of different *Lulworthia* isolates. The biology of marine fungi. Cambridge Press, Cambridge 49–60.
Scheidegger C, Mayrhofer H, Moberg R, Tehler A. 2001 – Evolutionary trends in the *Physciaceae*. The Lichenologist 33(1), 25–45.
Scheidegger C, Ruef B. 1988 – Die xanthonhaltigen, gesteinsbewohnenden Sippen der Flechtengattung Buellia De Not. (*Physciaceae*, *Lecanorales*) in Europa. - Nova Hedwigia 47, 433–468.
Scheidegger C. 1988 – Beiträge zu einer Revision gesteinsbewohnender Sippen der Flechtengattung Buellia de Not. in Europa. - Doctoral Thesis, University of Bern (Switzerland).
Scheidegger C. 1993 – A revision of European saxicolous species of the genus Buellia De Not. And formerly included genera. The Lichenologist 25, 315– 364.
Scheidegger C. 1995 – Reproductive strategies in *Vezdaea* (*Lecanorales*, lichenized *Ascomycetes*): a low-temperature scanning electron microscopy study of a ruderal species. Cryptogamic Botany 5, 163–171.
Scheuer C, Nograsek A. 1993 – *Trematosphaeria pachycarpa* and *Herbampulla crassirostris* gen. et spec. nov. (Ascomycetes). Mycotaxon 47, 415–424.
Scheuer C. 1988 – Ascomyceten auf Cyperaceen und Juncaceen im Ostalpenraum. Bibliotheca Mycologica 23, 1–274.
Schlatter DC, Burke I, Paulitz TC. 2017 – Succession of fungal and Oomycete communities in glyphosate-killed wheat roots. Phytopathology 108, 582–594.
Schmidt A. 1970 – Anatomisch-taxonomische Untersu- chungen an Europaischen Arten der Flechtenfamilie Cal- iciaceae. Mitt. Staatsinst. Allg. Bot. Hamburg 13, 111–166.
Schmidt AR, Dörfelt H, Perrichot V. 2007 – Carnivorous fungi from Cretaceous amber. Science 318, 1743.
Schmidt AR, Dörfelt H, Perrichot V. 2008 – *Palaeoanellus dimorphus* gen. et sp. nov. (*Deuteromycotina*): a Cretaceous predatory fungus. American Journal of Botany 95, 1328–1334.
Schmidt I. 1985 – Types and type collections of new higher marine and fresh-water fungi from the Baltic coast. Mycotaxon 24, 419–421.
Schmit JP, Shearer CA. 2003 – A checklist of mangrove-associated fungi, their geographical distribution and known host plants. Mycotaxon 85, 423–478.
Schmitt I, del Prado R, Grube M, Lumbsch HT. 2009 – Repeated evolution of closed fruiting bodies is linked to ascoma development in the largest group of lichenized fungi (*Lecanoromycetes*, *Ascomycota*). Molecular Phylogenetics and Evolution 52, 34–44.
Schmitt I, Fankhauser JD, Sweeney K, Spribille T et al. 2010 – Gyalectoid *Pertusaria* species form a sister-clade to *Coccotrema* (*Ostropomycetidae*, *Ascomycota*) and comprise the new lichen genus *Gyalectaria*. Mycology 1(1), 75–83.
Schmitt I, Lumbsch HT. 2004 – Molecular phylogeny of the *Pertusariaceae* supports secondary chemistry as an important systematic character set in lichen-forming *Ascomycetes*. Molecular Phylogenetics and Evolution 33(1), 43–55.
Schmitt I, Mueller G, Lumbsch HT. 2005 – Ascoma morphology is homoplaseous and phylogenetically misleading in some pyrenocarpous lichens. Mycologia 97, 362–374.
Schmitt I, Yamamoto Y, Lumbsch HT. 2006 – Phylogeny of *Pertusariales* (*Ascomycotina*): resurrection of *Ochrolechiaceae* and new circumscription of *Megasporaceae*. The Journal of the Hattori Botanical Laboratory 100, 753–764.

Schmull M, Miadlikowska J, Pelzer M, Stocker-Wörgoetter E. 2011 – Phylogenetic affiliations of members of the heterogeneous lichen-forming fungi of the genus *Lecidea sensu* Zahlbruckner (*Lecanoromycetes*, *Ascomycota*). Mycologia 103, 983–1003.
Schmull M, Spribille T. 2005 – *Schaereria dolodes* (Nyl. eHasse) Schmull & T Sprib.: a second corticolous species in the genus. The Lichenologist 37(6), 527–533.
Schneider G, Anke H, Sterner O. 1995 – Xylarin, an antifungal *Xylaria* metabolite with an unusual tricyclic uronic acid moiety. Natural Product Letters 7(4), 309–316.
Schneider G, Anke H, Sterner O. 1996 – Xylaramide, a new antifungal compound, and other secondary metabolites from *Xylaria longipes*. Zeitschrift fur Naturforschung - Section C Journal of Biosciences 51(11-12), 802–6.
Schneider G. 1979 – Die Flechtengattung *Psora sensu* Zahlbruckner. Bibliotheca Lichenologica 13. J. Cramer, Vaduz. 291
Schoch C, Sung GH, López-Giráldez F, Townsend JP et al. 2009a – The *Ascomycota* tree of life: A phylum wide phylogeny clarifies the origin and evolution of fundamental reproductive and ecological traits. Systematic Biology 58, 224–239.
Schoch CL, Crous PW, Groenewald JZ, Boehm EW et al. 2009b – A class-wide phylogenetic assessment of *Dothideomycetes*. Studies in Mycology 64, 1–15.
Schoch CL, Grube M. 2015 – *Pezizomycotina*: *Dothideomycetes* and *Arthoniomycetes*. In: (McLaughlin DJ, Spatafora JW, eds), The Mycota, systematics and evolution part B, VII. Springer.
Schoch CL, Shoemaker RA, Seifert KA, Hambelton S et al. 2006 – A multigene phylogeny of the *Dothideomycetes* using four nuclear loci. Mycologia 98, 1041–1052.
Schoch CL, Sung GH, Volkmann-Kohlmeyer B, Kohlmeyer J et al. 2007 – Marine fungal lineages in the *Hypocreomycetidae*. Mycological Research 111(2), 154–162.
Schoch CL, Wang Z, Townsend JP, Spatafora JW. 2009c – *Geoglossomycetes* cl. nov. *Geoglossales* ord. nov and taxa above class rank in the *Ascomycota* tree of life. Persoonia (22), 129–138.
Scholander PF. 1934 – On the apothecia in the lichen family *Umbilicariaceae*. Nytt Magazin for Naturvidenskaberne 75, 1–132.
Scholler M, Hagedorn G, Rubner A. 1999 – A reevaluation of predatory orbiliaceous fungi. II. A new generic concept. Sydowia 51, 89–113.
Schol-Schwarz MB. 1970 – Revision of the genus *Phialophora* (*Moniliales*). Persoonia 6, 59–94.
Schroeter B, Green TGA, Pannewitz S, Schlensog M et al. 2011 – Summer variability, winter dormancy: Lichen activity over 3 years at Botany Bay, 77°S latitude, continental Antarctica. Polar Biology 34(1), 13–22.
Schroeter B, Scheidegger C. 1995 – Water relations in lichens at subzero temperatures: structural changes and carbon dioxide exchange in the lichen *Umbilicaria aprina* from continental Antarctica. New Phytologist 131(2), 273–285.
Schubert K, Braun U. 2005 – Taxonomic revision of the genus *Cladosporium* sl 4. Species reallocated to *Asperisporium*, *Dischloridium*, *Fusicladium*, *Passalora*, *Pseudoasperisporium* and *Stenella*. Fungal Diversity 20, 187–208.
Schubert K, Groenewald JZ, Braun U, Dijksterhuis J M et al. 2007 – Biodiversity in the *Cladosporium herbarum* complex (*Davidiellaceae*, *Capnodiales*), with standardisation of methods for *Cladosporium* taxonomy and diagnostics. Studies in Mycology 58, 105–156.
Schubert K, Ritschel A, Braun U. 2003 – A monograph of *Fusicladium* s. lat. (*Hyphomycetes*). Schlechtendalia 9, 1–132.
Schultz M, Aptroot A. 2008 – Notes on poorly known, small cyanobacterial lichens from predominantly wet tropical to subtropical regions. Sauteria 15, 433–458.
Schultz M, Arendholz WR, Büdel B. 2001 – Origin and evolution of the lichenized *Ascomycetes* order Lichinales: monophyly and systematic relationships inferred from ascus, fruiting body and SSU rDNA evolution. Plant Biology 3, 116–123.
Schultz M, Büdel B. 2002 – Key to the genera of the *Lichinaceae*. The Lichenologist 34(1), 39–62.

Schultz M, Büdel B. 2003 – On the systematic position of the lichen genus *Heppia*. The Lichenologist 35, 151–156.
Schultz M, Porembski S, Büdel B. 2000 – Diversity of rock-inhabiting cyanobacterial lichens: studies on granite inselbergs along the Orinoco and in Guyana. Plant Biology 2, 482–495.
Schultz M, Wedin M, Diel H, Prieto M. 2015 – *Epiphloea* belongs to *Collemataceae* (*Lecanoromycetes*, lichenized *Ascomycota*). The Lichenologist 47, 369–378.
Schultz M. 1998 – Studies on lichens from southern Yemen (Arabian Peninsula). The Lichenologist 30, 293–297.
Schumacher RW, Waters AL, Peng J, Schumacher RA et al. 2022 – Structure and antimicrobial activity of rare lactone lipids from the sooty mold (*Scorias spongiosa*). Journal of Natural Products 85(5), 1436–1441.
Schumacher T, Sivertsen S. 1987 – *Sarcoleotia globosa* (Sommerf.: Fr.) Korf, taxonomy, ecology and distribution. In: Larsen, G.A. Amirati, J.F. Redhead, S.A. (Eds.), Arctic and Alpine Mycology 2. Plenum Press, New York and London 163–176.
Schumm F, Aptroot A. 2022 – Atlas of *Pyrenulaceae* and *Trypetheliaceae*. Books on Demand, Norderstedt. 2081
Schwan RF, Wheals AE. 2004 – The microbiology of cocoa fermentation and its role in chocolate quality. Critical Reviews in Food Science and Nutrition 44(4), 205–221.
Schweinitz LD. 1822 – Synopsis fungorum carolinae superioris. Schr Naturf Ges Leipzig 1, 1–105.
Scott IU, Cruz-Villegas V, Flynn HW, Miller D. 2004 – Delayed-Onset, Bleb-Associated Endophthalmitis Caused by *Lecythophora Mutabilis*. American Journal of Ophthalmology 137(3), 58385.
Scott JA, Malloch DW, Gloer JB. 1993 – *Polytolypa*, an undescribed genus in the *Onygenales*. Mycologia 85(3), 503–508.
Scott MG, Larson DW. 1986 – The Effect of winter field conditions on the distribution of two species of *Umbilicaria*. I. CO_2 exchange in reciprocally-transplanted thalli. The New Phytologist 101(1), 89–101.
Scott PM, van Walbeek W, MacLean WM. 1971 – Cladosporin, a new antifungal metabolite from *Cladosporium cladosporioides*. The Journal of Antibiotics 24, 747–755.
Seaver FJ, Chardón CE. 1926 – Botany of Porto Rico and the Virgin Islands. Mycology. Scientific Survey of Porto Rico and the Virgin Islands 8 1, 1–208.
Seaver FJ, Waterston JM. 1946 – Contributions to the Mycoflora of Bermuda—IV. Mycologia 38, 180–201.
Seaver FJ. 1928 – The North American cup-fungi (operculates). Hafner Publishing Co., Inc., New York
Seaver FJ. 1928a – Studies in tropical ascomycetes. V. Species of *Phyllachora*. Mycologia 20, 214–225.
Seaver FJ. 1928b – The North American cup-fungi (operculates). New York: Hafner Publishing Co, Inc. 377.
Seaver FJ. 1951 – The North American cup-fungi (non-operculates). Hafner Publishing Co., Inc., New York
Seaver FJ. 1961 – The North American cup-fungi (Inoperculates), supplemented edition. Hafner, New York, New York, USA.
Seeler EV. 1943 – "Several Fungicolous Fungi". Farlowia 119 –133.
Segeth MP, Bonnefoy A, Broenstrup M, Knauf M et al. 2003 – Coniosetin, a novel tetramic acid antibiotic from *Coniochaeta ellipsoidea* DSM 13856. The Journal of Antibiotics 56(2), 114–122.
Seifert K, Morgan-Jones G, Gams W, Kendrick B. 2011 – The Genera of *Hyphomycetes*. CBS Biodiversity Series no. 9, 1–997. CBS-KNAW Fungal Biodiversity Centre, Utrecht, Netherlands
Seifert KA. 1993 – Sapstain of commercial lumber by species of *Ophiostoma* and *Ceratocystis*. *Ceratocystis* and *Ophiostoma*: taxonomy, ecology and pathogenicity 141–151.

Seike T, Niki H. 2022 – Pheromone Response and Mating Behavior in Fission Yeast. Microbiology and Molecular Biology Reviews 86(4). e00130–22.
Seixas CDS, Barreto RW, Killgore E. 2007 – Fungal pathogens of *Miconia calvescens* (*Melastomataceae*) from Brazil, with reference to classical biological control. Mycologia 99, 99–111.
Selbmann L, Turchetti B, Yurkov A, Cecchini C et al. 2014 – Description of *Taphrina antarctica f.a.* sp. nov., a new anamorphic ascomycetous yeast species associated with Antarctic endolithic microbial communities and transfer of four *Lalaria* species in the genus *Taphrina*. Extremophiles 18(4), 707–721.
Selbmann L, Zucconi L, Isola D, Onofri S. 2015 – Rock black fungi: excellence in the extremes, from the Antarctic to space. Current Genetics 61, 335–345.
Selva SB. 1996 – Using lichens to assess ecological continuity in northeastern forests. In Eastern Old-Growth Forests: Prospects for Rediscovery and Recovery (M. Davis, ed.), 35–48.
Selva SB. 2014 – The calicioid lichens and fungi of the Acadian Forest Ecoregion of northeastern North America, II. The rest of the story. The Bryologist 117, 336 –367.
Senanayake IC, Al-Sadi AM, Bhat JD, Camporesi E et al. 2016 – *Phomatosporales* ord. nov. and *Phomatosporaceae* fam. nov., to accommodate *Lanspora*, *Phomatospora* and *Tenuimurus*, gen. nov. Mycosphere 7(5), 628–641.
Senanayake IC, Crous P, Groenewald J, Maharachchikumbura SSN et al. 2017a – Families of *Diaporthales* based on morphological and phylogenetic evidence. Studies in Mycology 86, 217–296.
Senanayake IC, Jeewon R, Chomnunti P, Wanasingha DN et al. 2018 – Taxonomic circumscription of *Diaporthales* based on multigene phylogeny and morphology. Fungal Diversity 93(1), 241–443.
Senanayake IC, Maharachchikumbura SS, Hyde KD, Bhat JD et al. 2015 – Towards unraveling relationships in *Xylariomycetidae* (*Sordariomycetes*). Fungal Diversity 73, 73–144.
Senanayake IC, Maharachchikumbura SSN, Jeewon R, Promputtha I et al. 2017b – Morphophylogenetic study of *Sydowiellaceae* reveals several new genera. Mycosphere 8(1), 172–217.
Senanayake IC, Pem D, Rathnayaka AR, Wijesinghe SN et al. 2022 – Predicting global numbers of teleomorphic *Ascomycetes*. Fungal Diversity 114(1), 237–278.
Senanayake IC, Rossi W, Leonardi M, Weir A et al. 2023 – Fungal diversity notes 1611–1716: taxonomic and phylogenetic contributions on fungal genera and species emphasis in south China. Fungal Diversity 122, 161–403.
Senn-Irlet B, Bieri G, Egli S. 2007 – Liste rouge des champignons supérieurs menacés en Suisse. L'environnement pratique (0718).
Seo C, HanYim J, Kum Lee H, Oh H. 2011 – PTP1B inhibitory secondary metabolites from the Antarctic lichen *Lecidella carpathica*. Mycology 2, 18–23.
Serrano L, Sosa D, Magdama F, Espinoza F et al. 2020 – *Neomyrmecridium asymmetricum* sp. nov. from Ecuador. Mycotaxon 135, 151–165.
Sert HB, Sterflinger K. 2010 – A new *Coniosporium* species from historical marble monuments. Mycololgical Progress 9(3), 353–359.
Sert HB, Sümbül H, Sterflinger K. 2007 – A new species of *Capnobotryella* from monument surfaces. Mycological Research 111(10), 1235–1241.
Sérusiaux E. 1979 – Contribution to the study of Lichens from Kivu (Zayre), Rwanda and Burundi, III, *Vezdaea,* a new genus for Africa. Mycotaxon 8, 135–139.
Servít M. 1946 – The new lichens of the Pyrenocarpaed group I. Studia Botanica Cechoslovaca 7, 49–111.
Servít M. 1950a. The new lichens of the Pyrenocarpaed group III. Studia Botanica Cechoslovaca 11, 7–41.
Servít M. 1950b. The new lichens of the Pyrenocarpaed group IV. Studia Botanica Cechoslovaca 11, 101–144.

Servít M. 1952 – Nove´ a ma´ lo zna´me´ druhy z c˘eledı´ Verrucariaceae a Dermatocarpaceae. Preslia 24, 345–390.
Servít M. 1953 – Species novae Verrucariarum et generum affinium. Rozpravy Ceskoslovenske´ Akademie Ve˘d 63, 1–33.
Servít M. 1954 – Lichenes Familiae Verrucariacearum. Nakladatelstvi Ceskoslovenske´ Akademie Ve˘d, Praha, 249.
Servít M. 1955 – Lichenes novi. Rozpravy Ceskoslovenske´ AkademieVe˘d 65, 1–45.
Seybold SJ, Bentz BJ, Fettig CJ, Lundquist JE et al. 2018 – Management of western North American bark beetles with semiochemicals. Annual Review of Entomology 63, 407–432.
Seyedmousavi S, Badali H, Chlebicki A, Zhao J et al. 2011 – Exophiala sideris, a novel black yeast isolated from environments polluted with toxic alkyl benzenes and arsenic. Fungal biology 115, 1030–1037.
Seyedmousavi S, Guillot J, Arné P, de Hoog GS et al. 2015–*Aspergillus* and aspergilloses in wild and domestic animals: a global health concern with parallels to human disease. Medical Mycology 53, 765–797.
Shafi SM, Sheikh MA, Nabi SU, Mir MA et al. 2019 – An overview of apple scab, its cause and management strategies. EC Microbiology 15, 1–4.
Shah JS, Pieciak W, Liu J, Buharin A et al. 1996 – Diversity of host species and strains of *Pneumocystis carinii* is based on rRNA sequences. Clinical and Vaccine Immunology 3, 119–127.
Shahim S, Gachande BD, Shaikh NF. 2019 – Isolation and screening of endophytic fungi for biosynthesis of silver nanoparticles. Think India Journal 22, 366–376.
Shahzad R, Waqas M, Khan AL, Asaf S et al. 2017 – Seed-borne endophytic *Bacillus amyloliquefaciens* RWL-1 produces gibberellins and regulates endogenous phytohormones of *Oryza sativa*. Plant Physiology and Biochemistry 115, 314–324.
Shang QJ, Hyde KD, Liu JK. 2021 – *Phaeoacremonium fusiformostromum* sp. nov. and a new record of *P. croatiense* from China. Phytotaxa 516(1), 59–72.
Shao L, Marin-Felix Y, Surup F, Stchigel AM et al. 2020 – Seven new cytotoxic and antimicrobial xanthoquinodins from *Jugulospora vestita*. Journal of Fungi 6(4), 188.
Shao LP, Shen RX, Zhang SX, Xiang CT et al. 1948 – Taxonomy of fungi. Beijing: China Forestry Publishing House. 1–370.
Sharma N, Kushwaha M, Arora D, Jain S et al. 2018 – New cytochalasin from *Rosellinia sanctaecruciana*, an endophytic fungus of *Albizia lebbeck*. Journal of Applied Microbiology 125, 111–20.
Sharma R, Saxena S, Kumar, A. 2017 – Indoor fungal contamination: Health risks and measurement techniques. Environmental Research 158, 706–717.
Shaw JJ, Spakowicz DJ, Dalal RS, Davis JH et al. 2015 – Biosynthesis and genomic analysis of medium-chain hydrocarbon production by the endophytic fungal isolate *Nigrograna mackinnonii* E5202H. Applied Microbiology and Biotechnology 99, 3715–3728.
She R, Wang HQ, Fornacca D, Li FT et al. 2023 – Independence effects of heat and ash on forest soil nematode-trapping fungi communities. Fire 6(1), 27.
Shear CL. 1929 – The life-history of *Sphaceloma ampelinum* de Bary. Phytopathology 19, 673–679.
Shear CL. 1938 – Mycological notes. II. Mycologia 30, 580–593.
Sheard JW. 1982 – The saxicolous species of the lichenized Ascomycete genus *Rinodina* (Ach.) Gray with blue epithecia. Bryologist 1, 88–95.
Shearer CA, Miller M. 1977 – Fungi of the Chesapeake Bay and Its Tributaries V. *Aniptodera chesapeakensis* gen. et sp. nov. Mycologia 69, 887–898.
Shearer CA, Motta JJ. 1973 – Ultrastructure and conidiogenesis in *Conioscypha* (*Hyphomycetes*). Canadian Journal of Botany 51, 1747–1751.
Shearer CA, Pang KL, Suetrong S, Raja HA. 2014 – Phylogeny of the *Dothideomycetes* and other classes of freshwater fissitunicate *Ascomycota*. In: Jones E, Hyde K, Pang K (eds) Freshwater Fungi. Walter de Gruyter, Berlin pp 25–46

Shearer CA, Raja HA, Miller AN, Nelson P et al. 2009 – The molecular phylogeny of freshwater *Dothideomycetes*. Studies in Mycology 64, 145–153.
Shearer CA, Zelski SE, Raja HA, Schmit JP et al. 2015 – Distributional patterns of freshwater *Ascomycetes* communities along an Andes to Amazon elevational gradient in Peru. Biodiversity and Conservation 24, 1877–1897.
Shearer CA. 1973 – Fungi of the Chesapeake Bay and its tributaries II. The genus *Conioscypha*. Mycologia 65, 128e136.
Shearer CA. 1993 – The freshwater *Ascomycetes*. Nova Hedwigia 56, 1–33.
Shearer CA. 2001 – The distribution of freshwater filamentous ascomycetes. In: Trichomycetes and other fungal groups (Misra JK, Horn BW, Robert W, eds). Lichtwardt Commemoration. Science Publishers, Plymouth, UK. 225–292.
Shen HW, Bao DF, Hyde KD, Su HY et al. 2021 – Two novel species and two new records of *Distoseptispora* from freshwater habitats in China and Thailand. MycoKeys 84, 79–101.
Shen M, Zhang JQ, Zhao LL, Groenewald JZ et al. 2020a– *Venturiales*. Studies in Mycology 96, 185–308.
Shen SK, Dowd PF. 1991 – Detoxification spectrum of the cigarette beetle symbiont *Symbiotaphrina kochii* in culture. Entomologia Experimentalis et Applicata 60(1), 51–59.
Shen SZ, Crowley JL, Wang Y, Bowring SA et al. 2011 – Calibrating the end-Permian mass extinction. Science 334, 1367–1372.
Shen XX, Opulente DA, Kominek J, Zhou X et al. 2018 – Tempo and mode of genome evolution in the budding yeast subphylum. Cell 175, 1533–1545.
Shen XX, Steenwyk JL, LaBella AL, Opulente DA et al. 2020b – Genome-scale phylogeny and contrasting modes of genome evolution in the fungal phylum Ascomycota. Science Advances 45, eabd0079.
Shenoy BD, Jeewon R, Wang H, Amandeep K et al. 2010 – Sequence data reveals phylogenetic affinities of fungal anamorphs *Bahusutrabeeja*, *Diplococcium*, *Natarajania*, *Paliphora*, *Polyschema*, *Rattania* and *Spadicoides*. Fungal Diversity 44, 161–169.
Shenoy BD, Jeewon R, Wu WP, Bhat DJ. 2006 – Ribosomal and RPB2 DNA sequence analyses suggest that *Sporidesmium* and morphologically similar genera are polyphyletic. Mycological Research 110, 916–928.
Sherwood MA. 1977a – Taxonomic studies in the *Phacidiales*: *Propolis* and *Propolomyces*. Mycotaxon 5(1), 320-330.
Sherwood MA. 1977b − The ostropalean fungi. Mycotaxon 5(1), 1–277.
Sherwood MA. 1978 – New *Ostropales* from the collections of the Farlow Herbarium. Occasional Papers of the Farlow Herbarium of Cryptogamic Botany 13, 39–47.
Sherwood MA. 1980 – Taxonomic studies in *Phacidiales*: the genus *Coccomyces* (*Rhytismataceae*). Occasional papers of the Farlow Herbarium of Cryptogamic Botany 15, 1–120.
Sherwood MA. 1981 – Convergent evolution in *Discomycetes* from bark and wood. Botanical Journal of the Linnean Society 82, 15–34.
Sherwood-Pike MA. 1987 – The ostropalean fungi III: the *Odontotremataceae*. Mycotaxon 28(1), 137–177.
Shi Y, Yan T, Yuan C, Li C et al. 2022 – Comparative physiological and transcriptome analysis provide insights into the response of *Cenococcum geophilum*, an ectomycorrhizal fungus to cadmium stress. Journal of Fungi 8(7), 724.
Shigemori H, Tenma M, Shimazaki K, aKobayashi JI. 1998 – Three new metabolites from the marine yeast *Aureobasidium pullulans*. Journal of Natural Products 61(5), 696–698.
Shimono Y, Arima T, Hyakumachi M, Hassan MM et al. 2021 – Isolation and characterization of mating type genes of *Pseudopyrenochaeta lycopersici*. Canadian Journal of Plant Pathology 43(6), 886–896.
Sieber TN. 2007 – Endophytic fungi in forest trees: are they mutualists? Fungal Biology Reviews 21, 75–89.

Sienkiewicz N, Jaroslawski S, Wyllie S, Fairlamb AH. 2008 – Chemical and genetic validation of dihydrofolate reductasethymidylate synthase as a drug target in African trypanosomes. Molecular Microbiology 69, 520–533.
Sierra DL. 2006 – Contribución al estudio de los Ascomicetes bitunicados de Cataluña. Acta botánica Barcinonensia 50, 5–434.
Sigler L, Abbott SP, Woodgyer AJ. 1994 – New records of nail and skin infection due to *Onychocola canadensis* and teleomorph *Arachnomyces nodosetosus* sp. nov. Journal of Medical and Veterinary Mycology 32, 275–285.
Sigler L, Carmichael JW. 1983 – Redisposition of some fungi referred to *Oidium microspermum* and a review of *Arthrographis*. Mycotaxon 18(2), 495–507.
Sigler L, Congly H. 1990 – Toenail infection caused by *Onychocola canadensis* gen. et sp. nov. Journal of Medical and Veterinary Mycology 28 (5), 405–417.
Sigler L, Tsuneda A, Carmichael JW. 1981 – *Phaeotheca* and *Phaeosclera*, two new genera of dematiaceous hyphomycetes and a redescription of *Sarcinomyces* Lindner. Mycotaxon 12, 449–467.
Sigler L. 2002 – Miscellaneous opportunistic fungi, *Microascaceae* and other *Ascomycetes*, *Hyphomycetes*, *Coelomycetes*, and *Basidiomycetes*. Pathogenic Fungi in Humans and Animals 2, 637–676.
Silva CF, Schwan RF, Dias ËS, Wheals AE. 2000 – Microbial diversity during maturation and natural processing of coffee cherries of *Coffea arabica* in Brazil. International Journal of Food Microbiology 60(2-3), 251–260.
Silva GH, Zeraik ML, de Oliveira CM, Teles HL et al. 2017 – Lactone derivatives produced by a *Phaeoacremonium* sp., an endophytic fungus from *Senna spectabilis*. Journal of Natural Products 80, 1674–1678.
Silva LRD Fortuna JL. 2020 – First record of *Geoglossum fallax* (*Geoglossaceae*, *Ascomycota*) in the southernmost region of the state of Bahia, northeastern Brazil. Bioscience Journal *36*(2), 602–605.
Silva NID, Thambugala KM, Tennakoon DS, Karunarathna SC et al. 2022 – Taxonomy and phylogenetic appraisal of dothideomycetous fungi associated with *Magnolia*, *Lilium longiflorum* and *Hedychium coronarium*. Journal of Fungi 8(10), 1094.
Simmons DR, De Beer ZW, Huang YT, Bateman C et al. 2016 – New *Raffaelea* species (*Ophiostomatales*) from the USA and Taiwan associated with ambrosia beetles and plant hosts. IMA Fungus 7, 265–273.
Simoni M, Annesi-Maesano I, Sigsgaard T, Norback D et al. 2010 – School air quality related to dry cough, rhinitis and nasal patency in children. European Respiratory Journal 35(4), 742–749.
Simonis JL, Raja HA, Shearer CA. 2008 – Extracellular enzymes and soft rot decay: are *Ascomycetes* important degraders in fresh water. Fungal Diversity 31, 135–146.
Sinclair K, Wakefield AE, Banerji S, Hopkin JM. 1991 – *Pneumocystis carinii* organisms derived from rat and human hosts are genetically distinct. Molecular and Biochemical Parasitology 45(1), 183–4.
Singh G, Calchera A, Schulz M, Drechsler M et al. 2021 – Climate-specific biosynthetic gene clusters in populations of a lichen-forming fungus. Environmental Microbiology 23(8), 4260–4275.
Singh G, Dal Grande F, Schmitt I. 2022 – Genome mining as a biotechnological tool for the discovery of novel biosynthetic genes in lichens. Frontiers in Fungal Biology 3, 993171.
Singh HB, Johri JK, Singh M, Singh A et al. 1999 – A new leaf spot disease of *Cuphea* spp. caused by *Chaetomella raphigera*. EPPO Bulletin 29(1-2), 213–214.
Singh SB, Zink DL, Liesch JM, Goetz MA et al. 1993 – Isolation and structure of chaetomellic acids A and B from *Chaetomella acutiseta*: farnesyl pyrophosphate mimic inhibitors of Ras farnesyl-protein transferase. Tetrahedron 49(27), 5917–5926.
Singh UB, Sahu A, Singh RK, Singh DP et al. 2012 – Evaluation of biocontrol potential of *Arthrobotrys oligospora* against *Meloidogyne graminicola* and *Rhizoctonia* solani in Rice (*Oryza sativa* L.). Biological control 60(3), 262–270.

Sipiczki M. 1995 – Phylogenesis of fission yeasts. Contradictions surrounding the origin of a century old genus. Antonie Leeuwenhoek 68, 119–149.
Sipiczki M. 2000 – Where does fission yeast sit on the tree of life?. Genome biology 1(2), 1–4.
Sipman HJM, Aptroot A. 2001 – Where are the missing lichens? Mycological Research 105, 1433–1439.
Sivanesan A, Chang HS. 1992 – *Ascotaiwania*, a new amphisphaeriaceous ascomycete genus on wood from Taiwan. Mycological Research 96, 481–484.
Sivanesan A, Shivas RG. 2002 – New species of *Lembosia* and *Lembosina* from Australia. Fungal Diversity 11, 159–168.
Sivanesan A. 1984 – Teleomorphs of *Clasterosporium anomalum* and *C. cyperi*. Transactions of the British Mycological Society 83(4), 710–718.
Sivanesan A. 1976 – New British species of *Rhamphoria*, *Trematosphaeria* and *Chaetosphaerella*. Transactions of the British Mycological Society 67(3), 469–475.
Sivichai S, Boonyuen N. 2010 – *Jahnula morakotii* sp. nov. and *J. appendicutata* from a peat swamp in Thailand. Mycotaxon 112, 475–481.
Sivichai S, HyweI-Jones N, Jones EBG. 1998 – Lignicolous freshwater *Ascomycota* from Thailand: 1. *Ascotaiwania sawada* and its anamorph state *Monotosporella*. Mycoscience 39, 307–311.
Six DL, Wingfield MJ. 2011 – The role of phytopathogenicity in bark beetle–fungus symbioses: a challenge to the classic paradigm. Annual Review of Entomology 56, 255–272.
Six DL. 2012 – Ecological and evolutionary determinants of bark beetle-fungus symbioses. Insects 3, 339–366.
Sjamsuridzal W, Tajiri Y, Nishida H, Thuan TB et al. 1997 – Evolutionary relationships of members of the genera *Taphrina*, *Protomyces*, *Schizosaccharomyces*, and related taxa within the archiascomycetes: integrated analysis of genotypic and phenotypic characters. Mycoscience 38, 267–280.
Sklenář F, Jurjević Ž, Peterson SW, et al. 2020–Increasing the species diversity in the *Aspergillus* section *Nidulantes*: six novel species mainly from the indoor environment. Mycologia 112, 342–370.
Sletvold N, Hestmark G. 1997 – Thallus growth asymmetry and habitat inclination in *Lasallia pustulata*. The Bryologist 100(4), 465–466.
Slifkin M, Bowers HM. 1975 – *Phialophora mutabilis* Endocarditis. American Journal of Clinical Pathology 63(1), 12030.
Slippers B, Boissin E, Phillips A, Groenewald JZ et al. 2013 – Phylogenetic lineages in the *Botryosphaeriales*: a systematic and evolutionary framework. Studies in Mycology 76, 31–49.
Slippers B, Crous PW, Jami F, Groenewald JZ et al. 2017 – Diversity in the *Botryosphaeriales*: Looking back, looking forward. Fungal Biology 121(4), 307–321.
Slippers B, Roux J, Wingfield MJ, Van der Walt FJJ et al. 2014 – Confronting the constraints of morphological taxonomy in the *Botryosphaeriales*. Persoonia: Molecular Phylogeny and Evolution of Fungi 33(1), 155–168.
Slippers B, Wingfield MJ. 2007– *Botryosphaeriaceae* as endophytes and latent pathogens of woody plants: diversity, ecology and impact. Fungal Biology Reviews 21, 90–106.
Smith AL. 1901 – On some fungi from the West Indies. The Journal of the Linnean Society. Botany 35, 1–19.
Smith AL. 1921 – Lichens. xxviii + 464, 135 flgs. Cambridge.
Smith AL. 1926 – *Cryptotheciaceae*, a family of primitive lichens. Transactions of the British Mycological Society. Worcester 11, 189–196.
Smith CW, Aptroot A, Coppins BJ, Fletcher A et al. 2009 – The Lichens of Great Britain and Ireland. British Lichen Society, London.
Smith GJD, Liew ECY, Hyde KD 2003 – The *Xylariales*: a monophyletic order containing 7 families. Fungal Diversity 13, 185–218.
Smith IM, Dunez J, Phillips DH, Lelliott RA et al. 1988 – European handbook of plant diseases. Blackwell Scientific Publications, Oxford, UK, 583.

Sobianski Herman T, Gomes RR, Queiroz Telles F, Pedroso CA et al. 2024 – Identification of CARD9 mutation in patients with chromoblastomycosis and evaluation of the immunological response. One Health Mycol 1, 14–23.
Søchting U, Lorentsen LB, Arup U. 2008 – The lichen genus *Caloplaca* (*Ascomycota*, *Lecanoromycetes*) on Svalbard. Notes and additions. Nova Hedwigia 87(1-2), 69–96.
Søchting U, Søgaard MZ, Ulf AR, Elvebakk A et al. 2014 – *Catenarina* (*Teloschistaceae*, *Ascomycota*), a new Southern Hemisphere genus with 7-chlorocatenarin. The Lichenologist 46(2), 175–187.
Sohrabi M. 2006 – Lichens and stone surfaces decay in the Imperial Palace of Persepolis (Shiraz, Iran). Notiziario della Società Lichenologica Italiana 19, 38.
Sokulska M, Kicia M, Wesołowska M, Hendrich AB. 2015 – *Pneumocystis jirovecii*—from a commensal to pathogen: clinical and diagnostic review. Parasitology Research 114, 3577–3585.
Sommerfelt SC. 1826 – Supplementum Florae Lapponicae (quam edidit Dr. Georgius Wahlenberg). Christianiae (Oslo): Borgianis et Grondahlianis.
Somrithipol S, Jones EG, Bahkali AH, Suetrong S et al. 2017 – *Lauriomyces*, a new lineage in the *Leotiomycetes* with three new species. Cryptogamie, Mycologie 38(2), 259–273.
Somrithipol S, Jones EG. 2007 – *Lauriomyces cylindricus* and *Lauriomyces ellipticus* spp. nov., two new hyphomycetes from tropical forest of Thailand. Nova Hedwigia 84(3–4), 479–486.
Somrithipol S, Kosol S, Jones EG. 2006 – *Lauriomyces sakaeratensis* sp. nov., a new hyphomycete on decaying *Dipterocarpus costatus* fruits from Sakaerat Biosphere Reserve, Thailand. Nova Hedwigia 82(1–2), 209–215.
Somrithipol S, Sakayaroj J, Rungjindamai N, Plaingam N et al. 2008 – Phylogenetic relationship of the coelomycete genus *Infundibulomyces* based on nuclear rDNA data. Mycologia 100, 735–741.
Somrithipol S, Sudhom N, Tippawan S, Jones EBG. 2007 – A new species of *Falcocladium* (*Hyphomycetes*) with turbinate vesicles from Thailand. Sydowia 59, 148–153.
Son YM, Kang HK, Na SY, Lee HY et al. 2010 – Chromoblastomycosis caused by *Phialophora richardsiae*. Annals of Dermatology 22, 362–366.
Song J, Liang JF, Mehrabi-Koushki M, Krisai-Greilhuber I, et al. 2019 – Fungal Systematics and Evolution: FUSE 5. Sydowia 71, 141–245.
Song JY, Wu HX, Li JC, Ding WF et al. 2023 – Taxonomy and evolution history of two new litter-decomposing *Ciliochorella* (*Amphisphaeriales*, *Sporocadaceae*). MycoKeys 100, 95.
Song Y, Menezes da Silva N, Vicente VA, Quan Y et al. 2021 – Dynamic genomic rearrangements in opportunistic *Phialophora* species involved in divergent disease types. Mycoses 64(5), 555–568.
Song YP, Ji NY. 2024 – Chemistry and biology of marine-derived *Trichoderma* metabolites. Natural Products and Bioprospecting 14(1), 1–54.
Song ZK, Zhu AH, Liu ZD, Qu Z et al. 2022 – Three New Species of *Hypoxylon* (*Xylariales*, *Ascomycota*) on a Multigene Phylogeny from Medog in Southwest China. Journal of Fungi 8(5), 500.
Soto-Medina E, Lücking RA. 2017 – New species of *Rhytidhysteron* (*Ascomycota*: *Patellariaceae*) from Colombia, with a provisional working key to known species in the world Artículo original. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 41, 59–63.
Sparapano L, Evidente AA. 1995 – Studies on structure-activity relationship of seiridins, phytotoxins produced by three species of *Seiridium*. Natural Toxins 3, 166–173.
Spatafora JW, Aime MC, Grigoriev IV, Martin F et al. 2017 – The fungal tree of life: from molecular systematics to genome-scale phylogenies. Microbiology Spectrum 5(5).
Spatafora JW, Blackwell M. 1994 – The polyphyletic origins of ophiostomatoid fungi. Mycological Research 98, 1–9.

Spatafora JW, Sung GH, Johnson D, Hesse C et al. 2006 – A five-gene phylogeny of *Pezizomycotina*. Mycologia 98, 1018–1028.
Species Fungorum 2023 – Available online: http://www.speciesfungorum.org/Names/Names.asp
Species Fungorum 2024 – Available online: http://www.speciesfungorum.org/Names/Names.asp
Species Fungorum 2025 – Available online: http://www.speciesfungorum.org/Names/Names.asp
Spegazzini C. 1881a – Fungi argentini additis nonnullis brasiliensibus montevideensibusque. *Pugillus quartus* (Continuacion). Anales de la Sociedad Científica Argentina 12(5), 193–227.
Spegazzini C. 1887 – [1888] Boln Acad. nac. Cienc. Córdoba 11(2), 216.
Spegazzini C. 1896 – Hongos de la cana de azucar. Revista de la Facultad de Agronomía Universidade Nacional de La Plata 2, 227–258.
Spegazzini C. 1909 – *Mycetes argentinenses* (Series IV). Anales del Museo Nacional de Buenos Aires 19, 257–458.
Spegazzini C. 1919 – Reliquiae mycologicae tropicae. Boletın de la Academia Nacional de Ciencias en Cordoba (Republica Argentina) 23, 365609.
Spegazzini CL. 1881b – Fungi argentini additis nonnullis brasiliensibus montevideensibusque. Pugillus quartus (Continuacion) Anales de la Sociedad Científica Argentina 12(3), 97–117.
Spier L, Van Dobben H, Van Dort K. 2010 – Is bark pH more important than tree species in determining the composition of nitrophytic or acidophytic lichen floras? Environmental pollution 158(12), 3607–3611.
Spies CF, Moyo P, Halleen F, Mostert L. 2018 – *Phaeoacremonium* species diversity on woody hosts in the Western Cape Province of South Africa. Persoonia-Molecular Phylogeny and Evolution of Fungi 40(1), 26–62.
Spies CFJ, Mostert L, Carlucci A, Moyo P et al. 2020 – Dieback and decline pathogens of olive trees in South Africa. Persoonia 45, 196–220.
Spooner BM, Legon N. 1999 – Profiles of fungi 35: *Catinella olivacea* (Batsch) Boud. Mycologist 35, 86.
Spooner BM. 1987 – *Helotiales* of Australasia: *Geoglossaceae*, *Orbiliaceae*, *Sclerotiniaceae*, *Hyaloscyphaceae*. Bibliotheca Mycologica (116), 1–711.
Spribille T, Björk CR, Ekman S, Elix JA et al. 2009 – Contributions to an epiphytic lichen flora of northwest North America: I. Eight new species from British Columbia inland rain forests. The Bryologist 112(1), 109–137.
Spribille T, Bjork CR. 2008 – New records and range extensions in the North American lignicolous lichen flora. Mycotaxon 105, 455–468.
Spribille T, Fryday AM, Pérez-Ortega S, Svensson M et al. 2020 – Lichens and associated fungi from Glacier Bay National Park, Alaska. The Lichenologist 52(2), 61–181.
Spribille T, Muggia L. 2013 – Expanded taxon sampling disentangles evolutionary relationships and reveals a new family in *Peltigerales* (*Lecanoromycetidae*, *Ascomycota*). Fungal Diversity 58, 171–184.
Spribille T, Pérez-Ortega S, Tønsberg T, Schirokauer D. 2010 – Lichens and lichenicolous fungi of the Klondike Gold Rush National Historic Park, Alaska, in a global biodiversity context. The Bryologist 113, 439–515.
Spribille T, Resl P, Ahti T, Pérez-Ortega S et al. 2014 – Molecular systematics of the wood-inhabiting, lichen-forming genus *Xylographa* (*Baeomycetales*, *Ostropomycetidae*) with eight new species. Acta Universitatis Upsaliensis, Symbolae Botanicae Upsalienses 37(1), 1.
Springer JP, Cutler HG, Crumley FG, Cox RH. 1981 – Plant growth regulatory effects and stereochemistry of cladosporin. Journal of Agricultural and Food Chemistry 29, 853–855.
Sri-indrasutdhi V, Boonyuen N, Sivichai S, Jones EBG. 2010 – Wood inhabiting freshwater fungi from Thailand: *Ascothailandia* gen. et sp. nov., *Canalisporium grenadoidia* sp. nov. with a key to *Canalisporium* species (*Sordariomycetes Ascomycota*). Mycoscience 51(6), 411– 420.
Stadler M, Sterner O, Anke H. 1993 – New biologically active compounds from the nematode-trapping fungus *Arthrobotrys oligospora* Fresen. Zeitschrift für Naturforschung C 48(11-12), 843–850.

Stadler M. 2011 – Importance of secondary metabolites in the *Xylariaceae* as parameters for assessment of their taxonomy, phylogeny, and functional biodiversity. Current Research in Environmental and Applied Mycology 1, 75–133.
Staiger B, Kalb K, Grube M. 2006 – Phylogeny and phenotypic variation in the lichen family *Graphidaceae* (*Ostropomycetidae*, *Ascomycota*). Mycological Research 110(7), 765–772.
Staiger B, Kalb K. 1995 – Haematomma-studien. I. Die Flechtengattung Haematomma. Bibliotheca Lichenologica 59, 1–198.
Starbäck K. 1899 – Ascomyceten der ersten Regnellschen Expedition 1. Bihang till Kungliga Svenska Vetenskaps-Akademiens Handlingar 25, 1–68.
Stchigel AM, Josep CA, Mac Cormack W, Guarro J. 2001 – *Antarctomyces psychrotrophicus* gen. et sp. nov., a new ascomycete from Antarctica. Mycological Research 105, 377–382.
Stchigel AM, Sutton DA, Cano-Lira JF, Cabañes FJ et al. 2013 – Phylogeny of chrysosporia infecting reptiles: proposal of the new family *Nannizziopsiaceae* and five new species. Persoonia 31(1), 86–100.
Stchigel AM, Sutton DA, Cano-Lira JF, Wiederhold N et al. 2017 – New species *Spiromastigoides albida* from a lung biopsy. Mycopathologia 182(11–12), 967–978.
Steel GS, Dickie IA, Sapsford SJ. 2022 – A risk to the forestry industry? Invasive pines as hosts of foliar fungi and potential pathogens. New Zealand Journal of Ecology 46, 1–13.
Stefani FO, Bérubé JA. 2006 – Biodiversity of foliar fungal endophytes in white spruce (*Picea glauca*) from southern Qué- bec. Botany 84(5), 777–790.
Stein B. 1879 – Flechten. J. U. Kern's Verlag, Wrocław.
Stenroos S, Högnabba F, Myllys L, Hyvönen J et al. 2006 – High selectivity in symbiotic associations of lichenized *Ascomycetes* and cyanobacteria. Cladistics 22(3), 230–238,
Stenroos S, Laukka T, Huhtinen S, Döbbeler P et al. 2010 − Multiple origins of symbioses between *Ascomycetes* and bryophytes suggested by a five-gene phylogeny. Cladistics 26, 281–300.
Stenroos SK, Depriest PT. 1998 – SSU rDNA phylogeny of cladoniiform lichens. American Journal of Botany 85(11), 1548–1559.
Stensiö KE, Wachtmeister CA. 1969 – 1,5,8-Trihydroxy-6-methoxy-3-methylantraquinone from *Laurera purpurina* (Nyl.) Zahlbr. Acta chemica Scandinavica 23, 144–148.
Stensrud Ø, Hywel-Jones NL, Schumacher T. 2005 – Towards a phylogenetic classification of *Cordyceps*: ITS nrDNA sequence data confirm divergent lineages and paraphyly. Mycological Research 109, 41–56.
Stepanchikova IS, Himelbrant DE, Chesnokov SV, Konoreva LA et al. 2022 – Modern and historical lichen biota of Karelian Isthmus: the case of Motornoe-Zaostrovje proposed protected area (Leningrad Region, Russia). Novitates Systematicae Plantarum non Vascularium 56(2), 371–404.
Sterflinger K, De Baere R, Hoog GS de, De Wachter R et al. 1997 – *Coniosporium perforans* and *C. apollinis*, two new rock–inhabiting fungi isolated from marble in the Sanctuary of Delos (Cyclades, Greece). Antonie van Leeuwenhoek 72, 349–353.
Sterflinger K, de Hoog GS, Haase G. 1999 – Phylogeny and ecology of meristematic *Ascomycetes*. Studies in Mycology 43, 5–22.
Stevens FL. 1927 – Fungi from Costa Rica and Panama. Illinois Biological Monographs 11, 157–255.
Stirton J. 1877-1878 – Descriptions of new lichens. Scottish Naturalist 4, 164–168.
Stizenberger E. 1862 – Beitrag sur Flechtensystematic. Ber. Tätigk. St Gall. Naturwiss. Ges., St Gallen 1861–1862, 124–182.
Stocker-Worgotter E, Elix J. 2009 – Experimental studies of lichen-forming fungi: formation of depsidones and shikimic-acid derivatives by the cultured mycobionts of three selected species of *Rhizocarpon* (*Lecideaceae*, lichenized *Ascomycota*). Bibliotheca Lichenologica, 495-512.
Stodůlková E, Man P, Kuzma M, Černý J et al. 2015 – A highly diverse spectrum of naphthoquinone derivatives produced by the endophytic fungus *Biatriospora* sp. CCF 4378. Folia Microbiologica 60, 259–267.

Stolk AC. 1969 – Four new species of *Penicillium*. Antonie van Leeuwenhoek 35(3), 261–274.
Stracquadanio C, Quiles JM, Meca G, Cacciola SO. 2020 – Antifungal activity of bioactive metabolites produced by *Trichoderma asperellum* and *Trichoderma atroviride* in liquid medium. Journal of Fungi 6(4), 263.
Strader CR, Pearce CJ, Oberlies NH. 2011 – Fingolimod (FTY720): a recently approved multiple sclerosis drug based on a fungal secondary metabolite. Journal of Natural Products 74(4), 900–907.
Stringer JR. 2002 – *Pneumocystis*. International journal of medical microbiology 292(5-6), 391–404.
Stringer SL, Hudson K, Blase MA, Walzer PD et al. 1989 – Sequence from ribosomal RNA of *Pneumocystis carinii* compared to those of four fungi suggests an ascomycetous affinity. Journal of Protozoology 36(01), 14S–16S.
Strobel G, Daisy B. 2003 – Bioprospecting for microbial endophytes and their natural products. Microbiology and Molecular Biology Reviews 67(4), 491–502.
Strobel GA, Dirkse E, Sears J, Markworth C. 2001 – Volatile antimicrobials from *Muscodor albus*, a novel endophytic fungus. Microbiology 147, 2943–50.
Strödel R. 1984 – Das olivfarbene Kelchbecherchen, *Catinella olivacea*. Beiträge zur Kenntnis der Pilze Mitteleuropas 1, 175–178.
Stuchlík D, Mencl K, Hubka V, Skorepova M. 2011 – Fungal melanonychia caused by *Onychocola canadensis*: first records of nail infections due to *Onychocola* in the Czech Republic. Czech Mycology 63(1), 83–91.
Studzinska-Sroka E, Galanty A, Bylka W. 2017 – Atranorin-an interesting lichen secondary metabolite. Mini Reviews in Medicinal Chemistry 17(17), 1633–1645.
Su HY, Hyde KD, Maharachchikumbura SSN, Ariyawansa HA et al. 2016a – The families *Distoseptisporaceae* fam. nov., *Kirschsteiniotheliaceae*, *Sporormiaceae* and *Torulaceae*, with new species from freshwater in Yunnan Province, China. Fungal Diversity 80, 375–409.
Su L, Deng H, Niu YC. 2016b – *Phialemoniopsis endophytica* sp. nov., a new species of endophytic fungi from Luffa cylindrica in Henan, China. Mycological Progress 15, e48.
Subramanian CV, Sekar G. 1982 – *Thaxteriellopsis lingicola* and its *Moorella* anamorph. Proceedings: Plant Sciences 91, 1–7.
Subramanian CV, Sekar G. 1990 – *Coronophorales* from India-a monograph. Kavaka 18, 19–90.
Subramanian CV. 1972 – The perfect states of *Aspergillus*. Current Science 41, 755–761.
Suetrong S, Boonyuen N, Pang KL, Ueapattanakit J et al. 2011 – A taxonomic revision and phylogenetic reconstruction of the *Jahnulales* (*Dothideomycetes*), and the new family *Manglicolaceae*. Fungal Diversity 51, 163–188.
Suetrong S, Klaysuban A, Sakayaroj J, Preedanon S et al. 2015a – *Tirisporellaceae*, a new family in the order *Diaporthales* (*Sordariomycetes*, *Ascomycota*). Cryptogamie, Mycologie 36(3), 319–330.
Suetrong S, Preedanon S, Klaysuban A, Gundool W et al. 2017 – Distribution and occurrence of manglicolous marine fungi from Eastern and Southern Thailand. Botanica Marina 60 (4), 503–514.
Suetrong S, Rungareerate P, Nor NABM, Alias SA et al. 2015b – *Bacusphaeria nypenthi* gen. et sp. nov. from the mangrove palm *Nypa fruticans*. Phytotaxa (In Press) [Q3, 1.087]
Suetrong S, Rungjindamai N, Sommai S, Rung-Areerate P et al. 2014 – *Wiesneriomyces* a new lineage of *Dothideomycetes* (*Ascomycota*) basal to *Tubeufiales*. Phytotaxa 176(1), 283–297.
Suetrong S, Schoch CL, Spatafora JW, Kohlmeyer J et al. 2009 – Molecular systematics of the marine *Dothideomycetes*. Studies in Mycology 64(1), 155–173.
Sugita R, Hirayama K, Shirouzu T, Tanaka K. 2022 – *Spirodecosporaceae* fam. nov. (*Xylariales*, *Sordariomycetes*) and two new species of *Spirodecospora*. Fungal Systematics and Evolution 10(1), 217–229.
Sugita R, Tanaka K. 2022 – *Thyridium* revised: Synonymisation of *Phialemoniopsis* under *Thyridium* and establishment of a new order, *Thyridiales*. MycoKeys 86, 147.

Sugiyama J, Hamamoto M. 2011 – *Saitoella* S. Goto, Sugiyama, Hamamoto & Komagata (1987). In C.P. Kurtzman, J.W. Fell and T. Boekhout (Eds.) The Yeasts, a Taxonomic Study (Fifth Edition), Vol. 2 (pp. 1313-1315) Amsterdam: Elsevier.
Sugiyama J, Hosaka K, Suh SO. 2006 – Early diverging *Ascomycota*: phylogenetic divergence and related evolutionary enigmas. Mycologia 98(6), 996–1005.
Sugiyama J, Nagai K, Komagata K. 1987 – Ubiquinone systems in strains of species in the black yeast genera *Phaeococcomyces*, *Exophiala*, *Hortaea*, and *Rhinocladiella*. The Journal of General and Applied Microbiology 33(2), 197–204.
Sugiyama J. 1998 – Relatedness, phylogeny, and evolution of the fungi. Mycoscience 39, 487–511
Sugiyama M, Summerbell RC, Mikawa T. 2002 – Molecular phylogeny of onygenalean fungi based on small subunit (SSU) and large subunit (LSU) ribosomal DNA sequences. Studies in Mycology 47, 5–23.
Suh MK, Lim JW, Lee YH, Ha GY et al. 2005 – A case of localized skin infection caused by *Cephalotheca foveolata*. Korean Journal of Dermatology 43(5), 665–668.
Suh MK, Lim JW, Lee YH, Ha GY et al. 2006 – Subcutaneous hyalohyphomycosis due to *Cephalotheca foveolata* in an immunocompetent host. British Journal of Dermatology 154, 1184–1189.
Suh SO, Blackwell M. 1999 – Molecular phylogeny of the cleistothecial fungi placed in *Cephalothecaceae* and *Pseudeurotiaceae*. Mycologia 91, 836–848.
Sui XN, Guo MJ, Wang QT, Wang HQ et al. 2024 – Taxonomy and phylogeny of *Colletotrichum* on important forest plants in China. Mycosphere 15(1), 4569–4743.
Suija A, de los Ríos A, Pérez-Ortega S. 2015a – A molecular reappraisal of *Abrothallus* species growing on lichens of the order *Peltigerales*. Phytotaxa 195, 201–226.
Suija A, Ertz D, Lawrey JD, Diederich P. 2015b – Multiple origin of the lichenicolous life habit in *Helotiales*, based on nuclear ribosomal sequences. Fungal Diversity 70, 55–72.
Suija A, Kaasalainen U, Kirika PM, Rikkinen J. 2018 – *Taitaia*, a novel lichenicolous fungus in tropical montane forests in Kenya (East Africa). The Lichenologist 50, 173–184.
Suija A, McMullin RT, Lõhmus P. 2023 – A phylogenetic assessment of a fungicolous lineage in *Coniocybomycetes*: *Chaenotricha*, a new genus of *Trichaptum*-inhabiting species. Fungal Systematics and Evolution 12(1), 255–270.
Suija A, Suu A, Lõhmus P. 2016 – Substrate specificity corresponds to distinct phylogenetic lineages: the case of *Chaenotheca brunneola*. Herzogia 29(2), 355–363
Suija A, van den Boom P, Zimmermann E, Zhurbenko MP et al. 2017 – Lichenicolous species of *Hainesia* belong to *Phacidiales* (*Leotiomycetes*) and are included in an extended concept of *Epithamnolia*. Mycologia 109(6), 882–899.
Sujetovienė G. 2010 – Road traffic pollution effects on epiphytic lichens. Ekologija 56(1–2), 64–71.
Sumarah MW, Puniani E, Blackwell BA, Miller JD. 2008 – Characterization of polyketide metabolites from foliar endophytes of *Picea glauca*. Journal of Natural Products 71(8), 1393–1398.
Summerbell RC, Gueidan C, Schroers H-J, Hoog GS de et al. 2011 – *Acremonium* phylogenetic overview and revision of *Gliomastix*, *Sarocladium*, and *Trichothecium*. Studies in Mycology 68, 139–162.
Summerell BA, Groenewald JZ, Carnegie A, Summerbell R et al. 2006 – *Eucalyptus* microfungi known from culture. 2. *Alysidiella Fusculina* and *Phlogicylindrium* genera nova with notes on some other poorly known taxa. Fungal Diversity 23, 323–350.
Sun BD, Zhou YG, Chen AJ, Houbraken J. 2019 – Phylogeny and a new species of the genus *Arachnomyces* (*Arachnomycetaceae*). Phytotaxa 394(1), 089–097.
Sun J, Yu S, Lu Y, Liu H et al. 2023 – Proposal of a new family *Pseudodiploösporeaceae* fam. nov. (*Hypocreales*) based on phylogeny of *Diploöspora longispora* and *Paecilomyces penicillatus*. Mycology 14(1), 60–73.

Sun JZ, Liu XZ, Hyde KD, Zhao Q et al. 2017a – *Calcarisporium xylariicola* sp. nov. and introduction of *Calcarisporiaceae* fam. nov. in *Hypocreales*. Mycological Progress 16(4), 433–445.
Sun LY, Li HY, Sun X, Guo LD. 2017b – *Dematipyriforma aquilaria* gen. et sp. nov., a New hyphomycetous taxon from *Aquilaria crassna*. Cryptogamie, Mycologie 38, 341–351.
Sun YR, Hyde KD, Liu NG. Jayawardena RS et al. 2025 – Micro-fungi in Southern China and Northern Thailand: emphasis on medicinal plants. Fungal Diversity.
Sun YR, Jayawardena RS, Hyde KD, Wang Y. 2021a – *Kirschsteiniothelia thailandica* sp. nov. (*Kirschsteiniotheliaceae*) from Thailand. Phytotaxa 490, 172–182.
Sun YR, Liu NG, Samarakoon MC, Jayawardena RS et al. 2021b – Morphology and phylogeny reveal *Vamsapriyaceae* fam. nov. (*Xylariales*, *Sordariomycetes*) with two novel *Vamsapriya* species. Journal of Fungi 7(11), 891.
Sun ZH, Li HH, Liang FL, Chen YC, Liu HX, Li SN, Tan GH, Zhang WM. 2016 – Two new secondary metabolites from the endophytic fungus *Endomelanconiopsis endophytica*. Molecules 21, 943.
Sung GH, Hywel-Jones NL, Sung JM, Luangsa-Ard JJ et al. 2007 – Phylogenetic classification of *Cordyceps* and the clavicipitaceous fungi. Studies in Mycology 57, 1–59.
Sung GH, Spatafora JW, Zare R, Hodge KT et al. 2001 – Arevision of *Verticillium* sect. *Prostrata*. II. Phylogenetic analyses of SSU and LSU nuclear rDNA sequences from anamorphs and teleomorphs of the *Clavicipitaceae*. Nova Hedwigia 72, 311 –328.
Surup F, Narmani A, Wendt L, Pfütze S et al. 2018 – Identification of fungal fossils and novel azaphilone pigments in ancient carbonised specimens of *Hypoxylon* fragiforme from forest soils of Châtillon-sur-Seine (Burgundy). Fungal Diversity 92, 345–356.
Suryanarayanan TS, Thirunavukkarasu N, Govindarajulu MB, Sasse F et al. 2009 – Fungal endophytes and bioprospecting. Fungal Biology Reviews 23(1-2), 9–19.
Suryanarayanan TS, Thirunavukkarasu N. 2017 – Endolichenic fungi: The lesser known fungal associates of lichens. Mycology 8, 189–196.
Sutherland GK. 1915 – New marine *Pyrenomycetes*. New Phytol 15, 35–48.
Sutton BC. 1963 – Coelomycetes II. *Neobarclaya*, *Mycohypallage*, *Bleptosporium* and *Cryptostictis*. Mycological Papers 88, 1–50.
Sutton BC. 1980 – The *Coelomycetes*. Fungi imperfecti with pycnidia, acervuli and stromata. Commonwealth Mycological Institute, Kew, 1–696.
Suwannarach N, Kumla J, Matsui K, Lumyong S. 2018 – Morphological and molecular evidence support a new endophytic fungus, *Chaetomella endophytica* from Japan. Mycoscience 59(6), 473–478.
Svrček M. 1969 – *Bolinia tubulina* (Alb. Et Schw. ex Fr.) Sacc. V Československu [*Bolinia tubulina* (Alb. Et Schw. ex Fr.) Sacc. in der Tschechoslowakei]. Čes Mykol 23, 118–122.
Swart L, Crous PW, Kang JC, Mchau GR et al. 2001 – Differentiation of species of *Elsinoë* associated with scab disease of *Proteaceae* based on morphology symptomatology and ITS sequence phylogeny. Mycologia 93, 366–379.
Swift ME. 1930 – A new species of *Chaetomella* on rose. Mycologia 22(4), 165–168.
Swift MJ, Heal OW, Anderson JM. 1979 – Decomposition in terrestrial ecosystems. University of California Press, Berkeley.
Syakalima M, Ramatla T, Lubanza N. 2019 – Opportunistic pathogenic fungi isolated from feces of feral pigeons in Mafikeng, North West Province of South Africa. Veterinary World 12(7), 1066-1069.
Sydow H. 1930 – Fungi venezuelani. Annales Mycologici 28, 29–224
Szcepańska K, Staniaszek-Kik M. 2012 – *Thelocarpon olivaceum* (lichenized Ascomycota), a lichen species new for Poland. Polish Botanical Journal 57, 483–485.
Szentiványi T, Haelewaters D, Pfliegler WP, Clément L et al. 2018 – *Laboulbeniales* (Fungi: *Ascomycota*) infection of bat flies (*Diptera*: *Nycteribiidae*) from *Miniopterus schreibersii* across Europe. Parasites & Vectors 11, 395.

Tabacchi R, Fkyerat A, Poliart C, Dubin GM. 2000 – Phytotoxins from fungi of esca of grapevine. Phytopathologia Mediterranea 39, 156–161.
Tabuchi H, Hamamoto T, Miki S, Tejima T et al. 1994 – Total Synthesis and Stereochemistry of Alternaric Acid. Journal of Organic Chemistry 59, 4749–4759.
Takegawa K, Tohda H, Sasaki M, Idiris A et al. 2009 – Production of heterologous proteins using the fission-yeast (*Schizosaccharomyces pombe*) expression system. Biotechnology and Applied Biochemistry 53(4), 227–235.
Talhinhas P, Baroncelli R 2023 – Hosts of *Colletotrichum*. Mycosphere 14(2), 158–261.
Tan J, Zhao H, Li J, Gong Y et al. 2023 – The devastating rice blast airborne pathogen *Magnaporthe oryzae*—A review on genes studied with mutant analysis. Pathogens 12(3), 379.
Tan MK, Timmer LW, Broadbent P, Priest M et al. 1996 – Differentiation by molecular analysis of *Elsinoë* sp. causing scab disease of Citrus and its epidemiological implications. Phytopathology 86, 1039–1044.
Tan YP, Steinrucken TV. 2024 – Nomenclatural novelties. Index of Australian Fungi 36.
Tanaka K, Hashimoto A, Matsumura M, Sato T. 2017 – *Brevicollum*, a new genus in *Neohendersoniaceae*, *Pleosporales*. Mycologia 109(4), 608–619.
Tanaka K, Hirata A. 1982 – Ascospore development in the fission yeast *Schizosaccharomyces pombe* and *S. japonicus*. Journal of Cell Science 56.
Tanaka K, Hirayama K, Yonezawa H, Hatakeyama S et al. 2009 – Molecular taxonomy of bambusicolous fungi: *Tetraplosphaeriaceae*, a new pleosporalean family with *Tetraploa*-like anamorphs, and notes on the phylogeny of selected species from bamboo. Studies in Mycology 64, 175–209.
Tanaka K, Hirayama K, Yonezawa H, Sato G et al. 2015 – Revision of the *Massarineae* (*Pleosporales*, *Dothideomycetes*). Studies in Mycology 82, 75–136.
Tanas S, Odabasoglu F, Halici Z, Cakir A et al. 2010 – Evaluation of anti-inflammatory and antioxidant activities of *Peltigera rufescens* lichen species in acute and chronic inflammation models. Journal of Natural Medicines 64, 42–49.
Tang AM, Jeewon R, Hyde KD. 2009 – A re-evaluation of the evolutionary relationships within the *Xylariaceae* based on ribosomal and protein-coding gene sequences. Fungal Diversity 34, 127–155.
Tang X, Jayawardena RS, Stephenson SL, Kang JC. 2022 – A new species *Pseudoplagiostoma dipterocarpicola* (*Pseudoplagiostomataceae*, *Diaporthales*) found in northern Thailand on members of the *Dipterocarpaceae.* Phytotaxa 543(4), 233–243.
Tang X, Lu YZ, Dissanayake LS, Goonasekara ID et al. 2023 – Two new fungal genera (*Diaporthales*) found on *Dipterocarpaceae* in Thailand. Frontiers in Microbiology 14, 1169052.
Taniguchi Y, Taketani T, Moriyama H, Moriki S et al. 2009 – Septic Shock Induced by *Lecythophora mutabilis* in a Patient with Mitochondrial Encephalomyopathy. Journal of Medical Microbiology 58(9), 125558.
Tanney JB, Nguyen HDT, Pinzari F, Seifert KA. 2015 – A century later: rediscovery, culturing and phylogenetic analysis of *Diploöspora rosea*, a rare onygenalean hyphomycete. Antonie van Leeuwenhoek 108(5), 1023–1035.
Tanney JB, Seifert KA. 2018 – *Phacidiaceae endophytes* of *Picea* rubens in Eastern Canada. Botany 96(9), 555–588.
Tappert R, Wolfe AP, McKellar RC, Tappert MC et al. 2011 – Characterizing modern and fossil gymnosperm exudates using micro-Fourier transform infrared spectroscopy. International Journal of Plant Sciences 172(1), 120–138.
Tarasova VN, Sonina AV, Androsova VI, Ahti T. 2013 – The present lichen flora of the city of Petrozavodsk. Folia Cryptogamica Estonica 50, 57–66.
Tassi F. 1904 – Origine e sviluppo delle Leptostromacee e loro rapporti con le famiglie affine. Bollettino del Laboratorio de Orto Botanico Reale Universita Siena 6, 3–124.

Tavares II. 1981 –Validation of the *Herpomycetineae* and *Herpomycetaceae* in the *Laboulbeniales*. Mycotaxon 13, 469–470
Tavares S, Inácio J, Fonseca Á, Oliveira C. 2004 – Direct detection of *Taphrina deformans* on peach trees using molecular methods. European Journal of Plant Pathology 110, 973–982.
Taylor EL, Taylor TN, Krings M. 2009a – Paleobotany: the biology and evolution of fossil plants. Academic Press.
Taylor JE, Hyde KD. 1999 – *Cannonia* gen. nov., from palms in the Southern Hemisphere. Mycological Research 103(11), 1398–1402.
Taylor JW. 2011 – One Fungus = One Name: DNA and fungal nomenclature twenty years after PCR. IMA Fungus 2(2), 113–120.
Taylor TN, Hass H, Kerp H. 1997 – A Cyanolichen from the Lower Devonian Rhynie Chert. American Journal of Botany 84, 992–1004.
Taylor TN, Krings M, Taylor EL. 2015a – 10 Fungal Diversity in the Fossil Record. In Systematics and Evolution, 259–278.
Taylor TN, Krings M, Taylor EL. 2015b – *Ascomycota*. In Fossil Fungi; Academic Press: Cambridge, MA, USA 129–171.
Taylor TN, Taylor EL, Krings M. 2009b – Palaeobotany. Elsevier publication, Amsterdam, The biology and evolution of fossil plants.
Taylor TN. 1994 – The fossil history of *Ascomycetes*. In Ascomycete Systematics: problems and perspectives in the nineties (pp. 167-174). Boston, MA: Springer US.
Tazik Z, Rahnama K, Iranshahi M, White JF et al. 2020 – *Ochroconisferulica* sp. nov. (*Venturiales*), a fungal endophyte from *Ferula ovina*. Nova Hedwigia 110, 369–381.
Tedersoo L, Bahram M, Põlme S, Kõljalg U et al. 2014. Global diversity and geography of soil fungi. Science 346, 2356688.
Tedersoo L, Hansen K, Perry BA, Kjøller R. 2006 – Molecular and morphological diversity of pezizalean ectomycorrhiza. New Phytologist 170, 581–596.
Tedersoo L, May TW, Smith ME. 2010 – Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. Mycorrhiza 20, 217–263.
Tedersoo L, Mikryukov V, Anslan S, Bahram M et al. 2021 – The global soil mycobiome consortium dataset for boosting fungal diversity research. Fungal Diversity 111, 573–588.
Tedersoo L, Sánchez-Ramírez S, Koljalg U, Bahram M et al. 2018 – High-level classification of the Fungi and a tool for evolutionary ecological analyses. Fungal Diversity 90, 135–159.
Tehler A, Baloch E, Tibell L, Wedin M. 2009 – The systematic position of *Schistophoron*. Bibliotheca Lichenologica 99, 383–392.
Tehler A, Dahlkild Å, Eldenäs P, Feige GB. 2004 – The phylogeny and taxonomy of Macaronesian, European and Mediterranean *Roccella* (*Roccellaceae*, *Arthoniales*). Symbolae Botanicae Upsalienses 34, 405–428.
Tehler A, Ertz D, Irestedt M. 2013 – The genus *Dirina* (*Roccellaceae, Arthoniales*) revisited. The Lichenologist 45, 427–476.
Tehler A, Farris JS, Lipscomb DL, Källersjö M. 2000 – Phylogenetic analyses of the fungi based on large rDNA data sets. Mycologia 92(3), 459–474.
Tehler A, Irestedt M, Bungartz F, Wedin M. 2009a – Evolution and reproduction modes in the *Roccella galapagoensis* aggregate (*Roccellaceae*, *Arthoniales*). Taxon 58, 438–456.
Tehler A, Irestedt M, Wedin M, Ertz D. 2009b – Origin, evolution and taxonomy of American *Roccella* (*Roccellaceae*, *Ascomycetes*). Systematics and Biodiversity 7, 307–317.
Tehler A, Irestedt M, Wedin M, Ertz D. 2010 – The Old World *Roccella* species outside Europe and Macaronesia: taxonomy, evolution and phylogeny. Systematics and Biodiversity 8, 223–246.
Tehler A, Irestedt M. 2007 – Parallel evolution of lichen growth forms in the family *Roccellaceae* (*Arthoniales*, *Euascomycetes*). Cladistics 23, 432–454.
Tehler A, Wedin M. 2008 – Systematics of lichenized fungi, chapter 17 in Nash III, T.H. Lichen Biology 2nd ed., 336–352.
Tehler A. 1983 – The genera *Dirina* and *Roccellina* (*Roccellaceae*). Opera Botanica 70, 1–86.

Tehler A. 1988 – *Dirina massiliensis* f. *aponina* (Massal.) Tehler, a pycnidial anamorph in the lichen genus *Dirina* (*Roccellaceae*). The Lichenologist 20, 398–399.
Tehler A. 1990 – A new approach to the phylogeny of *Euascomycetes* with a cladistic outline of *Arthoniales* focussing on *Roccellaceae*. Canadian Journal of Botany 68, 2458–2492.
Tehler A. 1993 – *Schismatomma* and three new or reinstated genera, a reassessment of generic relationships in *Arthoniales*. Cryptogamic Botany 3, 139–151.
Tehler A. 1996 – Systematics, phylogeny and classification. In: Nash III, T.H. (Ed.), Lichen Biology. University Press, Cambridge, 217–239.
Teixeira MDM, Moreno LF, Stielow B, Muszewska A et al. 2017 – Exploring the genomic diversity of black yeasts and relatives (*Chaetothyriales*, *Ascomycota*). Studies in Mycology 86, 1–28.
Temel F, Stone JK, Johnson GR. 2003 – First report of Swiss needle cast caused by *Phaeocryptopus gaeumannii* on Douglas-fir in Turkey. Plant Disease 87(12), 1536–1536.
Temina M, Kidron GJ. 2015 – The effect of dew on flint and limestone lichen communities in the Negev Desert. Flora 213, 77–84.
Temperini CV, Pardo AG, Pose GN. 2018 – Diversity of airborne *Cladosporium* species isolated from agricultural environments of northern Argentinean Patagonia: molecular characterization and plant pathogenicity. Aerobiologia 34, 227–239.
Temu SG, Tibell S, Tibuhwa DD, Tibell L. 2019 – Crustose Calicioid Lichens and Fungi in Mountain Cloud Forests of Tanzania. Microorganisms 7(11), 491.
Temu SG, Tibell S, Tibuhwa DD, Tibell L. 2024 – *Coniocybe* Ach. Revisited. Journal of Fungi 10(5), 363.
Teng SC. 1933 – Notes on *Hysteriales* from China. Sinensia 4, 129–144.
Teng SC. 1963 – Fungi of China. Science Press, Beijing. 1–808.
Tennakoon DS, Hongsanan S, De silva NI, Suwannarach N et al. 2023 – Molecular phylogeny and morphological characterization of *Paramicrothyrium bambusae sp*. nov. and *Tumidispora thailandica* sp. nov. from leaf litter. Phytotaxa 578, 112–124.
Tennakoon DS, Kuo CH, Maharachchikumbura SSN, Thambugala KM et al. 2021 – Taxonomic and phylogenetic contributions to *Celtis formosana*, *Ficus ampelas*, *F. septica*, *Macaranga tanarius* and *Morus australis* leaf litter inhabiting microfungi. Fungal Diversity 108, 1–215.
Terrier CA. 1942 – Essai sur la systématique des *Phacidiaceae* (Fr.) *sensu* Nannfeldt. Beitr. Krypt. Fl. Schweiz 9(2), 1−99.
Thakur A, Hui R, Hongyan Z, Tian Y et al. 2011 – Pro-apoptotic effects of P*aecilomyces hepiali*, a *Cordyceps sinensis* extract on human lung adenocarcinoma A549 cells *in vitro*. Journal of Cancer Research and Therapeutics 7(4), 421–426.
Thambugala KM, Ariyawansa HA, Li YM, Boonmee S et al. 2014 – *Dothideales*. Fungal Diversity 68, 105–158.
Thambugala KM, Chunfang Y, Camporesi E, Bahkali AH et al. 2015 – *Pseudodidymosphaeria* gen. nov. in *Massarinaceae*. Phytotaxa 231, 271–282.
Thambugala KM, Daranagama DA, Phillips AJ, Kannangara SD et al. 2020 – Fungi vs. fungi in biocontrol: An overview of fungal antagonists applied against fungal plant pathogens. Frontiers in Cellular and Infection Microbiology 10, 604923.
Thambugala KM, Daranagama DA, Phillips AJL, Bulgakov TS et al. 2017a – Microfungi on Tamarix. Fungal Diversity 82, 239–306.
Thambugala KM, Hyde KD, Eungwanichayapant PD, Romero AI et al. 2016 – Additions to the genus *Rhytidhysteron* in *Hysteriaceae*. Cryptogamie, Mycologie 37, 99–116.
Thambugala KM, Wanasinghe DN, Phillips AJL, Camporesi E et al. 2017b – Mycosphere notes 1–50: grass (*Poaceae*) inhabiting *Dothideomycetes*. Mycosphere 8, 697–796.
Thaxter R. 1896 – Contribution towards a monograph of the *Laboulbeniaceae*. Memoirs of the American Academy of Arts and Sciences 12, 187–429.
Thaxter R. 1902 – Preliminary diagnoses of new species of *Laboulbeniaceae*. V. Proceedings of the American Academy of Arts and Sciences 38, 9–57.

Thaxter R. 1908 – Contribution towards a monograph of the *Laboulbeniaceae.* II. Memoirs of the American Academy of Arts and Sciences 13, 217–469.
Thaxter R. 1920 – Second note on certain peculiar fungus-parasites of living insects. Botanical Gazette 69, 1–27.
Thaxter R. 1921 – Note on two remarkable *Ascomycetes*. Proceedings of the American Academy of Arts and Sciences 57, 423–436.
Thaxter R. 1931 – Contribution towards a monograph of the *Laboulbeniaceae*. Part V. Memoirs of the American Academy of Arts and Sciences 16, 7–435.
Theissen F, Sydow H. 1915 – Die *Dothideales*. Kritische-systematische Originaluntersuchungen. Annales Mycologici 13, 147–746.
Theissen F, Sydow H. 1918 – Vorentwürfe zu den *Pseudosphaeriales*. Ann Mycol 16, 1–34.
Theissen F. 1913 − *Hemisphaeriales*. Annales Mycologici 11, 425–467.
Theivendirarajah K, Chrystopher RK. 1987 – Microflora and microbial activity in palmyrah (*Borassus flabellifer*) palm wine in Sri Lanka. MIRCEN Journal of Applied Microbiology and Biotechnology 3, 23–31.
Thilagam LJ, Nayak BK, Nanda A. 2015 – Studies on the diversity of coprophilous microfungi from hybrid cow dung samples. International Journal of PharmTech Research 8, 135–138.
Thiyagaraja V, Lücking R, Ertz D, Coppins BJ et al. 2021a – Sequencing of the type species of *Arthopyrenia* places *Arthopyreniaceae* as a synonym of *Trypetheliaceae*. Mycosphere 12(1), 993–1011.
Thiyagaraja V, Lücking R, Ertz D, Karunarathna SC et al. 2021b – The evolution of life modes in *Stictidaceae*, with three novel taxa. Journal of Fungi 7(2), 105.
Thiyagaraja V, Lücking R, Ertz D, Wanasinghe DN et al. 2020 – Evolution of non-lichenized, saprotrophic species of *Arthonia* (*Ascomycota*, *Arthoniales*) and resurrection of *Naevia*, with notes on *Mycoporum*. Fungal Diversity 102, 205–224.
Thoen E, Aas AB, Vik U, Brysting AK et al. 2019 – A single ectomycorrhizal plant root system includes a diverse and spatially structured fungal community. Mycorrhiza 29, 167–180.
Thomas CF, Limper AH. 2007 – Current insights into the biology and pathogenesis of *Pneumocystis* pneumonia. Nature Reviews Microbiology 5, 298–308.
Thomson JW. 1967 – Notes on *Rhizocarpon* in the Arctic. Nova Hedmigia 14, 421–483.
Thomson JW. 1997 – American Arctic Lichens. 2. The Microlichens. The University of Wisconsin Press, Madison, U.S.A.
Thongkantha S, Jeewon R, Vijaykrishna D, Lumyong S et al. 2009 – Molecular phylogeny of *Magnaporthaceae* (*Sordariomycetes*) with a new species *Ophioceras chiangdaoense* from *Dracaena loureiroi* in Thailand. Fungal Diversity 34, 157–173.
Thor G. 1998 – Red-listed lichens in Sweden: habitats, threats, protection, and indicator value in boreal coniferous forests. Biodiversity and Conservation 7, 59–72.
Thor G, Wirth V. 1990 – *Candelariella viae-lacteae*, a new lichen species from Europe. Stuttgarter Beitrage zur Naturkunde, Serie A 445, 1–4.
Thor G. 1985 – A new species of *Lichenostigma*, a lichenicolous *Ascomycetes*. The Lichenologist 17(3), 269–272.
Thynne E, Mead OL, Chooi YH, McDonald MC et al. 2019 – Acquisition and loss of secondary metabolites shaped the evolutionary path of three emerging phytopathogens of wheat. Genome Biology and Evolution 11, 890–905.
Tian Q, Chomnunti P, Lumyong S, Liu JK, Hyde KD. 2021 – Phylogenetic relationships and morphological reappraisal of *Chaetothyriales*. Mycosphere 12(1), 1157–1261.
Tian XG, Bao DF, Karunarathna SC, Jayawardena RS et al. 2024 – Taxonomy and phylogeny of ascomycetes associated with selected economically important monocotyledons in China and Thailand. Mycosphere 15(1), 1–274.
Tian XG, Karunarathna SC, Xu R, Lu Y et al. 2022 – Three new species, two new records and four new collections of *Tubeufiaceae* from Thailand and China. Journal of Fungi 8, 206.

Tianpanich K, Prachya S, Wiyakrutta S, Mahidol C et al. 2011 –Radical scavenging and antioxidant activities of isocoumarins and a phthalide from the endophytic fungus *Colletotrichum* sp. Journal of Natural Products 74, 79–81.
Tibell L, Beck A. 2002 – Morphological variation, photobiont association and ITS phylogeny of *Chaenotheca phaeocephala* and *C. subroscida* (*Coniocybaceae*, lichenized *Ascomycetes*). Nordic Journal of Botany 21, 651–660.
Tibell L, Knutsson T. 2016 – *Calicium episcalaris* (*Caliciaceae*), a new lichen species from Sweden. Symbolae Botanicae Upsalienses 38, 49–52.
Tibell L, Tibell S, Van Der Pluijm A. 2019 – *Chaenotheca biesboschii* a new calicioid lichen from willow forests in the Netherlands. The Lichenologist 51(2), 123–135.
Tibell L, Wedin M. 2000 – *Mycocaliciales*, a new order for nonlichenized calicioid fungi. Mycologia 92(3), 577–581.
Tibell L. 1982 – *Caliciales* of Costa Rica. The Lichenologist 14(3), 219–254.
Tibell L. 1984 – A reappraisal of the taxonomy of *Caliciales*. Nova Hedwigia, Beiheft 79, 597–713.
Tibell L. 1992 – Crustose lichens as indicators of forest continuity in boreal coniferous forests. Nordic Journal of Botany 12, 427–450.
Tibell L. 1993 – The anamorphs of *Chaenotheca deludens*. Nordic Journal of Botany 13, 441–445.
Tibell L. 1996 – *Caliciales*. Flora Neotropica 69, 1–78.
Tibell L. 1997 – Anamorphs in mazaediate lichenized fungi and the *Mycocaliciaceae* ("*Caliciales* s. lat"). Symbolae Botanicae Upsalienses 32, 291–322.
Tibell L. 1999 – Calicioid lichens and fungi. In Nordic Lichen Flora 1 (Ahti T, Jørgensen PM, Kristinsson H, Moberg R, Søchting U, Thor G. eds), 20–94.
Tibell L. 2001 – Photobiont association and molecular phylogeny of the lichen genus *Chaenotheca*. Bryologist 104, 191–198.
Tibell L. 2003 – *Tholurna dissimilis* and generic delimitations in *Caliciaceae* inferred from nuclear ITS and LSU rDNA phylogenies (*Lecanorales*, lichenized ascomycetes). Mycological Research 107(12), 1403–1418.
Tibpromma S, Hyde KD, Bhat JD, Mortimer PE et al. 2018 – Identification of endophytic fungi from leaves of *Pandanaceae* based on their morphotypes and DNA sequence data from southern Thailand. MycoKeys 33, 25–67.
Tibpromma S, Hyde KD, Jeewon R, Maharachchikumbura SSN et al. 2017 – Fungal diversity notes 491–602: taxonomic and phylogenetic contributions to fungal taxa. Fungal Diversity 83(1), 1–261.
Tilak ST, Kale SB, Kale SVS. 1967 – Contribution to our knowledge of *Ascomycetes* of India XVI. Sydowia 21, 295–301.
Tim SKM. 1971 – The morphology and development of *Tripospora tripos* (Cooke) Lindau. Annals of Botany 35, 713–720.
Timdal E. 1984 – The genus *Hypocenomyce* (*Lecanorales*, *Lecideaceae*), with special emphasis on Norwegian and Swedish species. Nordic Journal of Botany 4, 83–108.
Timdal E. 1991 – A monograph of the genus *Toninia* (*Lecideaceae*, *Ascomycetes*). Opera Botanica 110, 1–137.
Timdal E. 1994 – *Boreoplaca ultrafrigida*, a new lichen genus and species from continental Siberia. Mycotaxon 51, 503–508.
Timdal E. 2001 – *Hypocenomyce oligospora* and *H. sierrae*, two new lichen species. Mycotaxon 77, 445–453.
Tisserat NA, Pair JC. 1997 – Susceptibility of selected juniper cultivars to cedar-apple rust, Kabatina tip blight, Cercospora needle blight and *Botryosphaeria* canker. Journal of Environmental Horticulture 15(3), 160–163.
Titov A. 2006 – Mikokalizievye griby (porjadok *Mycocaliciales*) Golarktiki [Mycocalicioid fungi (the order *Mycocaliciales*) of Holarctic]. KMK Scientific Press, Moskva 296.
Tønsberg T. 1992 – The sorediate and isidiate, corticolous, crustose lichens in Norway. Sommerfeltia 14, 1–331.

Topham PB. 1982 – Differentiation in *Umbilicaria krempelhuberi*. The Lichenologist 14, 86–87.
Torruella G, De Mendoza A, Grau-Bové X, Antó M et al. 2015 – Phylogenomics reveals convergent evolution of lifestyles in close relatives of animals and fungi. Current Biology 25, 2404–2410.
Torta L, Lo Piccolo S, Piazza G, Burruano S et al. 2015 – *Lulwoana* sp., a dark septate endophyte in roots of *Posidonia oceanica* (L.) Delile seagrass. Plant Biology 17(2), 505–511.
Tragust S, Tartally A, Espadaler X, Billen J. 2016 – Histopathology of *Laboulbeniales* (*Ascomycota*: *Laboulbeniales*): ectoparasitic fungi on ants (*Hymenoptera*: *Formicidae*). Myrmecological News 23, 81–89.
Trakunyingcharoen T, Lombard L, Groenewald JZ, Cheewangkoon R et al. 2015 – Caulicolous *Botryosphaeriales* from Thailand. Persoonia: Molecular Phylogeny and Evolution of Fungi 34, 87–99.
Trakunyingcharoen T, Lombard L, Groenewald JZ, Cheewangkoon R et al. 2014 – Mycoparasitic species of *Sphaerellopsis*, and allied lichenicolous and other genera. IMA Fungus 5, 391–414.
Trampe T. 2010 – Neotropical tar spot fungi: exploration of *Phyllachorales* in Panama. PhD thesis, Biowissenschaften, Johann Wolfgang Goethe-Universität, Frankfurt am Main, Germany.
Trappe JM. 1979 – The orders, families, and genera of hypogeous *Ascomycotina* (truffles and their relatives). Mycotaxon 9, 297–340.
Tretiach M, Modenesi P. 1999 – Critical notes on the lichen genus *Encephalographa* A. Massal.(? *Hysteriaceae*). Nova Hedwigia 527–544.
Trevisan V. 1861 – Synopsis generum Trypethelinarum. Flora 44, 17–26.
Triebel D. 1989 – Lecideicole Ascomyceten. Eine Revision der obligat lichenicolen Ascomyceten auf lecideoiden Flechten. - Bibliotheca Lichenologica 35, 1–278.
Triebel D.1993 – Notes on the genus *Sagediopsis* (*Verrucariales*, *Adelococcaceae*). Sendtnera 1, 273–280.
Trierveiler-Pereira L, Baltazar JM, Loguercio-Leite C. 2008 – *Xylobotryum portentosum* (Mont.) Pat. (*Ascomycota*): a second record from Brazil after a hundred years. Nova Hedwigia 87, 169–174.
Trierveiler-Pereira L, Baltazar JM. 2022 – *Xylobotryum portentosum* (Mont.) Pat. (*Xylobotryomycetes*, *Ascomycota*): a rare fungal species newly found in Southeastern Brazil. Biota Neotropica 22(4), e20221376.
Tripathi SKM. 2009 – Fungi from palaeoenvironments: their role in environmental interpretations. In: Misra JK, Deshmukh SK eds. Fungi from different environments. Progress in Mycological Research Series. Enfield: Science Publishers, 1–27.
Tripp EA, Lendemer JC. 2015 – *Candelariella clarkii* and *Lecidea hoganii*: two lichen species new to science from White Rocks Open Space, City of Boulder, Colorado. The Bryologist 118(2), 154–163.
Trovão J, Tiago I, Soares F, Paiva DS et al. 2019 – Description of *Aeminiaceae* fam. nov., *Aeminium* gen. nov. and *Aeminium ludgeri* sp. nov. (*Capnodiales*), isolated from a biodeteriorated art-piece in the old cathedral of Coimbra, Portugal. MycoKeys 45, 57–73.
Trung HV, Kuo PC, Tuan NN, Ngan NT et al. 2019 – Characterization of cytochalasins and steroids from the ascomycete *Daldinia concentrica* and their cytotoxicity. Natural Product Communications 14(5).
Tsang CC, Chan JFW, Ip PPC, Ngan AHY et al. 2014 – Subcutaneous phaeohyphomycotic nodule due to *Phialemoniopsis hongkongensis* sp. nov. Journal of Clinical Microbiology 52, 3280–3289.
Tsipouras A, Goetz MA, Hensens OD, Liesch JM et al. 1997 – Sporandol: A novel antiparasitic binaphthalene from *Chrysosporium meridarium*. Bioorganic & Medicinal Chemistry Letters 7(10), 1279–1282.
Tsui CKM, Goh TK, Hyde KD. 1997 – A new species of *Dactylaria* from Hong Kong. Sydowia 49(2), 182–186.
Tsui CKM, Hyde KD, Hodgkiss IJ. 2000 – Biodiversity of fungi on submerged wood in Hong Kong streams. Aquatic Microbial Ecology 21, 289–298.

Tsuneda A, Davey M, Hambleton S, Currah RS. 2008 – *Endosporium*, a new endoconidial genus allied to the *Myriangiales*. Botany 86, 1020–1033.
Tsuneda A, Hambleton S, Currah RS. 2011 – The anamorph genus *Knufia* and its phylogenetically allied species in *Coniosporium*, *Sarcinomyces*, and *Phaeococcomyces*. Botany 89(8), 523–536.
Tsuneda A, Tsuneda I, Currah RS. 2004 – Endoconidiogenesis in *Endoconidioma populi* and *Phaeotheca fissurella*. Mycologia 96, 1136–1142.
Tubaki K. 1957 – Biological and cultural studies of three species of *Protomyces*. Mycologia 49, 44–54.
Tubaki K. 1958 – Studies on the Japanese *Hyphomycetes*. V. Leaf and stem group with a discussion of the classification of the *Hyphomycetes* and their perfect stages. The Journal of the Hattori Botanical Laboratory 20, 142–244.
Tubaki K. 1975 – Notes on the Japanese hyphomycetes VII. *Cancellidium*, a new hyphomycete genus. Transactions of the Mycological Society of Japan 16, 357–360.
Tucker SC, Harris RC. 1980 – New or noteworthy pyrenocarpous lichens from Louisiana and Florida. Bryologist 83, 1–20.
Tuckerman E. 1872 – Genera lichenum: an arrangement of the North American lichens. Amherst [Mass.]: Edwin Nelson.
Tulasne LR, Tulasne C. 1865 – Selecta fungorum carpologia, vol. 3. Imperiale Typographeum, Parisiis
Tulasne LR. 1852 – Mémoire pour servir à l'histoire organographique et physiologique des lichens. Ann Sci Nat 17, 5–128.
Tulasne LR. 1860 – De quelques Sphéries fongicoles, à propos d'un mémoire de M. Antoine de Bary sur les Nyctalis. Annales des Sciences Naturelles, Botanique 13, 5–19.
Tuovila H, Schmidt AR, Beimforde, Dorfelt H et al. 2013 – Stuck in time – a new *Chaenothecopsis* species with proliferating ascomata from *Cunninghamia resin* and its fossil ancestors in European amber. Fungal Diversity 58, 199–213.
Turian G. 1977 – *Coniosporium aeroalgicolum* sp. nov. moisissure dematiee semi-lichenisante. Ber Schweiz Bot Ges 87, 19–24.
Turner J. 2004 – Explaining the global biodiversity gradient: energy, area, history and natural selection. Basic and Applied Ecology 5, 435–448.
U'Ren JM, Lutzoni F, Miadlikowska J, Arnold AE. 2010 – Community analysis reveals close affinities between endo- phytic and endolichenic fungi in mosses and lichens. Microbial Ecology 60(2), 340–353.
U'Ren JM, Miadlikowska J, Zimmerman NB, Lutzoni F et al. 2016 – Contributions of North American endophytes to the phylogeny, ecology, and taxonomy of *Xylariaceae* (*Sordariomycetes*, *Ascomycota*). Molecular Phylogenetics and Evolution 98, 210–32.
Udagawa SI, Toyazaki N. 1983 – A new species of *Conioscypha*. Mycotaxon 18, 131e137.
Udagawa SI, Uchiyama S. 1999 – Taxonomic studies on new or critical fungi of non-pathogenic *Onygenales* 1. Mycoscience 40 (3), 277–290.
Udayanga D, Miriyagalla SD, Manamgoda DS, Lewers KS et al. 2021 – Molecular reassessment of diaporthalean fungi associated with strawberry, including the leaf blight fungus, *Paraphomopsis obscurans* gen. et comb. nov. (*Melanconiellaceae*). IMA Fungus 12, 15
Uecker FA 1994 – On the ontogeny of the ascoma of *Glomerella cingulata*. Mycologia 86, 82–88.
Ullah J, Khanum Z, Khan IA, Khalid AN et al. 2021 – Metaproteomics reveals the structural and functional diversity of *Dermatocarpon miniatum* (L.) W. Mann. Microbiota. Fungal Biology 125(1), 32–38.
Unger F. 1833 – Die Exantheme der Pflanzen und einige mit diesen verwandte Krankheiten der Gewächse: pathogenetisch und nosographisch dargestellt. Wien: Gerold.
Untereiner WA, Bogale M, Carter A, cfv HW et al. 2013 – Molecular phylogeny of *Boliniales* (*Sordariomycetes*) with an assessment of the systematics of *Apiorhynchostoma*, *Endoxyla* and *Pseudovalsaria*. Mycologia 105, 564–588.

Untereiner WA, Scott JA, Naveau FA, Sigler L et al. 2004 – The *Ajellomycetaceae*, a new family of vertebrate-associated *Onygenales*. Mycologia 96(4), 812–821.
Untereiner WA. 1993 – A taxonomic revision of the genus *Endoxyla*. Mycologia 85, 294–310.
Upadhyay HP. 1981 – A monograph of *Ceratocystis* and *Ceratocystiopsis*. University of Georgia Press.
Urbanavichene IN, Urbanavichus GP. 2019 – Contributions to the lichen flora of the North Ossetia Nature Reserve (Republic of North Ossetia – Alania). I. Cluster "Shubi". Novitates Systematicae Plantarum non Vascularium 53(2), 349–368.
Úrbez-Torres JR, Haag P, Bowen P, O'Gorman DT. 2014. Grapevine trunk diseases in British Columbia: incidence and characterization of the fungal pathogens associated with black foot disease of grapevine. Plant Disease 98, 456–468.
Úrbez-Torres JR, Peduto F, Vossen PM, Krueger WH et al. 2013 – Olive twig and branch dieback: etiology, incidence, and distribution in California. Plant Disease 97, 231–244.
Urbez-Torres JR. 2011 – The status of *Botryosphaeriaceae* species infecting grapevines. Phytopathologia Mediterranea 50, S5–S45.
Urquhart AS, Mondo SJ, Mäkelä MR, Hane JK et al. 2018 – Genomic and genetic insights into a cosmopolitan fungus, *Paecilomyces variotii* (*Eurotiales*). Frontiers in Microbiology 9, 3058.
Üstün N, Bulam S, Peksen A. 2018 – Biochemical properties, biological activities and usage of truffles. In Proceedings of the Conference: International Congress on Engineering and Life Science, Kastamonu, Turkey 26–29.
Uzun Y, Kaya A. 2018 – *Rhizodiscina* Hafellner, a new genus record for Turkish *Dothideomycetes*. Acta Biologica Turcica 31(4), 141–145.
Vaca I, Chávez R. 2019 – Bioactive compounds produced by Antarctic filamentous fungi. In: Rosa L. (ed.) Fungi of Antarctica. Springer, Cham 265–283.
Vaghefi N, Pethybridge SJ, Ford R, Nicolas ME et al. 2012 – *Stagonosporopsis* spp. associated with ray blight disease of *Asteraceae*. Australasian Plant Pathology 41, 675–686.
Vainio E. 1890 – Etude sur la classification naturelle et la morphologie des lichens du Bresil. Acta Soc. Fauna Fl. Fenn. 7(1), 1–247; 7(2), 1–256.
Valadbeigi T, Von Brackel W. 2011 – Two new species of *Lichenostigma* (*Lichenotheliaceae*, lichenicolous fungi) from Iran. Willdenowia, 191–195.
Valenzuela-Lopez N, Cano-Lira JF, Guarro J, Sutton DA et al. 2018 – Coelomycetous *Dothideomycetes* with emphasis on the families *Cucurbitariaceae* and *Didymellaceae*. Studies in Mycology 90, 1–69.
Valladares F, Sancho LG, Ascaso C. 1996 – Functional analysis of the intrathalline and intracellular chlorophyll concentrations in the lichen family *Umbilicariaceae*. Annals of Botany 78, 471–477.
Valladares F, Sancho LG, Ascaso C. 1998 – Water storage in the lichen family *Umbilicariaceae*. Botanica Acta 111, 99–107.
Valle-Torres J, Ross TJ, Plewa D, Avellaneda MC et al. 2020 – Tar Spot: An understudied disease threatening corn production in the Americas. Plant Disease 104(10), 2541–2550.
Van Brummelen. 1992 – *Ramgea*, a new genus of *Pezizales* from the Netherlands. Persoonia-Molecular Phylogeny and Evolution of Fungi 14(4), 577– 582.
Van Brummelen J. 1985 – *Pseudoascozonus*, a new genus of *Pezizales*. Proceedings of the Indian Academy of Sciences 94, 363–367.
Van Caenegem W, Haelewaters D. 2024 – New insights into the DNA extraction and PCR amplification of minute ascomycetes in the genus *Laboulbenia* (*Pezizomycotina*, *Laboulbeniales*). IMA Fungus 15(1), 14.
Van Caenegem W, Blondelle A, Dumolein I, Santamaria B et al. 2023a – Five new species of *Gloeandromyces* (Fungi, *Laboulbeniales*) from tropical American bat flies (*Diptera*, *Streblidae*), revealed by morphology and phylogenetic reconstruction. Mycologia 115(5), 714–737.

Van Caenegem W, Ceryngier P, Romanowski J, Pfister DH et al. 2023b – *Hesperomyces* (Fungi, *Ascomycota*) associated with *Hyperaspis* ladybirds (*Coleoptera*, *Coccinellidae*): rethinking host specificity. Frontiers in Fungal Biology 3, 1040102.
Van de Wouw AP, Marcroft SJ, Howlett BJ. 2016 – Blackleg disease of canola in Australia. Crop and Pasture Science 67, 273–283.
van den Boom PPG, Giralt M. 1996 – Contribution to the flora of Portugal, lichens and lichenicolous fungi I. Nova Hedwigia 63 (1-2), 145–172.
van den Boom P, Etayo J. 2014 – New records of lichenicolous fungi and lichenicolous lichens from the Iberian Peninsula, with the description of four new species and one new genus. Opuscula Philolichenum 13, 44–79.
van den Boom PP, Lücking R, Sipman HJ. 2023 – Notes on *Graphidaceae* in Macaronesia, with Descriptions of Four New Species. Diversity 15(7), 817.
van den Brink J, Samson RA, Hagen F, Boekhout T et al. 2012 – Phylogeny of the industrial relevant, thermophilic genera *Myceliophthora* and *Corynascus*. Fungal Diversity 52, 197–207.
Van den Broeck D, Ertz D. 2016 – *Cryptophaea*, a new genus of byssoid *Arthoniaceae* (lichenized *Ascomycota*) and its phylogenetic position. Phytotaxa 261, 168–176.
Van den Broeck D, Lücking R, Gaya E, Chaves JL et al. 2017 – *Heterocyphelium leucampyx* (*Arthoniales*, *Ascomycota*): another orphaned mazaediate lichen finds its way home. The Lichenologist 49, 333–345.
van den Brule T, Punt M, Teertstra W, Houbraken J et al. 2019 – The most heat-resistant conidia observed to date are formed by distinct strains of *Paecilomyces variotii*. Environmental Microbiology 22, 986–999.
van der Kolk H. 2015 – *Thelocarpon pallidum*, een kleurloze stuifmeelkorst definitief in Nederland. Buxbaumiella 102, 31–34.
Van der Linde JA, Six DL, Wingfield MJ, Roux J. 2012 – New species of *Gondwanamyces* from dying *Euphorbia* tree in South Africa. Mycologia 104, 574–584.
van Dyk M, Spies CFJ, Mostert L, van der Rijst M et al. 2021 – Pathogenicity testing of fungal isolates associated with olive trunk diseases in South Africa. Plant Disease 105, 4060–4073.
van Nieuwenhuijzen EJ, Houbraken JA, Meijer M, Adan OC et al. 2016a – *Aureobasidium melanogenum*: a native of dark biofinishes on oil treated wood. Antonie Van Leeuwenhoek 109, 661–683.
Van Nieuwenhuijzen EJ, Miadlikowska JM, Houbraken JAMP, Adan OC et al. 2016b – Wood staining fungi revealed taxonomic novelties in *Pezizomycotina*: New order *Superstratomycetales* and new species *Cyanodermella oleoligni*. Studies in Mycology 85, 107–124.
Van Oorschot CA, De Hoog GS. 1982 – A new species of *Anthopsis*. Antonie van Leeuwenhoek 48, 61–65.
Van Oorschot CA. 1980 – A revision of *Chrysosporium* and allied genera. Studies in Mycology 20, 1–89.
Van Wyk M, Wingfield BD, Marin M, Wingfield MJ. 2010 – New *Ceratocystis* species infecting coffee, cacao, citrus and native trees in Colombia. Fungal Diversity 40, 103–117.
Vanderwolf KJ, Malloch D, McAlpine DF. 2016 – Ectomycota associated with arthropods from bat hibernacula in Eastern Canada, with particular reference to *Pseudogymnoascus destructans*. Insects 7, 16.
Vanga BR, Panda P, Shah AS, Thompson S et al. 2022 – DNA metabarcoding reveals high relative abundance of trunk disease fungi in grapevines from Marlborough, New Zealand. BMC Microbiology 22, 126.
Vargas-Asensio G, Pinto-Tomas A, Rivera B, Hernandez M et al. 2014 – Uncovering the cultivable microbial diversity of costa rican beetles and its ability to break down plant cell wall components. PLoS ONE 9(11), p.e113303.
Vasilyeva LN, Chernyshev A, Stephenson SL. 2010 – *Pyrenomycetes* of the Russian Far East 4: family *Nitschkiaceae* (*Coronophorales, Ascomycota*). Mycologia 102, 233–247.

Vasilyeva LN. 1997 – *Camarops pugillus* (Schwein.: Fr) Shear from the Russian far east. Mikol Fitoptolog 31, 5–7.
Vasilyeva LN. 1999a – Hysteriaceous fungi in the Russian far east I. *Hysterium*. Mikologiya i Fitopatologiya 33, 225–227.
Vasilyeva LN. 1999b – Hysteriaceous fungi in the Russian Far East II. The genus *Hysterographium*. Mikologiya i Fitopatologiya 33, 297–301.
Vasilyeva LN. 2000 – Hysteriaceous fungi in the Russian Far East III. *Glonium* and *Actidiographium*. Mikologiya i Fitopatologiya 34, 3–5.
Vasse M, Voglmayr H, Mayer V, Gueidan C et al. 2017 – A phylogenetic perspective on the association between ants (*Hymenoptera*: *Formicidae*) and black yeasts (*Ascomycota*: *Chaetothyriales*). Proceedings of the Royal Society B: Biological Sciences 284, 20162519.
Vašutová M, Jiroušek M, Hájek M. 2021 – High fungal substrate specificity limits the utility of environmental DNA to detect fungal diversity in bogs. Ecological Indicators 121, 107009.
Vázquez-Campos X, Kinsela AS, Waite TD, Collins RN et al. 2014 – *Fodinomyces uranophilus* gen. nov. sp. nov. and *Coniochaeta fodinicola* sp. nov., two uranium mine-inhabiting *Ascomycota* fungi from Northern Australia. Mycologia 106, 1073–1089.
Verkley G. 1994 – Ultrastructure of the ascus apical apparatus in *Leotia lubrica* and some *Geoglossaceae* (*Leotiales*, *Ascomycotina*). Persoonia: Molecular Phylogeny and Evolution of Fungi 15(4), 405–430.
Verkley GJ. 2002 – A revision of the genus *Sphaerographium* and the taxa assigned to *Rhynchophoma* (anamorphic *Ascomycetes*). Nova Hedwigia 75(3–4), 433–450.
Verkley GJM, Dukik K, Renfurm R, Göker M et al. 2014 – Novel genera and species of coniothyrium-like fungi in *Montagnulaceae* (*Ascomycota*). Persoonia 32, 25–51.
VEzda A, James PW. 1973 – *Sarrameanu paradoxa* A. Vezda & P. James gen. nov. et sp. nova, eine bemerken- swerte Flechte aus Neu-Kaledonien. Preslia, Praha 45, 305–3 10.
Vězda A, Kantvilas G. 1988 – *Sarrameana tasmanica*, a new Tasmanian lichen. The Lichenologist 20(2), 179–182.
Vězda A. 1963 – *Lichense Selecti Exsiccati, fasc. 8, n 184: Catillaria byssacea Vezda sp.nov.* Instituto Botanico Universitatis Agriculturae et Silviculturare, Brno.
Vězda A. 1970 – Neue oder wenig bekannte Flechten in der Tschechoslowakei. I. Folia Geobotanica et Phytotaxonomica 5, 307–337.
Vezda A. 1978 – Neue oder wenig bekannte Flechten in der Tschechoslowakei. II. Folia Geobot. Phytotaxa. 13, 397–420.
Vicente CS, Soares M, Faria J, Espada M et al. 2022 – Fungal communities of the pine wilt disease complex: studying the interaction of *Ophiostomatales* with *Bursaphelenchus xylophilus*. Frontiers in Plant Science 13, 1650.
Vicente F, Basilio A, Platas G, Collado J et al 2009 – Distribution of the antifungal agents sordarins across filamentous fungi. Mycological Research 113, 754–770.
Videira SI, Groenewald JZ, Braun U, Shin HD et al. 2016 – All that glitters is not *Ramularia*. Studies in Mycology 83, 49–163.
Videira SIR, Groenewald JZ, Nakashima C, Braun U et al. 2017 –*Mycosphaerellaceae* –chaos or clarity? Studies in Mycology 87, 257–421.
Vijaykrishna D, Hyde KD. 2006 – Inter-and intra stream variation of lignicolous freshwater fungi in tropical Australia. Fungal Diversity 21, 203–224.
Vijaykrishna D, Jeewon R, Hyde KD. 2006 – Molecular taxonomy, origins and evolution of freshwater *Ascomycetes*. Fungal Diversity 23, 351–390.
Vijaykrishna D, Mostert L, Jeewon R, Gams W et al. 2004 – *Pleurostomophora*, an anamorph of *Pleurostoma* (*Calosphaeriales*), a new anamorph genus morphologically similar to *Phialophora*. Studies in Mycology 50, 387–395.
Villanueva P, Vásquez G, Gil-Durán C, Oliva V et al. 2021. Description of the first four species of the genus *Pseudogymnoascus* from Antarctica. Frontiers in Microbiology 12, 713189.

Vishnu A, Khan MA, Bera M, Dilcher DL et al. 2017 – Fossil *Asterinaceae* in the phyllosphere of the eastern Himalayan Neogene Siwalikforest and their palaeoecological significance. Botanical Journal of the Linnean Society 185, 147–167.
Visscher H, Brinkhuis H, Dilcher DL, Elsik WC et al. 1996 – The terminal Paleozoic fungal event: evidence of terrestrial ecosystem destabilization and collapse. Proceedings of the National Academy of Sciences of the United States of America 93, 2155–2158.
Vitale S, Aiello D, Guarnaccia V, Luongo L et al. 2018 – *Liberomycespistaciae* sp. nov., the causal agent of pistachio cankers and decline in Italy. MycoKeys 40, 29.
Vitória NS, Bezerra JL, Gramacho KP, Luz EDMN. 2008 – *Camarotella torrendiella* comb. nov. and *C. acrocomiae*: etiologic agents of black leaf spot diseases on the coconut tree. Tropical Plant Pathology 33, 295–301.
Vittal BPR. 1975 – *Gangliostilbe indica*, a new synnematous hyphomycete from India. Kavaka 3, 69–71.
Vivi VK, Martins-Franchetti SM, Attili-Angelis D. 2019 – Biodegradation of PCL and PVC: *Chaetomium globosum* (ATCC 16021) activity. Folia Microbiologica 64, 1–7.
Vobis G. 1980 – Bau und Entwicklung der Flechten-Pycnidien und ihrer Conidien. Bibliotheca Lichenologica No. 14. J. Cramer, Vaduz. 141 pp.
Vogan AA, Miller AN, Silar P. 2021 – (2803) Proposal to change the conserved type of *Podospora*, nom,. cons. (*Ascomycota*). Taxon 70(2), 429–430.
Voglmayr H, Aguirre-Hudson MB, Wagner HG. 2019a – Lichens or endophytes? The enigmatic genus *Leptosillia* in the *Leptosilliaceae* fam. nov.(*Xylariales*), and *Furfurella* gen. nov.(*Delonicicolaceae*). Persoonia-Molecular Phylogeny and Evolution of Fungi 42, 228–260.
Voglmayr H, Amengual AP. 2018 – Three new species of *Stigmatodiscus* from Mallorca (Spain). Mycological Progress 17, 1189–1201.
Voglmayr H, Castlebury LA, Jaklitsch WM. 2017a – *Juglanconis* gen. nov. on *Juglandaceae*, and the new family *Juglanconidaceae* (*Diaporthales*). Persoonia 38, 136–155.
Voglmayr H, Fournier J, Jaklitsch WM. 2017b – *Stigmatodiscus pruni*, a new Dothideomycete with hysteriform ascomata. Sydowia 69, 29–35.
Voglmayr H, Fournier J, Jaklitsch WM. 2019b – Two new classes of *Ascomycota*: *Xylobotryomycetes* and *Candelariomycetes*. Persoonia: Molecular Phylogeny and Evolution of Fungi 42(1), 36–49.
Voglmayr H, Gardiennet A, Jaklitsch WM. 2016 – *Asterodiscus* and *Stigmatodiscus*, two new apothecial Dothideomycete genera and the new order *Stigmatodiscales*. Fungal Diversity 80, 271–284.
Voglmayr H, Jaklitsch WM. 2008 – *Prosthecium* species with *Stegonsporium* anamorphs on *Acer*. Mycological Research 112, 885–905.
Voglmayr H, Jaklitsch WM. 2011 – Molecular data reveal high host specificity in the phylogenetically isolated genus *Massaria* (*Ascomycota*, *Massariaceae*). Fungal Diversity 46, 133–170.
Voglmayr H, Jaklitsch WM. 2014 – *Stilbosporaceae* resurrected: generic reclassification and speciation. Persoonia 33, 61–82.
Voglmayr H, Rossman AY, Castlebury LA, Jaklitsch W. 2012 – Multigene phylogeny and taxonomy of the genus *Melanconiella* (*Diaporthales*). Fungal Diversity 57, 1–44.
von Arx J, Müller E. 1975 – A re-evaluation of the bitunicate *Ascomycetes* with keys to families and genera. Studies in Mycology 9, 1–159.
von Arx JA von. 1986 – On *Hamigera*, its Raperia anamorph and its classification in the *Onygenaceae*. Mycotaxon 26, 119–123.
von Arx JA, Müller E. 1954 – Die Gattungen der amerosporen Pyrenomyceten. Beiträge zur Kryptogamenflora der Schweiz 11(1), 1–434.
Von Arx JA, Samson RA. 1973 – Two new genera of the *Eurotiales*. Persoonia: Molecular Phylogeny and Evolution of Fungi 7(3), 377–380.

Von Arx JA. 1951 – Ueber die Gattung Laestadia und die Gnomoniaceen. Antonie van Leeuwenhoek 17, 259–272.
von Arx JA. 1952 – Studies on *Venturia* and related genera. Tijdschrift Ove Plantenziekten 58, 260–266.
von Höhnel FXR. 1917 – U¨ ber die Benennung Stellung und Nebenfruchtformen von Sphaerella Fries. Berichte der Deutschen Botanischen Gesellschaft 35, 627–631.
von Willdenow CL. 1787 – Florae Berolinensis Prodromus. Kessinger, Montana.
Vondrák J, Jaroslav ŠOUN. 2007 – *Lichenostigma svandae*, a new lichenicolous fungus on *Acarospora cervina*. The Lichenologist 39(3), 211–216.
Vondrák J, Palice ZD, Khodosovtsev AL, Postoyalkin S. 2010 – Additions to the diversity of rare or overlooked lichens and lichenicolous fungi in Ukrainian Carpathians. Chornomorski Botanical Journal. 6(1), 6–34.
Vondrak J, Pavel ŘÍ, Ulf AR, Søchting U. 2009 – The taxonomy of the *Caloplaca* citrina group (*Teloschistaceae*) in the Black Sea region; with contributions to the cryptic species concept in lichenology. The Lichenologist 41, 571–604.
Vorderman AG. 1894 – Analecta Op Bromatologisch Gebied: I II. Geneeskundig Tijdschrift voor Nederlandsch-Indië, 343–397.
Voronin LV. 1989 – *Phoma* Sacc. species from the water and fish of freshwater reservoirs. Mikologia i Fitopatologia 23, 19–27.
Vrålstad T, Myhre E, Schumacher T. 2002 – Molecular diversity and phylogenetic affinities of symbiotic root-associated *Ascomycetes* of the *Helotiales* in burnt and metal polluted habitats. New Phytologist 155, 131–148.
Vu D, Groenewald M, De Vries M, Gehrmann T et al. 2019 – Large-scale generation and analysis of filamentous fungal DNA barcodes boosts coverage for kingdom fungi and reveals thresholds for fungal species and higher taxon delimitation. Studies in Mycology 92, 135–154.
Vyas A, Freitas AV, Ralston ZA, Tang Z. 2021 – Fission yeast *Schizosaccharomyces pombe:* a unicellular "micromammal" model organism. Current Protocols 1(6), p.e151.
Wakana D, Itabashi T, Kawai K, Yaguchi T et al. 2014 – Cytotoxic anthrasteroid glycosides, malsterosides A–C, from *Malbranchea filamentosa*. The Journal of Antibiotics 67(8), 585–588.
Wakefield AE, Peters SE, Banerji S, Bridge PD et al. 1992 – *Pneumocystis carinii* shows DNA homology with the Ustomycetous red yeast fungi. Molecular Microbiology 6, 1903–1911.
Walker DM, Castlebury LA, Rossman AY, Mejía LC et al. 2012 – Phylogeny and taxonomy of *Ophiognomonia* (*Gnomoniaceae*, *Diaporthales*), including twenty-five new species in this highly diverse genus. Fungal Diversity 57(1), 85–147.
Walker J, Stovold GE. 1986 – *Arkoola nigra* gen. et sp. nov. (*Venturiaceae*) causing black leaf blight of soybean in Australia. Transactions of the British Mycological Society 87, 23–44.
Walker W F. 1985 – 5s ribosomal RNA sequences from *Ascomycetes* and evolutionary implications. Systematic and Applied Microbiology 6, 48–53.
Wallen RM, Perlin MH. 2018 – An overview of the function and maintenance of sexual reproduction in dikaryotic fungi. Frontiers in Microbiology 9, 503.
Walzer PD. 2013 – The ecology of pneumocystis: perspectives, personal recollections, and future research opportunities. Journal of Eukaryotic Microbiology 60(6), 634–645.
Wanasinghe DN, Bezerra JD, Xu J, Mortimer PE. 2023 – *Honghemyces pterolobii*, gen. et sp. nov. (*Bezerromycetaceae, Tubeufiales*), a new ascomycetous fungus from *Pterolobium macropterum* in Honghe, China. Sydowia 75, 13.
Wanasinghe DN, Hyde KD, Jeewon R, Crous PW et al. 2017a – Phylogenetic revision of *Camarosporium* (*Pleosporineae*, *Dothideomycetes*) and allied genera. Studies in Mycology 87, 207–256.
Wanasinghe DN, Hyde KD, Konta S, To-Anun C et al. 2017b – Saprobic *Dothideomycetes* in Thailand: *Neoaquastroma* gen. nov. (*Parabambusicolaceae*) introduced based on morphological and molecular data. Phytotaxa 302, 133–144.

Wanasinghe DN, Mortimer PE, Xu J. 2021 – Insight into the systematics of microfungi colonizing dead woody twigs of *Dodonaea viscosa* in Honghe (China). Journal of Fungi 7, e180.
Wanasinghe DN, Phukhamsakda C, Hyde KD, Jeewon R et al. 2018 – Fungal diversity notes 709–839: taxonomic and phylogenetic contributions to fungal taxa with an emphasis on fungi on *Rosaceae*. Fungal Diversity 89, 1–236.
Wang B, Li ZZ, Yao J. 2010a – Development status, tendency and strategy of fungal insecticides industry. Journal of Anhui Agricultural Sciences 38(12), 6269 –6270.
Wang C, Becker K, Pfütze S, Kuhnert E et al. 2019a – Investigating the function of cryptic cytochalasan cytochrome P450 monooxygenases using combinatorial biosynthesis. Organic Letters 21(21), 8756–60.
Wang CJK, Sutton BC. 1998 – *Diplococcium hughesii* sp. nov. with a *Selenosporella* synanamorph. Canadian Journal of Botany 76, 1608–1613.
Wang CJK. 1976 – *Spadicoides* in New York. Memoirs of the New York Botanical Garden 28, 218–228.
Wang F, Cale JA, Hussain A, Erbilgin N. 2020a – Exposure to fungal volatiles can influence volatile emissions from other ophiostomatoid fungi. Frontiers in Microbiology 11, 567462.
Wang GS, Yuan YL, Li K, Zhu JH et al. 2023a – Cytosporones with anti-inflammatory activities from the mangrove endophytic fungus *Phomopsis* sp. QYM-13. Marine Drugs 21(12), 631.
Wang H, Guo S, Huang M, Thorsten LH et al. 2010b – *Ascomycota* has a faster evolutionary rate and higher species diversity than *Basidiomycota*. Science China Life Sciences 53, 1163–1169.
Wang HJ, Gloer JB, Scott JA, Malloch D. 1995 – Coniochaetones A and B: new antifungal benzopyranones from the coprophilous fungus *Coniochaeta saccardoi*. Tetrahedron Letters 36(33), 5847–5850.
Wang K, Sipilä T, Overmyer K. 2016a– The isolation and characterization of resident yeasts from the phylloplane of *Arabidopsis thaliana*. Scientific Reports 6.
Wang K, Sipilä T, Overmyer K. 2021a – A novel *Arabidopsis* phyllosphere resident *Protomyces* species and a re-examination of genus *Protomyces* based on genome sequence data. IMA Fungus 12(1), 8.
Wang L, Dong JY, Song HC, Shen KZ et al. 2008 – Screening and isolation of antibacterial activities of the fermentative extracts of freshwater fungi from Yunnan Province, China. Annals of Microbiology 58, 579–584.
Wang L, Zhou HB, Frisvad JC, Samson RA. 2004a – *Penicillium persicinum*, a new griseofulvin, chrysogine and roquefortine C producing species from Qinghai province, China. Antonie Van Leeuwenhoek 86, 173–179.
Wang LL, Wang H, Xiong Y, Zhou X et al. 2022a – Advances in the control of crop pests by using entomopathogenic fungi. Journal of Tropical Biology 13(03), 309–314.
Wang LP, Xu JY, Li HC, Song LP et al. 2016b – The complete mitochondrial genome of *Paecilomyces hepiali* (*Ascomycota*, *Eurotiomycetes*). Mitochondrial DNA 27(2), 916–917.
Wang LS, Qian ZG. 2013 – Illustrated Medicinal Lichens of China. Yunnan, China.
Wang Q, Sun M, Zhang Y, Song Z et al. 2020b – Extensive chromosomal rearrangements and rapid evolution of novel effector superfamilies contribute to host adaptation and speciation in the basal ascomycetous fungi. Molecular Plant Pathology 21(3), 330–348.
Wang QT, Guo MJ, Lv T, Zhou H et al. 2023b – Phylogeny and taxonomy of *Rhytisma*-like species worldwide. Fungal Diversity 120(1), 77–119.
Wang TW, de Kesel A, Haelewaters D, Pfister DH. 2016c – Farlow Herbarium cockroach hosts new record of *Laboulbeniales* for North America. Rhodora 118(973), 26–31.
Wang X, Wedge DE, Cutler SJ. 2016d – Chemical and biological study of cladosporin, an antimicrobial inhibitor: a review. Natural Product Communications 11(10), 1595–1600.
Wang XW, Bai FY, Bensch K, Meijer M et al. 2019b – Phylogenetic re-evaluation of *Thielavia* with the introduction of a new family *Podosporaceae*. Studies in Mycology 93, 155–252.
Wang XW, Han PJ, Bai FY, Luo A et al. 2022b – Taxonomy, phylogeny and identification of *Chaetomiaceae* with emphasis on thermophilic species. Studies in Mycology 101, 121–243.

Wang XW, Houbraken J, Groenewald JZ, Meijer M et al. 2016e – Diversity and taxonomy of *Chaetomium* and chaetomium-like fungi from indoor environments. Studies in Mycology 84(1), 145–224.
Wang XW, Yang FY, Meijer M, Kraak B et al. 2019c– Redefining *Humicola sensu stricto* and related genera in the *Chaetomiaceae*. Studies in Mycology 93, 65–153.
Wang Y, Yang MH, Wang XB, Li TX et al. 2014a –Bioactive metabolites from the endophytic fungus *Alternaria alternata*. Fitoterapia 99, 153–158.
Wang YB, Wang Y, Fan Q, Duan DE et al. 2020c – Multigene phylogeny of the family *Cordycipitaceae* (*Hypocreales*): New taxa and the new systematic position of the Chinese cordycipitoid fungus *Paecilomyces hepiali*. Fungal Diversity 103(1), 1–46.
Wang YL, Lu Q, Decock C, Li YX et al. 2015 – *Cytospora* species from *Populus* and *Salix* in China with *C. davidiana* sp. nov. Fungal Biology 119(5), 420–432.
Wang YY, Liu B, Zhang XY, Zhou QM et al. 2014b – Genome characteristics reveal the impact of lichenization on lichen-forming fungus *Endocarpon pusillum* Hedwig (*Verrucariales*, *Ascomycota*). BMC Genomics 15, 1–18.
Wang YZ, Aptroot A, Hyde KD. 2004b – Revision of the genus *Amphisphaeria*. Hong Kong SAR, China. Fungal Diversity Research Sereies 13, 1–168.
Wang Z, Binder M, Hibbett DS. 2002 – A new species of *Cudonia* based on morphological and molecular data. Mycologia 94, 641–650.
Wang Z, Binder M, Schoch CL, Johnston PR et al. 2006a – Evolution of helotialean fungi (*Leotiomycetes*, *Pezizomycotina*): a nuclear rDNA phylogeny. Molecular Phylogenetics and Evolution 41(2), 295–312.
Wang Z, Johnston P, Takamatsu S, Spatafora J et al. 2006b – Toward a phylogenetic classification of the *Leotiomycetes* based on rDNA data. Mycologia 98(6), 1065–1075.
Wang Z, Johnston PR, Yang ZL, Townsend JW. 2009 – Evolution of reproductive morphology in leaf endophytes. PLoS ONE 4, e4246.
Wang Z, Nilsson RH, Lopez-Giraldez F, Zhuang WY et al. 2011 – Tasting soil fungal diversity with earth tongues: phylogenetic test of SATE alignments for environmental ITS data. Plos ONE 6(4), e19039.
Wang Z, Zhou Q, Zheng G, Fang J et al. 2021b – Abundance and diversity of ophiostomatoid fungi associated with the Great Spruce Bark Beetle (*Dendroctonus micans*) in the Northeastern Qinghai-Tibet Plateau. Frontiers in Microbiology 3082.
Watson W. 1929 – The classification of lichens. New Phytologist 28, 85–116.
Wazir JF, Ansari NA. 2004 – *Pneumocystis carinii* infection. Update and review. Archives of Pathology & Laboratory Medicine 1023–1027.
Webb JS, Nixon M, Eastwood IM, Greenhalgh M et al. 2000 – Fungal colonization and biodeterioration of plasticized polyvinyl chloride. Applied and Environmental Microbiology 66(8), 3194–200.
Weber B, Büdel B, Belnap J. 2016 – Biological soil crusts: An organizing principle in drylands. Ecological Studies 226, 548.
Weber E, Go¨ rke C, Begerow D. 2002 – The *Lecythophora-Coniocha*- eta complex II. Molecular studies based on sequences of large subunit of ribosomal DNA. Nova Hedwig 74, 187–200
Weber E. 2002 – The *Lecythophora-Coniochaeta* complex I. Morphological studies on *Lecythophora* species isolated from *Picea abies*. Nova Hedwig 74, 159–185.
Webster J, Weber R. 2007 – Introduction to Fungi (third edition). Cambridge: Cambridge University Press.
Webster J. 1955 – Graminicolous *Pyrenomycetes*. V. Conidial states of *Leptosphaeria michotii*, *L. microscopica*, *Pleospora vagans* and the perfect state of *Dinemasporium graminum*. Transactions of the British Mycological Society 38(4), 347–365.
Wedin M, Döring H, Ekman S. 2000a – Molecular phylogeny of the lichen families *Cladoniaceae*, *Sphaerophoraceae*, and *Stereocaulaceae* (*Lecanorales*, *Ascomycotina*). The Lichenologist 32(2), 171–187.

Wedin M, Döring H, Gilenstam G. 2004 – Saprotrophy and lichenization as options for the same fungal species on different substrata: environmental plasticity and fungal lifestyles in the *Stictis–Conotrema* complex. New Phytologist 164(3), 459–465.
Wedin M, Döring H, Gilenstam G. 2006 – *Stictis s. lat.* (*Ostropales*, *Ascomycota*) in northern Scandinavia, with a key and notes on morphological variation in relation to lifestyle. Mycological Research 110(7), 773–789.
Wedin M, Döring H, Könberg K, Gilenstam G. 2005a – Generic delimitations in the family *Stictidaceae* (*Ostropales*, *Ascomycota*): the Stictis–Conotrema problem. The Lichenologist 37(1), 67–75.
Wedin M, Döring H, Nordin A, Tibell L. 2000b – Small subunit rDNA phylogeny shows the lichen families *Caliciaceae* and *Physciaceae* (*Lecanorales*, *Ascomycotina*) to form a monophyletic group. Canadian Journal of Botany 78, 246–254.
Wedin M, Grube M. 2002 – Parsimony analyses of mtSSU and nITS rDNA sequences reveal the natural relationships of the lichen families *Physciaceae* and *Caliciaceae*. Taxon 51, 655–660.
Wedin M, Jørgensen PM, Ekman S. 2011 – *Vahliellaceae*, a new family of cyanobacterial lichens (*Peltigerales*, *Ascomycetes*). The Lichenologist 43(1), 67–72.
Wedin M, Jørgensen PM, Wiklund E. 2007 – *Massalongiaceae* fam. nov., an overlooked monophyletic group among the cyanobacterial lichens (*Peltigerales*, *Lecanoromycetes*, *Ascomycota*). The Lichenologist 39(1), 61–67.
Wedin M, Tibell L. 1997 – Phylogeny and evolution of *Caliciaceae*, *Mycocaliciaceae* and *Sphinctrinaceae* (*Ascomycota*), with notes on the evolution of the prototunicate ascus. Canadian Journal of Botany 75, 1236–1242.
Wedin M, Westberg M, Crewe AT, Tehler A et al. 2009a – Species delimitation and evolution of metal bioaccumulation in the lichenized *Acarospora smaragdula* (*Ascomycota*, Fungi) complex. Cladistics 25(2), 161–172.
Wedin M, Wiklund E, Crewe A, Döring H et al. 2005b – Phylogenetic relationships of *Lecanoromycetes* (*Ascomycota*) as revealed by analyses of mtSSU and nLSU rDNA sequence data. Mycological Research 109 (2), 159–172.
Wedin M, Wiklund E, Jørgensen PM, Ekman S. 2009b – Slippery when wet: phylogeny and character evolution in the gelatinous cyanobacterial lichens (*Peltigerales*, *Ascomycetes*). Molecular Phylogenetics and Evolution 53(3), 862–871.
Wedin M, Wiklund E. 2004 – The phylogenetic relationships of *Lecanorales* suborder *Peltigerineae* revisited. Symbolae Botanicae Upsalienses 34(1), 469–475.
Weerakoon G, Aptroot A, Lumbsch HT, Wolseley PA et al. 2012 – New molecular data on *Pyrenulaceae* from Sri Lanka reveal two well-supported groups within this family. Lichenologist 44, 639–647.
Wehmeyer LE. 1975 – The pyrenomycetous fungi. Mycologia Memoir No. 6. The New York Botanical Garden. J. Cramer Publishing, Germany.
Wei DL, Chang SC, Wei YH, Lin YW et al. 1992 − Production of cellulolytic enzymes from the *Xylaria* and *Hypoxylon* species of *Xylariaceae*. World Journal of Microbiology and Biotechnology 8, 141−146.
Wei DP, Gentekaki, Wanasinghe D, Tang et al. 2023 – Diversity, molecular dating and ancestral characters state reconstruction of entomopathogenic fungi in *Hypocreales*. Mycosphere 13(2), 281–351.
Wei DP, Wanasinghe DN, Gentekaki E, Thiyagaraja V et al. 2021a – Morphological and phylogenetic appraisal of novel and extant taxa of *Stictidaceae* from Northern Thailand. Journal of Fungi 7, 880.
Wei H, Duan R, Xu Q, Yang S et al. 2021b – Fungal spore indicators of vegetation and highland pastoralism in modern topsoil and dung, eastern Tibetan Plateau. Catena 202,105231.
Wei JC, Jiang YM. 1988 – A conspectus of the lichenized *Ascomycetes Umbilicariaceae* in China. Mycosystema 1, 73–106.

Wei JC, Jiang YM. 1993 – The Asian *Umbilicariaceae* (*Ascomycota*). Beijing: International Academic Publishers.
Wei LX, Zhang HX, Tan JL, Chu YS et al. 2011 – Arthrobotrisins A-C, oligosporons from the nematode-trapping fungus *Arthrobotrys oligospora*. Journal of Natural Products 74(6), 1526–1530.
Weir A, Beakes GW. 1996 – Correlative light-and scanning electron microscope studies on the developmental morphology of *Hesperomyces virescens*. Mycologia 88(5), 677–693.
Weir A, Blackwell M. 2001 – Molecular data support the *Laboulbeniales* as a separate class of *Ascomycota*, *Laboulbeniomycetes*. Mycological Research 105(10), 1182–1190.
Weir A, Hammond PM. 1997 – *Laboulbeniales* on beetles: Host utilization patterns and species richness of the parasites. Biodiversity and Conservation 6, 701–719.
Weir BS, Johnston PR, Damm U. 2012 – The *Colletotrichum gloeosporioides* species complex. Studies in Mycology 73, 115–180.
Weir JR. 1916 – *Hypoderma deformans*, an undescribed needle fungus of the western yellow pine. Journal of Agricultural Research 6, 277–288.
Weissenbacher-Lang C, Fuchs-Baumgartinger A, Guija-De-Arespacochaga A, Klang A et al. 2018 – Pneumocystosis in dogs: Metaanalysis of 43 published cases including clinical signs, diagnostic procedures, and treatment. Journal of Veterinary Diagnostic Investigation 30, 26–35.
Weissenbacher-Lang C, Kurelju˘sic´ B, Nedorost N, Matula B et al. 2016 – Retrospective analysis of bacterial and viral co-infections in *Pneumocystis* spp. positive lung samples of Austrian pigs with pneumonia. PLoS ONE 11, e0158479.
Wellman FL. 1972 – Tropical American plant disease. The Scarcccrow Press, Metuchen, 989.
Wemheuer F, Wemheuer B, Daniel R, Vidal S. 2019 – Deciphering bacterial and fungal endophyte communities in leaves of two maple trees with green islands. Scientific Reports 9(1), 14183.
Wen Z, Xing J, Liu C, Zhu X et al. 2022 – The effects of ectomycorrhizal inoculation on survival and growth of *Pinus thunbergia* seedlings planted in saline soil. Symbiosis 86, 71–80.
Wendt L, Sir EB, Kuhnert E, Heitkämper S et al. 2018 − Resurrection and emendation of the *Hypoxylaceae*, recognised from a multigene phylogeny of the *Xylariales*. Mycological Progress 17, 115−54.
Westberg M, Arup U, Kärnefelt I. 2007 – Phylogenetic studies in the *Candelariaceae* (lichenized *Ascomycota*) based on nuclear ITS DNA sequence data. Mycological Research 111(11), 1277–1284.
Westberg M, Arup U. 2010 – *Candelaria concolor* – a rare lichen in the Nordic countries. Graphis Scripta 22(2), 38–42.
Westberg M, Arup U. 2011 – *Candelaria pacifica* sp. nova (*Ascomycota*, *Candelariales*) and the identity of *Candelaria vulgaris*. Bibliotheca Lichenologica 106, 353–364.
Westberg M, Frödén P, Wedin M. 2009 – A monograph of the genus *Placomaronea* (*Ascomycota*, *Candelariales*). The Lichenologist 41(5), 513–527.
Westberg M, Frödén P. 2007 – *Candelaria fibrosoides* a new species from Peru. Bibliotheca Lichenologica 95, 549–554.
Westberg M, Millanes AM, Knudsen K, Wedin M. 2015 – Phylogeny of the *Acarosporaceae* (*Lecanoromycetes*, *Ascomycota*, Fungi) and the evolution of carbonized ascomata. Fungal Diversity 73, 145–158.
Westberg M, Morse CA, Wedin M. 2011 – Two new species of *Candelariella* and a key to the *Candelariales* (lichenized *Ascomycetes*) in North America. The Bryologist 114(2), 325–334.
Westberg M, Nash TH III. 2002 – *Candelina*. In: Nash THIII, Ryan BD, Gries C, Bungartz F (eds.): Lichen Flora of the Greater Sonoran Desert Region. I. Lichens Unlimited, Arizona State University, Tempe, Arizona.
Westberg M, Owe-Larsson B, Arup U. 2023 – *Halecania pannarica* new to Sweden. Graphis Scripta 35(1), 1–3.

Westberg M, Sohrabi M. 2012 – A conspectus of the lichen genus *Candelariella* (*Candelariaceae*, *Ascomycota*) in Southwest Asia with emphasis on Iran. Nova Hedwigia 95(3–4), 531–546.
Westberg M. 2004 – *Candelariella* In: Nash THIII, Ryan BD, Diederich P, Gries C, Bungartz F. (eds.): Lichen Flora of the Greater Sonoran Desert Region, II. Lichens Unlimited, Arizona State University, Tempe, Arizona.
Westberg M. 2005 – The lichen genus *Candelariella* in western North America. Doctoral thesis, Lund University. Södra Sandby. Lund.
Westberg M. 2007a – *Candelariella* (*Candelariaceae*) in western United States and northern Mexico: the species with biatorine apothecia. Bryologist 110(3), 365–374.
Westberg M. 2007b – *Candelariella* (*Candelariaceae*) in western United States and northern Mexico: the polysporous species. Bryologist 110(3), 375–390.
Westberg M. 2007c – *Candelariella* (*Candelariaceae*) in western United States and northern Mexico: the 8-spored, lecanorine species. Bryologist 110(3), 39–419.
Westberg M. 2010 – The identity of *Candelariella canadensis*. The Lichenologist 42(1), 119–122.
Whalley AJS, Edwards R. 1987 – Xylariaceous fungi: use of secondary metabolites. In: Rayner ADM, Brasier CM, Moore D (eds) The evolutionary biology of fungi. Cambridge University Press, Cambridge, 423–434.
Whalley AJS, Edwards R. 1995 – Secondary metabolites and systematic arrangement within the *Xylariaceae*. Canadian Journal of Botany 73, 802–810.
Whalley AJS. 1996 − The xylariaceous way of life. Mycological Research 100, 897−922.
Wibberg D, Stadler M, Lambert C, Bunk B et al. 2021 – High quality genome sequences of thirteen *Hypoxylaceae* (*Ascomycota*) strengthen the phylogenetic family backbone and enable the discovery of new taxa. Fungal Diversity 106, 7–28.
Wicklow DT, Hirschfield BJ. 1979 – Competitive hierarchy in post-fire *Ascomycetes*. Mycologia 71, 47–54.
Wijayawardene DNN, Hyde KD, Dai DQ, Sanchez-Garcia M et al. 2022a – Outline of Fungi and fungus-like taxa – 2021. Mycosphere 13, 53–453.
Wijayawardene DNN, McKenzie EHC, Hyde KD. 2012a – Towards incorporating anamorphic fungi in a natural classification–checklist and notes for 2011. Mycosphere 3(2), 157–228.
Wijayawardene N, Hyde K.D, Al-Ani L.K.T, Somayeh D et al. 2020 – Outline of Fungi and fungus-like taxa. Mycosphere 11, 1060–1456.
Wijayawardene NN, Crous PW, Kirk PM, Hawksworth DL et al. 2014a – Naming and outline of *Dothideomycetes*–2014 including proposals for the protection or suppression of generic names. Fungal Diversity 69, 1–55.
Wijayawardene NN, Dissanayake LS, LI QR, Dai DQ et al. 2021a – Yunnan–Guizhou Plateau: a mycological hotspot. Phytotaxa, 523, 1–31.
Wijayawardene NN, Hyde KD, Anand G, Dissanayake LS et al. 2021b – Towards incorporating asexually reproducing fungi in the natural classification and notes for pleomorphic genera. Mycosphere 12(1), 238–405.
Wijayawardene NN, Hyde KD, Camporesi E, Bhat DJ et al. 2014b – *Homortomyces tamaricis* sp. nov. and convergent evolution of *Homortomyces* and *Stilbospora*. Phytotaxa 176(1), 156–163.
Wijayawardene NN, Hyde KD, Lumbsch H, Liu JK et al. 2018 – Outline of *Ascomycota*: 2017. Fungal Diversity 88, 167–263.
Wijayawardene NN, Hyde KD, Rajeshkumar KC, Hawksworth DL et al. 2017a – Notes for genera-*Ascomycota*. Fungal Diversity 86, 1–594.
Wijayawardene NN, Hyde KD, Tibpromma S, Wanasinghe DN et al. 2017b – Towards incorporating asexual fungi in a natural classification: checklist and notes 2012–2016. Mycosphere 8(9), 1457–1554.
Wijayawardene NN, Hyde KD, Wanasinghe DN, Papizadeh M et al. 2016 – Taxonomy and phylogeny of dematiaceous *Coelomycetes*. Fungal Diversity 77(1), 1–316.
Wijayawardene NN, Mckenzie EHC, Chukeatirote E, Wang Y et al. 2012b – *Coelomycetes*. Cryptogamie, Mycologie 33(3), 215–244.

Wijayawardene NN, Phillips AJ, Pereira DS, Dai DQ et al. 2022b – Forecasting the number of species of asexually reproducing fungi (*Ascomycota* and *Basidiomycota*). Fungal Diversity 114(1), 463–490.
Wijayawardene NN, Phillips AJL, Tibpromma S, Dai DQ et al. 2021c – Looking for the undiscovered asexual taxa; case studies from lesser studied life modes and habitats. Mycosphere 12, 1290–1333.
Wikee S, Lombard L, Nakashima C, Motohashi K et al. 2013 – A phylogenetic re-evaluation of *Phyllosticta* (*Botryosphaeriales*). Studies in Mycology 76, 1–29.
Wiklund E, Wedin M. 2003 – The phylogenetic relationships of the cyanobacterial lichens in the *Lecanorales* suborder *Peltigerineae*. Cladistics 19(5), 419–431.
Wilberforce PW. 1999 – A new species of *Karstenia* on *Deschampsia caespitosa* from North Argyll, Scotland. Mycologist 13, 149–150.
Willdenow CL. 1787 – Florae berolinensis prodromus. Berlin. 439.
Wingfield MJ, Barnes I, De Beer ZW, Roux J et al. 2017 – Novel associations between ophiostomatoid fungi, insects and tree hosts: current status–future prospects. Biological Invasions 19, 3215–3228.
Wingfield MJ, Brockerhoff EG, Wingfield BD, Slippers B. 2015 – Planted Forest health: the need for a global strategy. Science 349, 832-836.
Wingfield MJ, De Beer ZW. 2018 – *Ophiostomatales*: complex, multifaceted, and still poorly understood. Fungal Biology Reviews 32, 1–6.
Wingfield MJ, van Wyk PS, Marasas WFO. 1988 – *Ceratocystiopsis proteae* sp. nov., with a new anamorph genus. Mycologia 80, 23–30.
Winka K, Ahlberg C, Eriksson OE. 1998a – Are there lichenized *Ostropales*?. The Lichenologist 30(4-5), 455–462.
Winka K, Eriksson OE, Bång Å. 1998b – Molecular evidence for recognizing the *Chaetothyriales*. Mycologia 90, 822–830.
Winka K. 2000 – Phylogenetic relationships within the *Ascomycota* based on 18S rDNA sequences. PhD Thesis. Sweden: Umea University.
Winter G. 1885 – Pilze: Ascomyceten. Rabenhorst's Kryptogamen Flora von Deutschland. Oesterreich und der Schweiz 1, 1–928.
Winter G. 1886 – Ascomyceten: Gymnoasceen und Pyenomyceten. In: Rabenhorst's Kryptogamen-Flora. Vol. 1. Leipzig, Germany: Eduard Kummer 928.
Winter G. 1887 – Ascomyceten. Rabenhorst's Kryptogamen-Flora 1, 1–928.
Winton LM, Manter DK, Stone JK, Hansen EM. 2003 – Comparison of biochemical, molecular, and visual methods to quantify *Phaeocryptopus gaeumannii* in Douglas-Fir foliage. Phytopathology 93(1), 121–126.
Winton LM, Stone JK, Hansen EM, Shoemaker RA et al. 2007 – The systematic position of *Phaeocryptopus gaeumannii*. Mycologia 99, 240–252.
Wirth V, Hauck M, Schultz M. 2013 – Die Flechten Deutschlands. Ulmer Verlag, Stuttgart, 1244.
Wirth V, Hauck M, von Brackel W, Cezanne RA et al. 2011 – Rote Liste und Artenverzeichnis der Flechten und flechtenbewohnenden Pilze Deutschlands [Red List and checklist of species of lichens and lichenicolous fungi of Germany]. Naturschutz und Biologische Vielfalt 70, 7–122.
Wirth V, Vézda A. 1972 – Zur Systematik der *Lecidea cyathoides*-Gruppe. - Beitrage Naturk. Forsch. Sudw.-Deutschl. 31, 91–92.
Wirth V. 1987 – Die Flechten Baden-Wirttembergs. Stuttgart.
Wittstein K, Cordsmeier A, Lambert C, Wendt L et al. 2020 − Identification of *Rosellinia* species as producers of cyclodepsipeptide PF1022 A and resurrection of the genus *Dematophora* as inferred from polythetic taxonomy. Studies in Mycology 96(1), 1−16.
Wong MKM, Goh TK, Hodgkiss IJ, Hyde KD et al. 1998a – Role of fungi in freshwater ecosystems. Biodiversity and Conservation 7, 1187–1206.
Wong PT, Tan YP, Weese TL, Shivas RG. 2022 – *Magnaporthiopsis* species associated with patch diseases of turfgrasses in Australia. Mycosphere 13(1), 602–611.

Wong PTW, Khemmuk W, Geering ADW et al. 2015 – *Budhanggurabania cynodonticola* Fungal Planet Description 359. Persoonia 34, 240–241.
Wong SW, Hyde KD, Jones EBG. 1998b – *Annulatascaceae*, a new ascomycete family from the tropics. Systema Ascomycetum 16, 17–25.
Wood AR, Damm U, van der Linde EJ, Groenewald JZ et al. 2016 – Finding the missing link: Resolving the *Coryneliomycetidae* within *Eurotiomycetes*. Persoonia 37, 37–56.
Wood V, Gwilliam R, Rajandream MA, Lyne M et al. 2002 – The genome sequence of *Schizosaccharomyces pombe*. Nature 415(6874), 871–880.
Woods RG, Coppins BJ. 2012 – A Conservation Evaluation of British Lichens and Lichenicolous Fungi. Joint Nature Conservation Committee, Peterborough.
Worobiec G, Worobiec E, Erdei B. 2020 – Fossil callimothalloid fungi: revised taxonomy, modern equivalents and palaeoecology. Fungal Biology 124(10), 835–44.
Worobiec G, Worobiec E. 2013 – Epiphyllous fungi from the Oligocene shallow-marine deposits of the Krabbedalen Formation, Kap Brewster, central East Greenland. Acta Palaeobotanica 53, 165–179.
Woronichin NN. 1925 – Über die *Capnodiales*. Annales Mycologici 23, 174–178.
Wu B, Wiese J, Labes A, Kramer A et al. 2015 – Lindgomycin, an unusual antibiotic polyketide from a marine fungus of the *Lindgomycetaceae*. Marine Drugs 13, 4617–4632.
Wu C, Wang Y, Yang Y. 2022 – *Pestalotiopsis* diversity: Species, dispositions, secondary metabolites, and bioactivities. Molecules 27, 8088.
Wu DK, Zhang CP, Zhu CY, Wang YL et al. 2013 – Metabolites from carnivorous fungus *Arthrobotrys entomopaga* and their functional roles in fungal predatory ability. Journal of Agricultural and Food Chemistry 61(17), 4108–4113.
Wu G, Schuelke TA, Broders K. 2019 – The genome of the butternut canker pathogen, *Ophiognomonia clavigignenti-juglandacearum* shows an elevated number of genes associated with secondary metabolism and protection from host resistance responses in comparison with other members of the *Diaporthales*. bioRxiv 820977.
Wu HX, Schoch CL, Boonmee S, Bahkali AH et al. 2011 − A reappraisal of *Microthyriaceae*. Fungal Diversity 51, 189–248.
Wu HX, Tian Q, Li WJ, Hyde KD. 2014a − A reappraisal of *Microthyriaceae*. Phytotaxa 176, 201−212.
Wu S, Zhao Z, Okada Y, Watanabe Y et al. 2014b – Physiological activity of Chinese lichen (*Gyrophora esculenta*) component, methyl 2,4-dihydroxy-6-methylbenzoate and the related compounds. Asian Journal of Chemistry 26, 702–708.
Wu W, Chen S. 2024 – Distribution patterns of *Calonectria* (*Ascomycota, Sordariomycetes, Hypocreales, Nectriaceae*) species complexes related to diseased leaves and soil habitats during leaf blight outbreak season in Eucalyptus plantations in southern China. MycoKeys 110, 117.
Wu W, Diao Y. 2022 – Anamorphic chaetosphaeriaceous fungi from China. Fungal Diversity. 116(1), 1–546.
Wu W, Diao Y. 2023 – The chalara-like anamorphs of *Leotiomycetes*. Fungal Diversity 119, 213–490.
Wu XK, Zavialova NE, Kodrul TM, Liu XY et al. 2021 – Northern hemisphere megafossil of *Dacrycarpus* (*Podocarpaceae*) from the Miocene of South China and its evolutionary and paleoecological implications. Journal of Systematics and Evolution 59(2), 352–74.
Wu Z, Yan S, Zhou S, Chen S. 2014c – Diversity of endophytic mycobiota in *Fortunearia sinensis*. Acta Ecologica Sinica 34(3), 160–164.
Wuczkowski M, Metzger E, Sterflinger K, Prillinger H. 2005 – Diversity of yeasts isolated from litter and soil of different natural forest sites in Austria. Die Bodenkultur 56(4), 201–208
Wyka S, Mondo S, Liu M, Nalam V et al. 2022 – A large accessory genome and high recombination rates may influence global distribution and broad host range of the fungal plant pathogen *Claviceps purpurea*. PLoS ONE 17(2), e0263496.

Wyka SA, Broders KD. 2016 – The new family *Septorioideaceae*, within the *Botryosphaeriales* and *Septorioides strobi* as a new species associated with needle defoliation of *Pinus strobus* in the United States. Fungal Biology 120, 1030–1040.
Wynns AA. 2015 – Convergent evolution of highly reduced fruiting bodies in *Pezizomycotina* suggests key adaptations to the bee habitat. BMC Evolutionary Biology 15, 145.
Xavier KV, KC AN, Crous PW, Groenewald JZ et al. 2019 – *Dwiroopa punicae* sp. nov. (*Dwiroopaceae* fam. nov., *Diaporthales*), associated with leaf spot and fruit rot of pomegranate (*Punica granatum*). Fungal Systematics and Evolution 4, 33–41.
Xavier-Leite AB, Goto BT, Lücking R, da Silva Cáceres ME. 2023 – New genera in the lichenized family *Gomphillaceae* (*Ascomycota*: *Graphidales*). Mycological Progress 22(12), 88.
Xia YL, Luo FF, Shang YF, Chen PL et al. 2017 – Fungal cordycepin biosynthesis is coupled with the production of the safeguard molecule pentostatin. Cell Chemical Biology 24(12), 1479–1489.
Xiao XJ, Ma J, Zhang LJ, Liu NG et al. 2023a – Additions to the Genus *Helicosporium* (*Tubeufiaceae*, *Tubeufiales*) from China with an Identification Key to *Helicosporium* Taxa. Journal of Fungi 9, 775.
Xiao YP, Wang YB, Hyde KD, Eleni G et al. 2023b. – *Polycephalomycetaceae*, a new family of clavicipitoid fungi segregates from *Ophiocordycipitaceae*. Fungal Diversity 120, 1–76.
Xie CM, Wang LS, Zhao ZT, Zhang YY et al. 2022 – Revision of Immersaria and a new lecanorine genus in *Lecideaceae* (lichenised *Ascomycota*, *Lecanoromycetes*). MycoKeys 87, 99.
Xie L, Chen YL, Long YY, Zhang Y et al. 2019 – Three new species of *Conlarium* from sugarcane rhizosphere in southern China. MycoKeys 56,1.
Xu B, Li C, Sung C. 2014 – Telomerase inhibitory effects of medicinal mushrooms and lichens, and their anticancer activity. International Journal of Medicinal Mushrooms 16, 17–28.
Xu H, Zhou L, Wang M, Wei L et al. 2022a – Chemical constituents from marine derived fungus *Talaromyces cellulolyticus* SHJ-3 and its chemotaxonomic significance. Biochemical Systematics and Ecology 100, 104377.
Xu RJ, Boonmee S, Dong W, Guo YY et al. 2024a – *Savoryella claviformis* (*Savoryellaceae*), a new freshwater hyphomycetous species from the Tibetan Plateau, China. Studies in Fungi 9, e009.
Xu RJ, Thiyagaraja V, Li Y, Zhou DQ et al. 2024b – Two novel lignicolous freshwater fungi, *Conioscypha xizangensis* and *Cordana linzhiensis*, from the Tibetan Plateau, China. New Zealand Journal of Botany 9, 1–7.
Xu WF, Hou XM, Yao FH, Zheng N et al. 2017 − Xylapeptide A, an antibacterial cyclopentapeptide with an uncommon L-pipecolinic acid moiety from the associated fungus *Xylaria* sp. (GDG-102). Scientific Reports 7(1), 6937.
Xu XH, Su ZZ, Wang C, Kubicek CP et al. 2014 – The rice endophyte *Harpophora oryzae* genome reveals evolution from a pathogen to a mutualistic endophyte. Scientific Reports 4(1), 5783.
Xu XL, Zeng Q, Lv YC, Jeewon R et al. 2021 – Insight into the systematics of novel entomopathogenic fungi associated with armored scale insect, *Kuwanaspis howardi* (*Hemiptera*: *Diaspididae*) in China. Journal of Fungi 7, 628.
Xu Y, Mafezoli J, Oliverira MCF, U'ren JM et al. 2015 – Anteaglonialides A-F and Palmarumycins CE1-CE3 from *Anteaglonium* sp. FL0768, a fungal endophyte of the spike moss *Selaginella arenicola*. Journal of Natural Products 78, 2738–2747.
Xu Z, Xiong B, Xu J. 2019 – Chemical investigation of secondary metabolites produced by mangrove endophytic fungus *Phyllosticta capitalensis*. Natural Product Research 35, 1561–1565.
Yacharoen S, Tian Q, Chomnunti P, Boonmee S et al. 2015 – *Patellariaceae* revisited. Mycosphere 6, 290–326.
Yaguchi T, Sano A, Yarita K, Suh MK et al. 2006 – New species of *Cephalotheca* isolated from a Korean patient. Mycotaxon 96, 309–322.
Yahr R. 2015 – The status of the conservation priority species *Calicium corynellum* in the British Isles. The Lichenologist 47(4), 205–214.

Yakovchenko L, Ahti T, Westberg M. 2013 – *Candelariella biatorina* new to Asia from the Russian Far East. Herzogia 26, 207–212.
Yakovchenko L, Davydov EA, Ohmura Y. 2016 – *Candelariella placodizans* (*Candelariaceae*) reported new to mainland China and Taiwan based on morphological, chemical and molecular phylogenetic analyses. Taiwania 61(2), 159–164.
Yakovchenko LS, Davydov E, Ohmura Y. 2022 – *Candelariella xanthostigmoides* (*Candelariaceae*, *Ascomycota*) - a new lichen record to East Asia from Japan. Turczaninowia 25(1), 124–128.
Yakovchenko LS, Davydov EA. 2018 – *Sporastatia crassulata*, a new species from the Altai Mountains with a key to *Sporastatia* and remarks on some additional species. The Lichenologist 50, 439–450.
Yakovchenko LS, Davydov EA. 2024 – *Candelariella ahtii* (*Candelariaceae*, *Ascomycota*) – a new species of lichen from Central and North East Asia, and a key for 8-spored *Candelariella*. The Lichenologist 56(5), 287–300.
Yakovchenko LS, Ismailov AB, Westberg M. 2012 – *Candelariella antennaria* new to Russia, Kazakhstan, Nepal and India. Turczaninowia 15(4), 27–30.
Yakovchenko LS, Vondrák J, Ohmura Y, Korchikov ES et al. 2017 – *Candelariella blastidiata* sp. nov. (*Ascomycota*, *Candelariaceae*) from Eurasia and North America, and a key for grey thalli *Candelariella*. The Lichenologist 49(2), 117–126.
Yamada T, Tsukamoto H, Shiraishi T, Nomura T, Oku H. 1990 – Detection of indoleacetic acid biosynthesis in some species of *Taphrina* causing hyperplastic diseases in plants. Annals of the Phytopathological Society of Japan 56, 532–540.
Yamaguchi K, Chuaseeharonnachai C, Huhtinen S, Tsurumi Y et al. 2020 – Phylogeny and taxonomic revision of the genus *Candelabrum*, aero-aquatic fungi. Mycoscience 61(6), 265–281.
Yamamoto W. 1955 – On the so-called host range of sooty mould fungi. Annales of the Phytopathology Society of Japan 19, 97–103.
Yang C, Baral HO, Xu X, Liu Y. 2019a – *Parakarstenia phyllostachydis*, a new genus and species of non-lichenized *Odontotremataceae* (*Ostropales*, *Ascomycota*). Mycological Progress 18, 833–845.
Yang CL, Xu XL, Liu YG, Hyde KD et al. 2019b – A new species of *Phyllachora* (*Phyllachoraceae*, *Phyllachorales*) on *Phyllostachys heteroclada* from Sichuan, China. Phytotaxa 3, 392.
Yang EF, Dai DQ, Bhat JD, Dawoud TM et al. 2023a – Taxonomic and Phylogenetic Studies of Saprobic Fungi Associated with *Mangifera indica* in Yunnan, China. Journal of Fungi 9, 680.
Yang H, Sun G, Batzer J, Crous P et al. 2010 – Novel fungal genera and species associated with the sooty blotch and flyspeck complex on apple in China and the USA. Persoonia 24, 29–37.
Yang J, Liu JK, Hyde KD, Jones EB et al. 2017a – Two new species in *Fuscosporellaceae* from freshwater habitats in Thailand. Mycosphere 8, 1893–1903.
Yang J, Liu LL, Jones EBG, Hyde KD et al. 2023b – Freshwater fungi from karst landscapes in China and Thailand. Fungal Diversity 119, 1–212.
Yang J, Maharachchikumbura SSN, Bhat DJ, Hyde KD et al. 2016a – *Fuscosporellale*s, a new order of aquatic and terrestrial *Hypocreomycetidae* (*Sordariomycetes*). Cryptogamie, Mycologie 37(4), 449–475.
Yang J, Maharachchikumbura SSN, Hyde KD, Bhat DJ et al. 2015 – *Aquapteridospora lignicola* gen. et sp. nov., a new hyphomycetous taxon (*Sordariomycetes*) from wood submerged in a freshwater stream. Cryptogamie, Mycologie 36, 469–478.
Yang L, Bao DF, Luo ZL, Su XJ et al. 2022a – *Neoascotaiwania aquatica* sp. nov. from a freshwater habitat in Yunnan province, China. Phytotaxa 531 (2), 120–128.
Yang P, Shi W, Wang H, Liu H. 2016b – Screening of freshwater fungi for decolorizing multiple synthetic dyes. Brazilian Journal of Microbiology 47, 828–834.
Yang PW, Wen ML, Li YG, Fan HC et al. 2014 – Trichothecin from *Cordana musae* AGROO73: isolation, structure elucidation and antifungal activity on plant pathogenic fungi. Southwest China Journal of Agricultural Sciences 27(1), 142–146.

Yang Q, Fan XL, Du Z, Tian CM. 2017b – *Diaporthosporellaceae*, a novel family of *Diaporthales* (*Sordariomycetes*, *Ascomycota*). Mycoscience 59(3), 229–235.
Yang Q, Hollinger J, Leavitt SD, Wei X. 2022b – Two new species and two new records of the lichen-forming fungal genus *Peltula* (*Ascomycota*: *Peltulaceae*) from China. Biology 11, 1518.
Yang SW, Buevich A, Chan TM, Terracciano J et al. 2003 – A new antifungal sterol sulfate, Sch 601324, from *Chrysosporium* sp. The Journal of Antibiotics 56(4), 419–422.
Yang SW, Chan TM, Terracciano J, Boehm E et al. 2009 – Caryophyllenes from a fungal culture of C*hrysosporium pilosum*. Journal of Natural Products 72(3), 484–487.
Yang T, Groenewald JZ, Cheewangkoon R, Jami F et al. 2017c – Families, genera, and species of *Botryosphaeriales*. Fungal Biology 121(4), 322–346.
Yang Y, Liu XZ. 2006 – A new generic approach to the taxonomy of predatory anamorphic *Orbiliaceae* (*Ascomycotina*). Mycotaxon 97, 153–161
Yang Y, Yang E, An Z, Liu XZ. 2007 – Evolution of nematode-trapping cells of predatory fungi of the *Orbiliaceae* based on evidence from rRNA-encoding DNA and multiprotein sequences. Proceedings of the National Academy of Sciences 104, 8379–8384.
Yao JM, Wang YC, Zhu YG. 1992 – A new variety of the pathogen of maize take-all. Acta Mycologica Sinica 11, 99–104.
Yasanthika WE, Tennakoon DS, de Farias ARG, Chethana KT et al. 2023 – Isolation and characterization of novel *Dothideomycetes* species from forest soils in Chiang Rai and Krabi (Thailand): additions to the diversity of *Curvularia* and *Verruconis*. Phytotaxa 609, 17–44.
Yasin UZU. 2018 – *Rhizodiscina* Hafellner, a new genus record for Turkish *Dothideomycetes*. Acta Biologica Turcica 31(4), 141–145.
Yen LTH, Yamaguchi K, Tsurumi Y, Hopet DV et al. 2018 − *Hamatispora*, a new genus of aquatic fungi in *Microthyriales* isolated from fallen leaves in Vietnam. Mycoscience 59, 467−472.
Yeung QYY, Jeewon R, Hyde KD. 2006 – *Cancellidium pinicola* sp. nov. from *Pinus massoniana* and its phylogeny. Cryptogamie, Mycologie 27, 295–304.
Yin ML, Wingfield MJ, Zhou XD, de Beer ZW. 2020 – Phylogenetic re-evaluation of the *Grosmania penicillata* complex (*Ascomycota*, *Ophiostomatales*), with the description of five new species from China and USA. Fungal Biology 124, 110–124.
Yin ML, Wingfield MJ, Zhou XD, Linnakoski R et al. 2019 – Taxonomy and phylogeny of the *Leptographium olivaceum* complex (*Ophiostomatales*, *Ascomycota*), including descriptions of six new species from China and Europe. MycoKeys 60, 93.
Yoneda A, Kuo HW, Ishihara M, Azadi P et al. 2014 – *Glycosylation variants* of a β-glucosidase secreted by a Taiwanese fungus, *Chaetomella raphigera*, exhibit variant-specific catalytic and biochemical properties. PLoS ONE 9(9), e106306.
Yoshimura I. 1993 – Use of "Iwatake", an edible lichen, *Umbilicaria esculenta*. Bulletin of Kochi Gakuen College 24, 803–808.
Ypma-Wong MF, Fonzi WA, Sypherd PS. 1992 – Fungus-specific translation elongation factor 3 gene present in *Pneumocystis carinii*. Infection & Immunity 60, 4140–4145.
Yu FM, Jayawardena RS, Luangharn T, Zeng XY et al. 2024a – Species diversity of fungal pathogens on cultivated mushrooms: a case study on morels (*Morchella*, *Pezizales*). Fungal Diversity 125(1), 157–220.
Yu G, Sun Z, Peng J, Zhu M et al. 2019 − Secondary metabolites produced by combined culture of *Penicillium crustosum* and a *Xylaria* sp. Journal of Natural Products 82, 2013–2017.
Yu X, Hu X, Pop M, Wernet N et al. 2021 – Fatal attraction of Caenorhabditis elegans to predatory fungi through 6-methyl-salicylic acid. Nature Communications 12(1), 5462.
Yu XD, Dong W, Bhat DJ, Boonmee S et al. 2018 – *Cylindroconidiis aquaticus* gen. et sp. nov., a new lineage of aquatic hyphomycetes in *Sclerococcaceae* (*Eurotiomycetes*). Phytotaxa 372(1), 079–087

Yu XD, Zhang SN, Liu JK. 2023 – Additions to bambusicolous fungi of *Savoryellaceae* from Southwest China. Journal of Fungi 9, 571.
Yu XD, Zhang SN, Liu JK. 2024b – Novel hyphomycetous fungi associated with bamboo from Sichuan, China. Phytotaxa 634(3), 235–254.
Yu Z, Mo M, Zhang Y, Zhang KQ. 2014 – Taxonomy of Nematode-Trapping Fungi from *Orbiliaceae*, *Ascomycota*. In: Zhang KQ, Hyde K (eds) Neamtode-Trapping Fungi. Springer, Dordrecht, pp 41–210
Yuan C, Yang HX, Guo YH, Fan L et al. 2019 − New α- pyrones from an endophytic fungus, *Hypoxylon investiens* J2. RSC Advances 9, 27419–23.
Yuan ZL, Lin FC, Zhang CL, Kubicek CP. 2010 – A new species of *Harpophora* (*Magnaporthaceae*) recovered from healthy wild rice (*Oryza granulata*) roots, representing a novel member of a beneficial dark septate endophyte. FEMS Microbiology Letters 307, 94–101.
Yue JZ, Eriksson OE. 1987 – *Sinosphaeria bambusicola* gen. et sp. nov., (*Thyridiaceae* fam. nov.). Systema Ascomycetum 6, 229–236.
Yuen TK, Hyde KD, Hodgkiss IJ. 1998 – Physiological growth parameters and enzyme production in tropical freshwater fungi. Material und Organismen 32, 2–16.
Yukawa M, Maki T. 1931 – *Schizosaccharomyces japonicus* nov. spec. Fukuoka, Japan: La Bul Sci Falkultato Terkultura Kjusu Imp Univ 4, 218–26.
Yun CS, Motoyama T, Osada H. 2017 – Regulatory mechanism of mycotoxin tenuazonic acid production in *Pyricularia oryzae*. ACS Chemical Biology 12(9), 2270–2274.
Yun HY, Rossman AY. 2011 – *Tubakia seoraksanensis*, a new species from Korea. Mycotaxon 115(1), 369–373.
Yuzon J, Roux C, Lendemer JC, Gueidan C. 2014 – Molecular phylogeny and taxonomy of the endolithic lichen genus *Bagliettoa* (*Ascomycota*: *Verrucariaceae*). Taxon 63(6), 1177–1192.
Zachariah SA, Nayaka S, Gupta P, Varghese SK. 2019 – The lichen genus *Pyxine* (*Caliciaceae*) in Kerala state with *P. dactyloschmidtii* as new to India. Hattoria 10, 109–117.
Zahlbruckner A (1898) Beiträge zur Flechtenflora Niederösterreichs V. Verhandlungen der Kaiserlich-Königlichen ZoologischBotanischen Gesellschaft in Wien 48:349–370.
Zahlbruckner A. 1903–1907 – Lichenes (Flechten). In: Engler K., Prantl K. (eds) Die Natürliche Pflanzenfamilien. Teil I, Abt. 1, 49–96 (1903), 97–144 (1905), 145–192 (1906), 193–249 (1907). Leipzig.
Zahlbruckner A. 1905 – ('1907') Lichenes (Flechten). B. Specieller Teil. In Die naturlichen Pflanzenfamilien. I Teil, 1 Apt (Engler, A. & Prantl, K., eds). Leipzig.
Zahlbruckner A. 1907 – Lichenes (Flechten). B. Spezieller Teil. - In: ENGLER, A. & PRANTL, K. Die natürlichen Pflanzenfamilien. 1.Teil, Abteilung 1, 49–249.
Zahlbruckner A. 1921–1922 – Catalogus Lichenum Universalis Band 1. Gebru¨ der Borntraeger, Leipzig.
Zahlbruckner A. 1925 – Catalogus lichenum universalis. Leipzig, Germany: Gebru¨ der Borntra¨ger-Verlag 3, 1–899.
Zahlbruckner A. 1926 – Lichenes. Spezieller Teil, in: Engler-Prantl, Die nat. Pflanzenfam. Ⅱ Aufl. 8, 61–263.
Zahlbruckner A. 1928 – Catalogus Lichenum Universalis, 5. Borntraeger, Leipzig, Germany. 481–754.
Zahlbruckner A. 1930 – Catalogus Lichenum Universalis VI. Borntraeger. Leipzig.
Zahlbruckner A. 1932 – Catalogus lichenum universalis. Leipzig: Gebru¨ der Borntra¨ger-Verlag 8, 1–612.
Zahradníková M, Andersen HL, Tønsberg T, Beck A. 2017a – Molecular evidence of *Apatococcus*, including *A. fuscideae* sp. nov., as photobiont in the genus *Fuscidea*. Protist 168(4): 425–438.
Zahradníková M, Tønsberg T, Andersen HL. 2017b – The taxonomy of the lichen *Fuscidea cyathoides* (*Fuscideaceae*, *Umbilicariomycetidae*, *Ascomycota*) in Europe. Lichenologist 49(6), 547–560.

Zahradníková M. 2017 – [Thesis:] Taxonomy and phylogeny of the family *Fuscideaceae* (*Umbilicariales*, *Ascomycota*) with special emphasis on *Fuscidea*. AIT Bjerch AS, University of Bergen, 196 pp.
Zajc J, Zalar P, Gunde-Cimerman N. 2017 – Yeasts in hypersaline habitats. in: Buzzini P, Lachance M-A, Yurkov A (eds) Yeasts in natural ecosystems: diversity. Springer International Publishing, Cham, 293–329.
Zakaria L. 2024 – An Overview of *Aspergillus* species associated with plant diseases. Pathogens 13, 813.
Zalar P, De Hoog GD, Gunde-Cimerman N. 1999a – Ecology of halotolerant dothideaceous black yeasts. Studies in Mycology 43, 38–48.
Zalar P, De Hoog GS, Gunde-Cimerman N. 1999b – Taxonomy of the endoconidial black yeast genera *Phaeotheca* and *Hyphospora*. Studies in Mycology 43, 49–56.
Zare R, Gams W, Starink-Willemse M, Summerbell RC. 2007 – *Gibellulopsis*, a suitable genus for *Verticillium nigrescens*, and *Musicillium*, a new genus for *V. theobromae*. Nova Hedwigia 85, 463–489.
Zedda L, Rambold G. 2015 – The Diversity of Lichenised Fungi: Ecosystem Functions and Ecosystem Services In: Upreti, Dalip K. ; Divakar, Pradeep K. ; Shukla, Vertika ; Bajpai, Rajesh (Hrsg.): Recent Advances in Lichenology : Modern Methods and Approaches in Lichen Systematics and Culture Techniques. Volume 2. – New Delhi: Springer India, 121–145.
Zeilinger S, Gupta VK, Dahms TE, Silva RN et al. 2016 – Friends or foes? Emerging insights from fungal interactions with plants. FEMS Microbiology Reviews 40(2), 182–207.
Zelski SE, Balto JA, Do C, Raja HA et al. 2014 – Phylogeny and morphology of dematiaceous freshwater microfungi from Perú. IMA Fungus 5, 425–438.
Zelski SE, Raja HA, Miller AN, Shearer CA. 2015 – *Conioscypha peruensis* sp. nov., its phylogenetic placement based on 28S rRNA gene, and a report of *Conioscypha gracilis* comb. nov. from Peru. Mycoscience 56, 319e325.
Zeng M, Gentekaki E, Zeng XY, Tian Q et al. 2022a – Evolutionary relationships and allied species of *Pyronemataceae*, with segregation of the novel family *Pyropyxidaceae*. Mycosphere 13(2), 207–280.
Zeng WN, Jin C, Wang B, Chen LY et al. 2022b – Secondary metabolites from the mangrove-derived fungus *Penicillium* sp. TGM112 and their bioactivities. Chemistry of Natural compounds 58(3), 574–577.
Zeng X, Qian S, Lu Y, Li Y et al. 2022c – A novel nitrogen-containing glyceride from fungal saprobe *Tubeufia rubra* reverses MDR of tumor cell lines to Doxorubicin. Records of Natural Products 16(6), 622–632.
Zeng XY, Jeewon R, Hongsanan S, Hyde KD et al. 2020 – Unravelling evolutionary relationships between epifoliar *Meliolaceae* and angiosperms. Journal of Systematics and Evolution 60, 23–42.
Zeng XY, Jeewon R, Wen TC, Hongsanan S et al. 2018 – Simplified and efficient DNA extraction protocol for *Meliolaceae* specimens. Mycological Progress 17, 403–415.
Zeng XY, Wu HX, Hongsanan S, Jeewon R. 2019 – Taxonomy and the evolutionary history of *Micropeltidaceae*. Fungal Diversity 97, 393–436.
Zeng XY, Zhao JJ, Hongsanan S, Chomnunti P et al. 2017 – A checklist for identifying *Meliolales* species. Mycosphere 8, 218–359.
Zhang C, Aptroot A, Liu H, Jiang S. 2020a –Two new species of *Anisomeridium* (lichenized *Dothideomycetes*, *Ascomycota*) from China. Phytotaxa 458(2), 167–172.
Zhang CJ, Yang ZL, Shen JP, Sun YF et al. 2018a – Impacts of long-term nitrogen addition, watering and mowing on ammonia oxidizers, denitrifiers and plant communities in a temperate steppe. Applied Soil Ecology 130, 241–250.
Zhang D, Tao X, Chen RD, Liu JM et al. 2015a – Pericoanosin A, a polyketide synthase–nonribosomal peptide synthetase hybrid metabolite with new carbon skeleton from the endophytic fungus *Periconia* sp. Organic Letters 17, 4304–4307.

Zhang D, Tao X, Liu JM, Chen RD et al. 2016a – Pericoanosin G, a new cytochalasan with unprecedented 7/6/5 tricyclic ring system from the endophytic fungus *Periconia* sp. Tetrahedron Lett 57, 796–799.
Zhang F, Boonmee S, Monkai J, Yang XY et al. 2022a – *Drechslerella daliensis* and *D.xiaguanensis* (*Orbiliales*, *Orbiliaceae*), two new nematode-trapping fungi from Yunnan, China. Biodiversity Data Journal 10, e96642.
Zhang F, Boonmee S, Yang YQ, Zhou FP et al. 2023a – *Arthrobotrys blastospora* sp. nov.(*Orbiliomycetes*): A living fossil displaying morphological traits of mesozoic carnivorous fungi. Journal of Fungi 9(4), 451.
Zhang F, Yang YQ, Zhou FP, Xiao W et al. 2023b – Morphological and phylogenetic characterization of five novel nematode-trapping fungi (*Orbiliomycetes*) from Yunnan, China. Journal of Fungi 9(7), 735.
Zhang H, Dong W, Hyde KD, Maharachchikumbura SS et al. 2017a – Towards a natural classification of *Annulatascaceae*-like taxa: introducing *Atractosporales* ord. nov. and six new families. Fungal Diversity 85, 75–110.
Zhang H, Zhu R, Qing Y, Yang H et al. 2022b – Polyphasic Identification of *Distoseptispora* with six new species from fresh water. Journal of Fungi 8(10), 1063.
Zhang J, Liang JH, Zhao JC, Wang YL et al. 2018b – Xylarianins A−D from the endophytic fungus *Xylaria* sp. SYPF 8246 as natural inhibitors of human carboxylesterase 2. Bioorganic Chemistry 81, 350–5.
Zhang JF, Liu JK, Hyde KD, Chen YY et al. 2017b – Two new species of *Dyfrolomyces* (*Dyfrolomycetaceae*, *Dothideomycetes*) from karst landforms. Phytotaxa 313(3), 267–277.
Zhang JF, Liu JK, Hyde KD, Chen YY et al. 2023c – *Ascomycetes* from karst landscapes of Guizhou Province, China. Fungal Diversity 122, 1–160.
Zhang JF, Liu JK, Jeewon R, Wanasinghe DN et al. 2019a – Fungi from Asian Karst formations III. Molecular and morphological characterization reveal new taxa in *Phaeosphaeriaceae*. Mycosphere 10(1), 202–220.
Zhang L, Fasoyin OE, Molnár I, Xu Y. 2020b – Secondary metabolites from hypocrealean entomopathogenic fungi: novel bioactive compounds. Natural Product Reports 37(9), 1181–1206.
Zhang M, Koko TW, Hyde KD. 2011a – Towards a monograph of *Dothideomycetes*: Studies on *Diademaceae*. Cryptogamie, Mycologie 32, 115–126.
Zhang M, Li JJ, Wu HY, Geng YH et al. 2014 – First report of *Chaetomella raphigera* causing leaf spot on *Rosa chinensis* in China. Plant Disease 98(4), 569–569.
Zhang N, Blackwell M. 2001 – Molecular phylogeny of dogwood anthracnose fungus (*Discula destructiva*) and the *Diaporthales*. Mycologia 93, 355–365.
Zhang N, Blackwell M. 2002 – Molecular phylogeny of *Melanospora* and similar pyrenomycetous fungi. Mycological Research 106(2), 148–155.
Zhang N, Cai G, Price DC, Crouch JA et al. 2018c – Genome wide analysis of the transition to pathogenic lifestyles in *Magnaporthales* fungi. Scientific Reports 8(1), 5862.
Zhang N, Castelbury LA, Miller AN, Huhndorf SM et al. 2006 – An overview of the systematics of the *Sordariomycetes* based on a four-gene phylogeny. Mycologia 98, 1076–1087.
Zhang N, Luo J, Rossman AY, Aoki T et al. 2016b – Generic names in *Magnaporthales*. IMA Fungus 7, 155–159.
Zhang N, Wang Z. 2015 – 3 *Pezizomycotina*: *Sordariomycetes* and *Leotiomycetes*. Systematics and evolution: Part B, 57–88.
Zhang N. 2002 – Molecular phylogeny of *Melanospora* and *Diaporthales*, and population genetics of dogwood anthracnose fungus. Doctoral dissertations 439. http://digitalcommons.lsu.edu/gradschool_dissertations/439. (Accessed 10 Feb 2024)
Zhang P, Li X, Yuan XL, Du YM et al. 2018d – Antifungal prenylated diphenyl ethers from *Arthrinium arundinis*, an endophytic fungus isolated from the leaves of tobacco (*Nicotiana tabacum* L.). Molecules 23, 3179.

Zhang P, Pang W, Zhang Y, Alonazi MA et al. 2024a – *Cenococcum geophilum* impedes Cadmium toxicity in *Pinus massoniana* by modulating nitrogen metabolism. Science of The Total Environment 946, 174296.
Zhang Q, Nizamani MM, Feng Y, Yang YQ et al. 2023d – Genome-scale and multi-gene phylogenetic analyses of *Colletotrichum* spp. host preference and associated with medicinal plants. Mycosphere 14(2), 1–106.
Zhang SN, Abdel-Wahab MA, Jones EBG, Hyde KD et al. 2019b – Additions to the genus *Savoryella* (*Savoryellaceae*), with the asexual morphs *Savoryella nypae* comb. nov. and *S. sarushimana* sp. nov. Phytotaxa 408(3), 195–207.
Zhang SN, Hyde KD, Jones EG, Cheewangkoon R et al. 2017c – *Novomicrothelia pandanicola* sp. nov., a non-lichenized *Trypetheliaceae* species from Pandanus. Phytotaxa 321(3), 254–264.
Zhang T, Wang NF, Liu HY, Zhang YQ et al. 2016c – Soil pH is a key determinant of soil fungal community composition in the Ny-Ålesund Region, Svalbard (High Arctic). Frontiers in Microbiology 7, 227.
Zhang T, Zhang X, Yang Q, Wei X. 2022c – Hidden species diversity was explored in two genera of catapyrenioid lichens (*Verrucariaceae*, *Ascomycota*) from the deserts of China. Journal of Fungi 8(7), 729.
Zhang W, Draeger S, Schulz B, Krohn K. 2009a –Ring B aromatic steroids from an endophytic fungus, *Colletotrichum* sp. Natural Product Communications 4, 1449–1454.
Zhang W, Fan Y, Deng W et al. 2024b – Characterization of genome-wide phylogenetic conflict uncovers evolutionary modes of carnivorous fungi. mBio. 29: e02133–24
Zhang W, Groenewald JZ, Lombard L, Schumacher RK et al. 2021a – Evaluating species in *Botryosphaeriales*. Persoonia: Molecular Phylogeny and Evolution of Fungi 46, 63–115.
Zhang WW, Lai YL, Cheng XL et al. 2015b – Genomic analysis of *Hypocreales* reveals the evolutionary process of host jumping and range. The 12th Cross Strait Mycology Academic Symposium Handbook, Poster Paper Abstract Collection. 2. did not match any articles
Zhang X, Zhang J, He J, Li M et al. 2024c – Physiological and transcriptome responses of *Pinus massoniana* seedlings inoculated by various ecotypes of the ectomycorrhizal fungus *Cenococcum geophilum* during the early stage of drought stress. Journal of Fungi 10(1), 71.
Zhang XY, Bao J, Wang GH, He F. 2012a – Diversity and antimicrobial activity of cultural fungi isolated from six species of the South China Sea Gorgonians. Microbial Ecology 64, 617–627.
Zhang Y, Crous PW, Schoch CL, Bahkali AH et al. 2011b – A molecular, morphological and ecological re-appraisal of *Venturiales* – a new order of *Dothideomycetes*. Fungal Diversity 51, 249–277.
Zhang Y, Crous PW, Schoch CL, Hyde KD. 2012b – *Pleosporales*. Fungal Diversity 53, 1–221.
Zhang Y, Fournier J, Crous PW, Pointing SB et al. 2009b – Phylogenetic and morphological assessment of two new species of *Amniculicola* and their allies (*Pleosporales*). Persoonia 23, 48–54.
Zhang Y, Schoch CL, Fournier J, Crous PW et al. 2009c – Multi-locus phylogeny of *Pleosporales*: a taxonomic, ecological and evolutionary re-evaluation. Studies in Mycology 64, 85–102.
Zhang Y, Zhang Y, Liu M, Shi X et al. 2008 – Dark septate endophyte (DSE) fungi isolated from metal polluted soils: their taxonomic position, tolerance, and accumulation of heavy metals *in vitro*. The Journal of Microbiology 46, 624–632.
Zhang YX, Chen JW, Manawasinghe IS, Lin YH et al. 2023e – Identification and characterization of *Colletotrichum* species associated with ornamental plants in Southern China. Mycosphere 14(2), 262–302.
Zhang YY, Wang XY, Liu D, Shi et al. 2018e – New species and new records of *Ophioparmaceae* (lichenized *Ascomycota*) from China. The Lichenologist 50(1), 89–99.
Zhang ZF, Liu F, Zhou X, Liu XZ et al. 2017d – Culturable mycobiota from Karst caves in China, with descriptions of 20 new species. Persoonia 39(1), 1–31.

Zhang ZY, Dong CB, Chen WH, Mou QR et al. 2020c – The Enigmatic *Thelebolaceae* (*Thelebolales*, *Leotiomycetes*): One New Genus *Solomyces* and Five New Species. Frontiers in Microbiology 11, 572596.
Zhang ZY, Han YF, Chen WH, Liang ZQ. 2019c – Phylogeny and taxonomy of three new *Ctenomyces* (*Arthrodermataceae*, *Onygenales*) species from China. MycoKeys 47, 1–16.
Zhang ZY, Han YF, Chen WH, Tao G. 2023f – Additions to *Thelebolales* (*Leotiomycetes*, *Ascomycota*): *Pseudogeomyces lindneri* gen. et sp. nov. and *Pseudogymnoascus campensis* sp. nov. MycoKeys 95, 47–60.
Zhang ZY, Pan H, Tao G, Li X et al. 2024d – Culturable mycobiota from Guizhou wildlife park in China. Mycosphere 15(1), 654–763.
Zhang ZY, Ren YL, Li X, Chen WH et al. 2022d – New taxonomic framework for *Arthrodermataceae*: a comprehensive analysis based on their phylogenetic reconstruction, divergence time estimation, phylogenetic split network, and phylogeography. Antonie van Leeuwenhoek 115(11), 1319–1333.
Zhang ZY, Shao QY, Li X, Chen WH et al. 2021b – Culturable fungi from urban soils in China I: Description of 10 new taxa. Microbiology Spectrum 9(2), e00867–e21.
Zhang ZY, Zhou SY, Eurwilaichitr L, Ingsriswang S et al. 2021c – Culturable mycobiota from Karst caves in China II, with descriptions of 33 new species. Fungal Diversity 106(1), 29–136.
Zhao G, Yu P, Liu X. 2012 – *Cancellidium* and *Canalisporium* (hyphomycetes) from China. Nova Hedwigia 96, 221–236.
Zhao GZ, Liu XZ, Wu WP. 2007 – Helicosporous *Hyphomycetes* from China. Fungal Diversity 26, 313–524.
Zhao GZ, Wu WP, Liu B, Liu X. 2006 – Two new species of *Xenosporium* (*Hyphomycetes*) lacking secondary conidia. Nova Hedwigia 82, 127–134.
Zhao JY, Fan XY, Zou XF, Yang PW et al. 2022a – Study on chemical composition and antioxidant activity of solid fermented product of soil fungus *Aspergillus fumigatus*. Natural Product Research and Development 34(1), 70–75.
Zhao R, Chen KY, Mao LJ, Zhang CL. 2024 – Eleven new species of *Trichoderma* (*Hypocreaceae*, *Hypocreales*) from China. Mycology, 1–30.
Zhao X, Fan Y, Xiang M, Chen Y et al. 2022b – DdaCrz1, a C2H2-Type transcription factor, regulates growth, conidiation, and stress resistance in the nematode-trapping fungus *Drechslerella dactyloides*. Journal of Fungi 8, 750.
Zhao X, Leavitt SD, Zhao ZT, Zhang LL et al. 2016 – Towards a revised generic classification of lecanoroid lichens (*Lecanoraceae*, *Ascomycota*) based on molecular, morphological and chemical evidence. Fungal Diversity 78, 293–304.
Zhao XX, Zhao ZT, Miao CC, Ren ZJ et al. 2017 – Five *Lecidea* lichens new to China, Mycotaxon 132(2), 317–326.
Zheng H, Qiao M, Guo J, Castañeda-Ruiz et al. 2022 – *Keqinzhangia aquatica* gen. et sp. nov. and *Pseudocoronospora hainanense* gen. et sp. nov., isolated from freshwater in southern China. Antonie van Leeuwenhoek 115, 203–213.
Zheng H, Wan Y, Li J, Castañeda-Ruiz RF et al. 2020 – *Phialolunulospora vermispora* (*Chaetosphaeriaceae*, *Sordariomycetes*), a novel asexual genus and species from freshwater in southern China. Mycokeys 76, 17–30.
Zhong LF, Ling J, Luo LX, Yang CN et al. 2023 – *Lecanicilliums* A-F, thiodiketopiperazine-class lkaloids from a mangrove sediment-derived fungus *Lecanicillium kalimantanense*. Marine Drugs 1(11), 575.
Zhou J, Li X, Huang PW, Dai CC. 2018 – Endophytism or saprophytism: decoding the lifestyle transition of the generalist fungus *Phomopsis liquidambari*. Microbiological Research 206, 99–112.
Zhou N, Zhang Y, Liu F, Cai L. 2016 – Halophilic and thermotolerant *Gymnoascus* species from several special environments, China. Mycologia 108(1), 179–191.

Zhou QM, Wei JC. 2007 – A new order *Umbilicariales* J. C. Wei & Q. M. Zhou (*Ascomycota*). Mycosystema 26, 40–45.
Zhu HY, Tian CM, Fan XL. 2018 – Studies of botryosphaerialean fungi associated with canker and dieback of tree hosts in Dongling Mountain of China. Phytotaxa 348, 63–76.
Zhu L, Song J, Zhou JL, Si J et al. 2019 – Species diversity, phylogeny, divergence time, and biogeography of the genus *Sanghuangporus* (*Basidiomycota*). Frontiers in Microbiology 10, 812.
Zhuang WY, Wang Z. 1998 – Discomycetes of tropical China. I. Collections from Hainan Island. Mycotaxon 67, 21–31.
Zhuang WY, Zeng ZQ. 2017 – *Cocoonihabitus sinensis* gen. et sp. nov. on remaining leaf veins of cocoons in a new family (*Cocoonihabitaceae* fam. nov.) of *Hypocreales*. Mycosystema 12, 1591–1598
Zhuang WY. 2020 – *Hypocreales*. Chinese Fungi. Beijing.
Zhurbenko MP, Etayo J. 2013 – *Biazrovia*, a new genus of lichenicolous *Ascomycetes* from Asia. Mycobio 1, 51–56.
Zhurbenko MP, Ohmura Y. 2020 – Contributions to the knowledge of lichenicolous fungi growing on baeomycetoid lichens and *Icmadophila,* with a key to the species. The Lichenologist 52(6), 437–453.
Zhurbenko MP, Yakovchenko LS. 2014 – A new species, *Sagediopsis vasilyevae*, and other lichenicolous fungi from Zabaikal'skii Territory of Russia, southern Siberia. Folia Cryptogamica Estonica 51, 121–130
Zin NA, Badaluddin NA. 2020 – Biological functions of *Trichoderma* spp. for agriculture applications. Annals of Agricultural Sciences 65(2), 168–178.
Zipfel RD, De Beer ZW, Jacobs K, Wingfield BD et al. 2006 – Multi-gene phylogenies define *Ceratocystiopsis* and *Grosmannia* distinct from *Ophiostoma*. Studies in Mycology 55, 75–97.
Zogg H. 1962 – Die *Hysteriaceae* s. Str. Und *Lophiaceae*, unter besonderer Berücksichtigung der mitteleuropäischen Formen. Beiträge zur Kryptogamenflora der Schweiz, Band 11, 1–190.
Zou JM. 2021 – Secondary metabolites and their bioactivities of three rhizospheric fungi from *Panax notoginseng*. Kunming: Master's Thesis of Yunnan University.
Zou WX, Meng JC, Lu H, Chen GX et al. 2000 –Metabolites of *Colletotrichum gloeosporioides*, an endophytic fungus in *Artemisia mongolica*. Journal of Natural Products 63, 1529–1530.
Zschacke H. 1913 – Die mitteleuropa¨ischen Verrucariaceen. I. Hedwigia 54, 183–198.
Zschacke H. 1914 – Die mitteleuropa¨ischen Verrucariaceen. II. Hedwigia 55, 286–324.
Zschacke H. 1918 – Die mitteleuropa¨ischen Verrucariaceen. Nachtra¨ge zu I und II. Hedwigia 60, 1–9.
Zschacke H. 1921 – Die mitteleuropa¨ischen Verrucariaceen III. Hedwigia 62, 90–154.
Zschacke H. 1924 – Die mitteleuropa¨ischen Verrucariaceen IV. Hedwigia 65, 46–64.
Zschacke H. 1927 – Die mitteleuropa¨ischen Verrucariaceen V. Hedwigia 67, 45–85.
Zschacke H. 1933–1934 – *Epigloeaceae*, *Verrucariaceae* und *Dermatocarpaceae*. In: Zahlbruckner A (ed), Dr L. Rabenhorst's Kryptogamen-Flora von Deutschland, O¨ sterreich und der Schweiz. Akademische Verlagsanstalt, Leipzig 44–695.
Zubaer A, Wai A, Patel N, Perillo J et al. 2021 – The mitogenomes of *Ophiostoma minus* and *Ophiostoma piliferum* and comparisons with other members of the *Ophiostomatales*. Frontiers in Microbiology 12, 618649.
Zucconi L, Gagliardi M, Isola D, Onofri S et al. 2012 – Biodeterioration agents dwelling in or on the wall paintings of the Holy Saviour's cave (Vallerano, Italy). International Biodeterioration & Biodegradation 70, 40– 46.
Zukal H. 1891 – Halbflechten. Flora 49, 92–107.
Zukal H. 1893 – "Mykologische Mitteilungen". Österreichische Botanische Zeitschrift (in German). 43 (7), 241–247.