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ARTICLE

Towards an integrative morpho-molecular classification of the *Lulworthiomycetidae*

Dayarathne MC[1], Jones EBG[2]*, Rämä T[3], Hagestad OC[4], Abdel-Wahab MA[5], Bahkali AH[2], Prematunga C[1], Azevedo E[6], Hyde KD[1], Caeiro MF[7], Barata M[8], Sarma VV[9], Devadatha B[10], Guo SY[11], Sakayaroj J[12] and Pang KL[11]*

[1] Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand.
[2] Botany and Microbiology Department, Faculty of Science, King Saud University, P.O Box 2455, Riyadh 11451, Saudi Arabia
[3] Norwegian College of Fishery Science, UiT, The Arctic University of Norway, Tromsø, Norway
[4] Marbank, Institute of Marine Research, Tromsø, Norway
[5] Department of Botany and Microbiology, Faculty of Science, Sohag University, Sohag 82524, Egypt
[6] CE3C – Centro de Ecologia, Evolução e Alterações climáticas, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal and CESAM Lisboa – Centro de Estudos do Ambiente e do Mar, Universidade de Aveiro, Aveiro, Portugal
[7] CESAM Lisboa – Centro de Estudos do Ambiente e do Mar, Universidade de Aveiro, Aveiro, Portugal and Departamento de Biologia Vegetal, Faculdade de Ciências, Universidade de Lisboa, Portugal
[8] CE3C – Centro de Ecologia, Evolução e Alterações climáticas, Departamento de Biologia Vegetal, Faculdade de Ciências, Universidade de Lisboa, Portugal
[9] Fungal Biotechnology Laboratory, Department of Biotechnology, School of Life Sciences, Pondicherry University, R.V. Nagar, Kalapet, Pondicherry-605014, India
[10] Microbial Type Culture Collection and Gene Bank (MTCC), CSIR-Institute of Microbial Technology, Chandigarh, 160036, India
[11] Institute of Marine Biology and Center of Excellence for the Oceans, National Taiwan Ocean University, 2 Pei-Ning Road, Keelung 202301
[12] Department of Biology School of Science, Walailak University, 222 Thaiburi, Thasala district, Nakhonsithammarat 80161, Thailand

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Abstract

This study re-evaluates the classification of the *Lulworthiomycetidae* based on phylogenetic analyses of 18S, 28S and ITS (internal transcribed spacers and 5.8S) regions of rDNA and protein coding genes (TEF1α, RPB1, RPB2, TUB2, MCM7) along with comprehensive morphological comparisons. Based on the current phylogenetic data we consider the genus *Spathulospora* as a member of the *Lulworthiales*, *Lulworthiomycetidae*, and redundancy of the taxon *Spathulosporales*. This study confirms *Lulworthia* as polyphyletic with the characteristic filiform, long ascospores with an end chamber, which is found in many genera: *Halazoon*, *Halophilomyces, Lulwoana*, *Lulwoidea*, *Matsusporium*, *Paralulworthia*, *Paramoleospora*, *Rostrupiella*, and *Sammeyersia*. These genera can be distinguished by morphology, their asexual morphs and molecular phylogeny. The *Lulworthiomycetidae* includes 23 genera and 69 species. One new genus (*Lindriella*) and eight new species (*Hydea mangrovei*, *Lulworthia norwegica*, *Matsusporium japonica*, *Moromyces*

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***Corresponding Author:** E. B. Gareth Jones – e-mail – torperadgj@gmail.com, K. L. Pang Jones – e-mail – klpang@ntou.edu.tw
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mangrovis, *Paralulworthia lignicola*, *Rostrupiella longispora*, *Sammeyersia yanbuensis*, *S. thailandica*) are introduced, with four new combinations.

Key words – 9 new taxa – ecology – marine Ascomycota – life below water – taxonomy.

INTRODUCTION

Currently, 2,118 marine fungi are reported worldwide, from a wide range of substrates (seagrasses, seaweeds, invertebrates, driftwood, sediments, sea foam) and ecosystems, and particularly speciose in mangroves, salt marsh, deep-sea and salterns (Jones et al. 2019, marinefungi.org, accessed August 2024). All the major taxonomic groups are represented in marine habitats, with the Ascomycota being the dominant class (Jones et al. 2019, Calabon et al. 2021, 2023, Devadatha et al. 2021, Poli et al. 2022). Most are saprobes, while a smaller number are known to be mutualistic symbionts, parasitic or pathogenic on mangrove plants and very few are animal pathogens (Hyde & Lee 1998, Raghukumar 2017, Pang et al. 2021). Many taxonomic groups are known only from marine habitats, including the families *Etheirophoraceae*, *Halojulellaceae*, *Halotthiaceae*, *Juncigenaceae*, *Manglicolaceae* and *Torpedosporaceae*, the order *Koralionastetales*, and including the subclasses *Lulworthiomycetidae*, the subject of this review. The only account of the *Lulworthiales* has been conducted by Johnson and Sparrow (1961) and Kohlmeyer and Kohlmeyer (1979), both before the advent of molecular phylogeny. Abdel-Wahab et al. (2010) studied taxonomy of selected asexual morphs and introduced *Halazoon*, *Hydea*, *Matsusporium*, *Moleospora* and *Moromyces*, some previously assigned to the *Halosphaeriaceae*. Some of these asexual morphs have now been linked to their sexual morphs which includes *Halazoon purpurea*, *Matsusporium japonica* as highlighted in this monograph.

Morphological characteristics still play a crucial role in identifying and determining relationships among fungal species even though using molecular data is the current trend in fungal classification. Furthermore, the nomenclatural type specimens constitute an integral part of fungal classification and nomenclature (Dayarathne 2016). Some of the described species of genera in *Lulworthiaceae* and *Koralionastetaceae* lack molecular data or are taxonomically problematic. In this modern era, it is possible to prepare advanced morphological accounts for earlier observed, poorly illustrated materials due to greatly improved microscopes, which allows more reliable phenotypic characterizations. Therefore, this monograph provides a complete morpho-molecular account for taxa of *Lulworthiaceae* and *Koralionastetaceae*, introduces several novel taxa and confirms the placements of those fungal families within the natural classification system.

History

Lulworthiomycetidae (Index Fungorum number: IF551131)

Maharachchikumbura et al. (2015) introduced this subclass for a lineage of marine fungi that is unrelated to *Halosphaeriaceae* (*Microascales*, *Hypocreomycetidae*), which includes the orders *Lulworthiales* (*Lulworthiaceae*) and *Koralionastetales* (*Koralionastetaceae*). The divergence time for *Lulworthiomycetidae* has been estimated as 257 MYA (Hyde et al. 2020) and 310 MYA (Dayarathne et al. 2019).

Lulworthiales **(Index Fungorum number**: **IF90552)**

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 the *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 with the latter subsequently referred to a new order *Koralionastetales* (Campbell et al. 2009). The order *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).

***Koralionastetales* (Index Fungorum number: IF512605)**

Campbell et al. (2009) erected the order *Koralionastetales* based on a phylogenetic study of 18S and 28S rDNA sequences and the unique morphological features of the genera *Koralionastes* and *Pontogeneia* in the family *Koralionastetaceae* (Kohlmeyer & Volkmann-Kohlmeyer 1987a). This was based on sequence data from only two species: *Koralionastes ellipticus* (DNA obtained from herbarium material) and *Pontogeneia microdictyi* (fresh material collected in Bahamas: Sweetings Cay, on thalli of *Microdictyon* sp.) (Campbell et al. 2009). Furthermore, ascospores of *Koralionastes* and *Pontogeneia* are thick-walled and differ significantly from the long filiform ascospores with terminal end chambers containing mucilage found in the order *Lulworthiales*.

***Lulworthiaceae* (Index Fungorum number: IF82091)**

The family *Lulworthiaceae* comprises mostly saprobes occurring on wood or growing on sea grasses and salt marsh plants (Kohlmeyer et al. 2000, Jones et al. 2015, Azevedo et al. 2017, Gonçalves et al. 2021, Poli et al. 2021). Extending from the single gene analysis to multi-gene phylogeny of *Lulworthiaceae*, several attempts were reported in resolving the phylogenetic relationships of the family by examining selected genera and related taxa (Spatafora et al. 1998, Anderson et al. 2001, Sakayaroj et al. 2005, 2011, Abdel-Wahab et al. 2010, Maharachchikumbura et al. 2015, 2016, Hyde et al. 2020). Kohlmeyer et al. (2000) inaugurated the family *Lulworthiaceae* in *Lulworthiales* to accommodate halosphaerialean species with filiform ascospores (Campbell 2005). The type genus *Lulworthia* was described by Sutherland (1916) to introduce the species *Lulworthia fucicola*, a taxon occurring on the seaweed, commonly known as the bladder wrack, at Lulworth Cove on the coast of Dorset, UK. Nevertheless, initially only the genera *Lulworthia* and *Lindra* were established in the family *Halosphaeriaceae* (*Halosphaeriales*) (Muller & von Arx 1962). Additional genera currently positioned in *Lulworthiaceae* based on morphology and/or phylogeny are *Orbimyces* (Barghoorn & Linder 1944), *Zalerion* (Moore & Meyers 1962), *Cumulospora* (Schmidt 1985), *Kohlmeyeriella* (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), *Paramoleospora* (Li et al. 2023), *Rambellisea* (Braconcin et al. 2024) and *Halophilomyces* (Chen et al. 2024). There were over 1,400 sequences (rDNA and protein coding genes) in the GenBank for taxa of *Lulworthiaceae* (data retrieved on 14 March 2023). However, further phylogenetic analyses with more taxon sampling and phylogenetic trees with several markers were urgent for resolving the polyphyly of the key genera *Lindra* and *Lulworthia* (Azevedo et al. 2017) and to establish the phylogenetic placements of genera with uncertain taxonomic positions such as *Spathulospora* and *Orbimyces*.

***Koralionastetaceae* (Index Fungorum number: IF82025)**

Koralionastetaceae was introduced by Kohlmeyer and Volkmann-Kohlmeyer (1987a) to accommodate *Koralionastes.* Kohlmeyer (1975) investigated five perithecial ascomycetes parasitizing marine Phaeophyta and introduced *Pontogeneia* as the second genus of this family. Ordinal and higher classification of *Koralionastetaceae* was initially unresolved and *Koralionastes* was placed under Ascomycota *genera incertae sedis* by Eriksson (2006). Phylogenetic analyses by Campbell et al. (2009) with 18S and 28S rDNA sequence data placed *Koralionastes* and *Pontogeneia* in a new order *Koralionastetales* which is sister to *Lulworthiales*. *Koralionastetaceae* members are coral and algal inhabiting fungi and play a major role in heterotrophic conversion of reef biomass to nutrients (Raghukumar & Ravindran 2012). There are 13 species (five species of

Koralionastes and eight species of *Pontogeneia*) in the *Koralionastetaceae* (Wijayawardene et al. 2017, 2022, Hyde et al. 2020).

Molecular phylogenetic studies

The strictly marine fungi in the *Sordariomycetes* families *Lulworthiaceae* and *Koralionastetaceae* have been studied using molecular phylogenetics since Spatafora et al. (1998). The number of reference sequences for several species and several genetic loci has been increasing.

Lulworthiaceae

First hints of the existence of the family *Lulworthiaceae* were obtained through a phylogenetic study on marine fungi that showed the order *Halosphaeriales* having terrestrial origins (Spatafora et al. 1998). In the study, it was noticed that *Halosphaeriales* was split into two lineages and one of them comprised *Lulworthia* and *Lindra* species. Later, the family *Lulworthiaceae* was established based on phylogenetic analyses of the partial 18S and 28S sequences of four *Lulworthia sensu stricto* and three *Lindra* isolates (Kohlmeyer et al. 2000). Despite the limited taxon sampling in those early days of molecular phylogenetics, there was no doubt that a new family was discovered and in the later studies it was confirmed that the family contained fungi that were restricted in their occurrence to marine habitats. In publications that followed, several isolates of *Lulworthiaceae* and adjacent marine taxa, such as fungi in the genera *Kohlmeyeriella*, *Haloguignardia* and *Spathulospora*, were included, still relying on 18S and 28S sequences (Harvey 2004, Inderbitzin et al. 2004, Campbell et al. 2005). *Spathulospora* was inferred to be a secondary invader of the sea and derived from *Lulworthiales* taxa, and with that, the theory of *Spathulospora* fungi representing the evolutionary origins of the whole kingdom Ascomycota was abandoned (Kohlmeyer & Kohlmeyer 1979, Inderbitzin et al. 2004). It was also shown that *Kohlmeyeriella* and *Haloguignardia* belong to *Lulworthiaceae* (Campbell et al. 2005). At the same time a broader picture of the systematics of fungi was established using not only 18S and 28S rRNA gene sequences, but also the internal transcribed spacer regions of rDNA and protein coding genes, sampled also from a few *Lulworthiaceae* species (James et al. 2006, Schoch et al. 2009).

In recent years, there has been higher level molecular analyses undertaken based on a narrow selection of taxa and rDNA genes that have contributed to the designation of the subclass *Lulworthiomycetidae* and knowledge on *Lulworthiales* hosting species that are the most basal "marine-based taxa" in *Sordariomycetes* (Maharachchikumbura et al. 2015, Dayarathne et al. 2019). There have been a few papers with descriptions of new *Lulworthiaceae* taxa based on multilocus data, but these have not used all available sequence data to revise the molecular systematics within the family (Azevedo et al. 2017, Poli et al. 2021). Consequently, we are lacking an overview of the systematics of *Lulworthiaceae* based on multi-locus data with the representation of both rDNA and protein coding genes.

Koralionastetaceae

For *Koralionastetaceae* there are only seven rRNA gene sequences available in the GenBank and no genome sequences in Mycocosm, to the present day (Grigoriev et al. 2014, Sayers et al. 2019). For this reason, few phylogenetic studies were conducted with species in this family, which contains the genera *Pontogeneia* and *Koralionastes.* The family was shown to be a sister group to *Lulworthiaceae* within the order *Lulworthiales* by Campbell et al. (2009). Since this publication, no new sequence data has been established for the family. The type species of the family *Koralionastes ovalis* remains unsequenced and consequently the systematic placement and circumscription of *Koralionastetaceae* are unverified.

Ecology and mode of life of *Lulworthiaceae* and *Koralionastetaceae*

Generally, *Lulworthiaceae* taxa are endophytes, pathogens and/or saprobes, although sometimes they occur as parasites or secondary invaders of injured plant tissues or those infected by other organisms. *Lulworthia* sp. was recorded on *Spartina maritima* plants from three salt

marshes of the rivers Tejo Sado and Mira (Barata 2002, 2006) and Castro Marim and Ria Aveiro (Calado et al. 2015, 2019), fruit bodies occurred more frequently in flooded plant portions (basal portions) associated with stems and/or leaf sheaths of a salt marsh plant *Spartina,* sediments in marine mangroves (Li et al. 2023). *Lindra thalassiae* was reported to degrade turtle grass, an ecologically important marine flowering plant (Orpurt et al. 1964). *Haloguignardia* sp. and *Lulworthia kniepii* were reported as parasites on red and brown algae (Kohlmeyer 1974, Alongi et al. 1999). Gall formation in species of *Cystoseira* and *Sargassum* was generally caused by *Haloguignardia* spp. (Apt 1988, Alongi et al. 1999). To date, five *Haloguignardia* species are recorded *viz*., *H. oceanica*, *H. decidua* and *H. tumejacierzs* parasitic on *Sargassum* spp.; *H. irritans* parasitic on species of *Halidrys* and *Cystoseira*; *H. cystoseirae* described as a parasite on *Cystoseira balearica* [=*Cystoseira brachycarpa*] by Kohlmeyer and Demoulin (1981) from Corsica (France). During a study of the morphological phenology of a population of *Cystoseira elegans* from Capo Passero (southeast Sicily, Italy), numerous galls were found on thalli of *Cystoseira*. They were induced by a fungus identified as *H. cystoseirae* based on papers by Kohlmeyer and Demoulin (1981) and Kohlmeyer and Volkmann-Kohlmeyer (1991). The occurrence of *Lulwoana* was also reported in extreme environments such as saline soils (Hujslová et al. 2010). As well it was believed that *Lulwoana* sp. in *Posidonia oceanica* roots helped the host to capture mineral nutrients, through lytic activity by living as an endophyte (Torta et al. 2015). Nambiar and Raveendran (2015) reported that *Matsusporium tropicalis* was commonly found on four substrates including calcareous animal shells, "chicken bone", endoskeleton of *Seibia* and feathers. *Paralulworthia* species have been reported as endophytes of the seagrass *Posidonia oceanica*, from seawater contaminated by oil spills and submerged wood (Poli et al. 2021), while *Halophilomyces hongkongensis* is endophytic in roots of *Halophila ovalis* (Chen et al. 2024). Most members of the *Lulworthiaceae* have been recovered from submerged wood or driftwood. Recently, species of *Paramoleospora* from marine mangrove sediments (Li et al. 2023) and *Rambellisea* were isolated from the marine tunicate *Halocynthia papillosa* (Braconcini et al. 2024).

Koralionastetaceae comprises coral and algal inhabiting taxa which are integral members of heterotrophic conversion of reef biomass to nutrients (Raghukumar & Ravindran 2012). *Koralionastes* has been reported to have a unique association with crustaceous sponges and corals, developing their ascomata on or within these hosts (Kohlmeyer & Volkmann-Kohlmeyer 1990, Wang 2006). *Koralionastes* is the only marine fungal group which has been identified in marine sponges (Wang et al. 2008). *Pontogeneia* has been recorded as parasites of marine Chlorophyta and Phaeophyta (Walker 2012).

General morphology of *Lulworthiaceae* and *Koralionastetaceae*

The sexual morphs of *Lulworthiaceae* generally comprise long necked ascomata and hyaline, filiform long ascospores, generally with apical chambers filled with mucilage (Jones 1994). *Paralulworthia* differs with the presence of 1–3 septate ascospores that are hyaline to brown (Poli et al. 2020). The algicolous genera *Haloguignardia, Pontogeneia* and *Spathulospora* also lack the filiform ascospores found in *Lulworthia. Haloguignardia* has elongated ellipsoidal to fusiform ascospores that are tapering at their apices (Alongi et al. 1999), while *Spathulospora* species have hairy ascomata and subglobose ascospores with appendages (Inderbitzin et al. 2004). *Koralionastes* spores are hyaline, thick-walled, ellipsoidal to fusiform, unevenly multi-septate, that germinate into hyphae bearing phialidic antheridia with enteroblastic spermatia, considered primitive of *Koralionastetaceae*.

Ascomata

Ascomatal shape, color, nature of ascomatal neck and ascomatal position on the substrate are important characters in delineating *Lulworthiaceae* at the familial level (Kohlmeyer et al. 2000, Campbell et al. 2005, Azevedo et al. 2017). Ascomata of *Lulworthiaceae* can be superficial or deeply immersed, immersed or partly immersed in wood usually with a long neck that are vertically or horizontally laying on the substrates (Kohlmeyer et al. 2000, Campbell et al. 2005, Azevedo

et al. 2017). They are globose to subglobose, cylindrical or ellipsoid in shape and ostiolate with a papilla or a cylindrical, straight, or irregular long neck (Kohlmeyer et al. 2000, Campbell et al. 2005). Sutherland (1916) described ascomata of *L. fucicola* as carbonaceous with almost hyaline bases and without any trace of a neck-like ostiole. Considering the ascomatal pigmentation they can be dark brown, black or purple (*Halazoon purpurea=Lulworthia purpurea*) (Alongi et al. 1999, Kohlmeyer et al. 2000, Jones et al. 2015). However, *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 2003) and these structures are clearly absent in other *Lulworthiaceae* and *Koralionastetaceae* species (Kohlmeyer 1973, Kohlmeyer & Volkmann-Kohlmeyer 1987a).

Asci

Asci of *Lulworthiaceae* members are 8-spored, often clavate to fusiform, unitunicate, thin-walled, usually without apical apparatus or deliquescing early (Sutherland 1916, Kohlmeyer 1973, Campbell et al. 2005, Azevedo et al. 2017). Further, they can be with or without a short stalk (Kohlmeyer & Volkmann-Kohlmeyer 1989). Asci of *Rostrupiella* species are cylindrical with tips rounded which become pointed (Koch et al. 2007), while asci of *Spathulospora* are arranged in a hymenium but without paraphyses (Inderbitzin et al. 2004). *Koralionastes* species have clavate to ellipsoidal or fusiform, pedicellate, deliquescent asci.

Ascospores

Ascospore dimensions and presence/absence of regular septa vary greatly within the order and ascospores range from ellipsoid, fusiform to filiform with or without septa. *Lulworthia* species have ascospores with mucus (*L. fucicola*) releasing a drop of mucilage when in water (Jones et al. 2009, Abdel-Wahab et al. 2010). *Paralulworthia gigaspora* and *P. posidoniae* differ from all members of the family in possessing dark brown ascospores that are 1-3-septate at maturity, constricted at septa (particularly the central one), ellipsoid to fusiform, pointed at both ends, thin-walled, and light to dark brown at maturity (Poli et al. 2020), but these details are questioned in this monograph.

Conidial morphology

Asexual genera *Cumulospora*, *Halazoon*, *Hydea*, *Matsusporium*, *Moleospora*, *Moromyces, Paramoleospora,* and *Zalerion* are hyphomycetes which comprise 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 (Poli et al. 2020, 2021, Chen et al. 2024).

MATERIALS AND METHODS

Specimens, morphological observation and redrawing

Nomenclatural type specimens, or appropriate authenticated specimens, were loaned from accessible herbaria: BIOTEC Bangkok Herbarium (BBH), New York State Museum (NY), Mae Fah Luang University Herbarium (MFLU), Royal Botanic Gardens, Kew (K), Queensland Department of Agriculture and Fisheries (BRIP), Plant Protection Research Institute (PREM), National Museum in Prague (PR), Swedish Museum of Natural History (S), and U.S. National Fungus Collections (BPI). The herbarium material was rehydrated with water or 5% KOH which was added on top of the fungal structures until fully absorbed. Micro-morphological characters were examined from rehydrated ascomata with a Motic SMZ 168 stereomicroscope. Morphologies of ascomata, asci, ascospores and other special tissues (when necessary) were photographed with a Canon 550D digital camera fitted to the Nikon ECLIPSE 80i compound microscope or Moticam S12 camera mounted on Olympus SZX16 and BX43 microscopes. Illustrations were assembled

with Adobe Photoshop v. CS6 extended version and measurements were taken using Tarosoft v. 0.9.0.7 or Fiji/ImageJ (Schindelin et al. 2012). Frequently type specimens were in poor condition or were lost or could not be located, hence, only ascomatal morphology could be observed. Therefore, morphological information for these taxa was obtained depending on the protologue and hand drawings were made for some of the taxa. Taxonomic descriptions were registered in Index Fungorum numbers (Index Fungorum 2025).

Micromorphology characters of *Lulworthia fucicola* GJ 589_FCUL as widefield images were acquired at the Faculty of Sciences of the University of Lisbon's Microscopy Facility on a Leica DMI4000 microscope coupled to a Leica DFC365 12-bit camera, using a 63x/1.4NA objective with DIC optics. Basic image histogram manipulations and cropping were done using Fiji/ImageJ (Schindelin et al. 2012).

Molecular study

For the sequences created in this study, genomic DNA was isolated using a modified CTAB protocol (Murray & Thompson 1980, Rämä et al. 2014) or as described in Azevedo et al. (2017). In some cases, mycelia were used as templates directly in PCR as described in Hagestad et al. (2020). For *Lulworthia fucicola* GJ 589_FCUL, PCR took place in a reaction volume of 25 µl and consisted of 12.5 µl of DreamTaq Green PCR Master Mix (2X) (Thermo Scientific) or My Taq Red Mix (2X) (Bioline), 0.5 µl of 10 µM forward and reverse primer (Table 1), 10.5 µl of water and 1 µl of the extracted DNA template. The cyclic PCR program consisted of an initial 5 min denaturation at 95°C, followed by 40 cycles of 30s (15s) at 95°C, 30s (15s) at primer specific annealing temperature (Table 1) and 1 min (30s) at 72°C (synthesis), and termination with a 10 min elongation step at 72°C (time in parentheses indicated PCR reactions with My Taq Red Mix). Details on PCR product visualization, purification and sequencing were described in Azevedo et al. (2017), Rämä et al. (2014) and Hagestad et al. (2020).

Table 1 Details of primers used in the phylogenetic study and their annealing temperature.

Gene locus	Primer name	Primer sequence	Annealing temperature (°C)	Reference
ITS	ITS5	GGAAGTAAAAGTCGTAACAAGG	47	White et al. (1990)
	ITS4	TCCTCCGCTTATTGATATGC		
28S	LR0R	ACCCGCTGAACTTAAGC	47	Vilgalys & Hester (1990), Rehner & Samuels (1994)
	LR5	TCCTGAGGGAAACTTCG		
18S	NS1	GTAGTCATATGCTTGTCTC	42	White et al. (1990), Gargas & Taylor (1992)
	NS4	CTTCCGTCAATTCCTTTAAG		
	NS24	AAACCTTGTTACGACTTTTA		
TEF1-α	EF1-983F	GCYCCYGGHCAYCGTGAYTTYAT	47	Rehner & Buckley (2005), Stielow et al. (2015)
	EF1-2218R	ATGACACCRACRGCRACRGTYTG		
	EF1-1620R	GACGTTGAADCCRACRTTGTC		
RPB1	RPB1-Af	GARTGYCCDGGDCAYTTYGG	47	Stiller & Hall (1997), Matheny et al. (2002)
	RPB1-Cr	CCNGCDATNTCRTTRTCCATRTA		
RPB2	fRPB2-5f	GAYGAYMGWGATCAYTTYGG	60	Liu et al. (1999)
	fRPB2-7Cr	ATGGGYAARCAAGCYATGGG		
TUB2	Btub2Fd2	GTBCACCTYCARACCGGYCARTG	58	Woudenberg et al. (2009)
	Btub4Rd	CCRGAYTGRCCRAARACRAAGTTGTC		
MCM7	Mcm7-709for	ACIMGIGTITCVGAYGTHAARCC	47	Schmittt et al. (2009)
	Mcm7-	GAYTTDGCIACICCIGGRTCWCCCA		

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Abbreviations: ITS: internal transcribed spacer regions, 28S: 28S Ribosomal RNA, 18S: 18S Ribosomal RNA, TEF1-α: translation elongation factor 1-alpha, RPB1: RNA polymerase largest subunit I, and RPB2: RNA polymerase largest subunit II, TUB2: β-tubulin, MCM7: Mini-chromosome maintenance complex component 7.

Phylogenetic analysis

Sequences created in this study were imported into Geneious Prime® (https://geneious.com/), trimmed to 0.05 error probability, primer regions removed and assembled into consensus sequences that were manually proofread. Other sequences used in this study were downloaded from the NCBI nucleotide database. All sequences used can be found in Table 2. Alignments were made for each gene (18S, ITS, 28S rDNA, TEF1α, RPB1, RPB2, TUB2, MCM7, and mtSSU (mitochondrial 16S rDNA). Portions of 5' and 3' ends of poor quality and single nucleotide insertion in sequences were removed as they are likely sequencing errors.

For the main tree (Fig. 1), sequences of the 18S and 28S rDNA of species of the *Lulworthiales* were downloaded from GenBank (Table 2) and aligned individually in the program MUSCLE (Edgar 2004) in MEGA11 (Tamura et al. 2021). Multiple sequences for each species were used when available to confirm the authenticity of the sequences while doubtful sequences were removed from the analysis. The combined 18S and 28S rDNA dataset contained 123 taxa and a total of 3239 nucleotide positions. A model test was run in MEGA11 (Tamura et al. 2021) to find out the best nucleotide substitution model which was TN93+G. A maximum likelihood analysis including bootstrapping, was performed in IQ-TREE web server (Nguyen et al. 2015) with TN+F+R3 as the best fit model with Model Finder (Kalyaanamoorthy et al. 2017). The ML branch support analysis was performed with ultrafast bootstrap (UFBoot) (Hoang et al. 2018) with the following settings: number of bootstrap alignments set at 1000, maximum iteration set at 1000, minimum correlation coefficient set at 0.99, 1000 replicates of SH-aLRT branch test.

For Bayesian analysis, the alignment was entered into BEAUti v2.6.7 for prior settings and generation of XML files for Bayesian analysis in BEAST v2.6.7 and analyzed simultaneously (Bouckaert et al. 2019) with the following analytical settings: TN93, estimated base frequency, gamma+invariant sites, number of gamma categories set at 5, a strict clock, Coalescent: Constant Size as the speciation model, running 50 million generations with parameters and trees sampled every 1000 generations. The first 10% of the trees were treated as burn-in and discarded based on the effective sample size (ESS) of the parameter statistics in Tracer v1.7.2 (Rambaut et al. 2018). A summary tree was produced using TreeAnnotator v1.10.4 (Bouckaert et al. 2019) and viewed and edited in FigTree v1.4.4 (available at https://github.com/rambaut/figtree/releases).

For the multilocus analyses with 18S, ITS, 28S, TEF1α, TUB2, RPB1, RPB2 and MCM7 sequences (Figs. 2–3), individual gene alignments were produced in Geneious Prime (2022.1.1-Build 2022-03-15) using MAFFT v.7.490, algorithm E/L/G-INS-i and manually corrected (Katoh & Stanley 2013). After cleaning the ends of alignments as described above, the individual alignments were concatenated into a multilocus alignment, which was subjected to Bayesian inference (BI) and maximum likelihood (ML) analyses. Before analyzing the alignment was tested for which partitions could be merged, the optimal evolutionary model and the model parameters with IQ-TREE v.1.6.12 for both Bayesian and ML analysis (Nguyen et al. 2015). The partitions, models and parameters were used for the analysis in MrBayes (v.3.2.7a - MPI and Beagle enabled version) and RAxML v.8.2.11 (Ronquist et al. 2012, Stamatakis 2006).

Table 2 GenBank accession numbers for the taxa used in the phylogenetic analyses.

Taxa	Isolate no.	18S rDNA	28S rDNA	ITS rDNA	TEF1-α	RPB1	RPB2	TUB2	MCM7	mitochondrial 16S rDNA
Achroceratosphaeria potamia	JF 08139	GQ996541	GQ996538							
Lindra obtusa	CBS 79183	AY878996	AY878955							
Cumulospora marina	GR53	GU256625	GU256626							
Cumulospora marina	MF46	GU252136	GU252135							
Cumulospora marina	SUMCC H-15016		OP646427							
Halazoon fuscus	NBRC105256	GU252148	GU252147							
Halazoon melhae	MF819	GU252144	GU252143							
Halazoon purpurea (*Lulworthia* cf. *purpurea*)	CBS 21960	AY879004	AY878962							
Halazoon purpurea (*Lulworthia* cf. *purpurea*)	CMG 54	MT235698	MT235739	MT235722						
Halazoon purpurea (*Lulworthia* cf. *purpurea*)	CMG 55	MT235699	MT235740	MT235723						
Halazoon purpurea (*Lulworthia* cf. *purpurea*)	CMG 56	MT235700	MT235741	MT235724						
Halazoon purpurea (*Lulworthia* cf. *purpurea*)	CMG 57	MT235701	MT235742	MT235725						
Halazoon purpurea (*Lulworthia* cf. *purpurea*)	CMG 58	MT235702	MT235743	MT235726						
Halazoon purpurea (*Lulworthia* cf. *purpurea*)	CMG 59	MT235703	MT235744	MT235727						
Halazoon purpurea (*Lulworthia* cf. *purpurea*)	CMG 60	MT235704	MT235745	MT235728						
Halazoon purpurea (*Lulworthia* cf. *purpurea*)	CMG 61	MT235705	MT235746	MT235729						
Halazoon purpurea (*Lulworthia* cf. *purpurea*)	CMG 62	MT235706	MT235747	MT235730						
Halazoon purpurea (*Lulworthia* cf. *purpurea*)	CMG 63	MT235707	MT235748	MT235731						

Table 2 Continued

Taxa	Isolate no.	18S rDNA	28S rDNA	ITS rDNA	TEF1-α	RPB1	RPB2	TUB2	MCM7	mitochondrial 16S rDNA
Halazoon purpurea (Lulworthia cf. *purpurea*)	FCUL070108CF8		JN886818							
Halazoon purpurea (Lulworthia cf. *purpurea*)	FCUL070108CF9		JN886817							
Halazoon purpurea (Lulworthia cf. *purpurea*)	FCUL170907CF7		JN886815							
Halazoon purpurea (Lulworthia cf. *purpurea*)	FCUL170907CP5	KT347201	JN886824	KT347219						
Halazoon purpurea (Lulworthia cf. *purpurea*)	FCUL280207CF8		JN886807							
Halazoon purpurea (Lulworthia cf. *purpurea*)	FCUL280207CF9	KT347202	JN886808	KT347218						
Haloguignardia irritans		AY566252		AY581935						
Halophilomyces hongkongensis	HOMAR1	PP347844	PP347858							
Halophilomyces hongkongensis	HOMAR2	PP347845	PP347859							
Halophilomyces hongkongensis	HOMAR3	PP347846	PP347860							
Halophilomyces hongkongensis	HOMAR4	PP347847	PP347861							
Hydea mangrovei	MCD177A	OP884604	OP884601							
Hydea mangrovei	NFCCI-4386	OP908067	OP908068							
Hydea pygmea	NBRC33069	GU252134	GU252133							
Kohlmeyeriella crassa	IFO32133	AY879005	AY878963							
Kohlmeyeriella crassa	IFO32134	AY879006	AY878964							
Kohlmeyeriella crassa	NBRC 32133		LC146742							
Kohlmeyeriella tubulata	PP0989	AY878997	AF491264							
Kohlmeyeriella tubulata	PP1105	AY878998	AF491265							
Koralionastes ellipticus	JK5769; PC 35	EU863581	EU863585							

Table 2 Continued

Taxa	Isolate no.	18S rDNA	28S rDNA	ITS rDNA	TEF1-α	RPB1	RPB2	TUB2	MCM7	mitochondrial 16S rDNA
Koralionastes ellipticus	JK5771; PC 305	EU863580	EU863583							
Lindra obtusa	AFTOL_ID_5012	FJ176847	FJ176902		FJ238416		FJ238382			FJ190661
Lindra obtusa	CBS 113030	AY879001	AY878959							
Lindra obtusa	IFO31317	AY879002	AY878960							
Lindria obtusa	m269	FJ176847	FJ176902							
Lindriella thalassiae	AFTOL_ID_413	DQ470994	DQ470947	DQ491508	DQ471065	DQ471139	FJ238382			FJ190593
Lindriella crassa	ATCC 56663	AY878999								
Lindriella thalassiae	JK4322	AF195632	AF195633		Genome		Genome	Genome	Genome	Genome
Lindriella thalassiae	JK5090	AF195634	AF195635							
Lindriella thalassiae	JK5090A	U46874	U46891							
Lindriella thalassiae	JK5091A	AY879000								
Lindriella thalassiae	Kohlmeyer 4743	AF047580	AF047581							
Lulwoana uniseptata	AFTOL_ID_5014	FJ176849	FJ176904				FJ238383			
Lulwoana uniseptata	CBS 280.54		MH868873	MH857330						
Lulwoana uniseptata	CBS 16760	AY879034	AY878991							
Lulwoana uniseptata	CMG 64	MT235708	MT235749							
Lulwoana uniseptata	CMG 65	MT235709	MT235750	MT235733						
Lulwoana uniseptata	CMG 66	MT235710	MT235751							
Lulwoana uniseptata	CMG 67	MT235711	MT235752							
Lulwoana uniseptata	FCUL010407SP2	KT347204	JN886805							
Lulwoana uniseptata	FCUL280207CP1	KT347203	JN886806							

Table 2 Continued

Taxa	Isolate no.	18S rDNA	28S rDNA	ITS rDNA	TEF1-α	RPB1	RPB2	TUB2	MCM7	mitochondrial 16S rDNA
Lulwoana uniseptata	IFO7836	AY879038	AY878995							
Lulwoana uniseptata	KMPB14648	AY879035	AY878992							
Lulwoana uniseptata	KMPB150	AY879036	AY878993							
Lulwoana uniseptata	KMPB82	AY879037	AY878994							
Lulwoana uniseptata	NBRC 32137	AY879031 NG_078728	AY878988 NG_088005							
Lulwoana uniseptata	PP4032	AY879032	AY878989							
Lulwoana uniseptata	PP4033	AY879033	AY878990							
Lulwoana uniseptata		EU848591	EU848592							
Lulwoidea lignoarenaria	AFTOL_ID_5013	FJ176848	FJ176903		FJ238417					FJ713612
Lulwoidea lignoarenaria	ATCC 64644	AY879009								
Lulwoidea lignoarenaria	IFO32135	AY879010	AY878968							
Lulwoidea lignoarenaria	PP1933		AF491272							
Lulwoidea lignoarenaria	PP915	FJ176848	FJ176903							
Lulworthia atlantica	CBS 139632	KY202429	KY202429	KY202429						
Lulworthia atlantica	FCUL061107CP3	KT347196	JN886825	KT347208	OQ296422	OQ296420			OQ296424	
Lulworthia atlantica	FCUL010407SP6	KT347197	JN886836							
Lulworthia atlantica	FCUL090707CF10	KT347199	JN886814							
Lulworthia atlantica	FCUL210208SP4	KT347193	JN886843							
Lulworthia cf. *opaca*	CBS 21860	AY879003	AY878961							
Lulworthia cf. *purpurea*	LF847	KM096220								
Lulworthia floridana	DA13	OP908050	OP908057							

Table 2 Continued

Taxa	Isolate no.	18S rDNA	28S rDNA	ITS rDNA	TEF1-α	RPB1	RPB2	TUB2	MCM7	mitochondrial 16S rDNA
Lulworthia floridana	DA15	OP908051	OP908058							
Lulworthia floridana	DA12	OP908049	OP908056							
Lulworthia fucicola	ATCC 64288	AY879007	AY878965							
Lulworthia fucicola	GJ 589_FCUL	OM760532	OM760533	OM760531						
Lulworthia fucicola	PP1249	AY879008	AY878966							
Lulworthia fucicola	DA10	OP908048	OP908055							
Lulworthia fucicola	DA8	OP908046	OP908053							
Lulworthia fucicola	DA9	OP908047	OP908054							
Lulworthia fundyensis	AW2347	MH465136	MH458750	MH465123						
Lulworthia medusa	JK5581	AF195636	AF195637							
Lulworthia norwegica	M16HELTRa3202.II.1	MK531776	MK531707	MK543190	OP715912			OP715913	OP715899	
Lulworthia norwegica	TRä3123A	OP680778	OP648294	OP683562	OP715908	OP715900	OP715904		OP715895	
Lulworthia norwegica	TRä3129A	OP683563	OP648295	OP683563	OP715909	OP715901	OP715905		OP715896	
Lulworthia norwegica	TRä3129C	OP680779	OP648296	OP683564	OP715910	OP715902	OP715906		OP715897	
Lulworthia sp.	PP2597	AY879030	AY878987							
Matsusporium japonica	SUMCC H-08001	OP646428	OP646426							
Matsusporium tropicale	IT061	GU256631								
Matsusporium tropicale	NBRC 32499	GU252142	GU252141							
Microdochium lycopodinum	CBS 125585		KP858952	NR_145223			KP859125	KP859080		
Moleospora maritima	MF836	GU252138	GU252137							
Moromyces mangrovis	MCD032	OP884603	OP884599							
Moromyces varius	GR78		EU848578							

Table 2 Continued

Taxa	Isolate no.	18S rDNA	28S rDNA	ITS rDNA	TEF1-α	RPB1	RPB2	TUB2	MCM7	mitochondrial 16S rDNA
Paralulworthia gigaspora (*P. elbensis*)	MUT 377	MZ357753	MZ357732	MZ357710	MZ407516	MZ365271	MZ357215	MZ407536		
Paralulworthia gigaspora (*P. elbensis*)	MUT 5422	MZ357766	MZ357745	MZ357723	MZ407525		MZ357228	MZ407549		
Paralulworthia gigaspora (*P. elbensis*)	MUT 5438	MZ357755	MZ357734	MZ357712	MZ407518		MZ357217	MZ407538		
Paralulworthia gigaspora (*P. elbensis*)	MUT 5461	MZ357768	MZ357747	MZ357725	MZ407527		MZ357230	MZ407551		
Paralulworthia gigaspora (*P. candida*)	MUT 5430	NG_078762	MZ357746	NR_175739	MZ407526		MZ357229	MZ407550		
Paralulworthia gigaspora	MUT 1753	MZ357773	MZ357752	MZ357730	MZ407532	MZ365285	MZ357235	MZ407556		
Paralulworthia gigaspora	MUT 263	MZ357772	MZ357751	MZ357729	MZ407531		MZ357234	MZ407555		
Paralulworthia gigaspora	MUT 435	MN649246/ NG_070318	MN649250	NR_169703	MZ407533	MZ365286	MZ357236	MZ407557		
Paralulworthia gigaspora	MUT 465	MZ357769	MZ357748	MZ357726	MZ407528	MZ365282	MZ357231	MZ407552		
Paralulworthia gigaspora	MUT 5085	MZ357758	MZ357737	MZ357715	MZ407521	MZ365274	MZ357220	MZ407541		
Paralulworthia gigaspora	MUT 5086	MZ357759	MZ357738	MZ357716	MZ407522	MZ365275	MZ357221	MZ407542		
Paralulworthia gigaspora	MUT 5093	MZ357761	MZ357740	MZ357718		MZ365277	MZ357223	MZ407544		
Paralulworthia gigaspora	MUT 5094	MZ357762	MZ357741	MZ357719	MZ407524	MZ365278	MZ357224	MZ407545		
Paralulworthia gigaspora	MUT 5413	MN649247	MN649251	MN649243	MZ407534	MZ365287	MZ357237	MZ407558		
Paralulworthia gigaspora	MUT 672	MN649248	MN649252	MN649244						
Paralulworthia gigaspora (*P. halima*)	CBS 208.64		MH870049	MH858421						
Paralulworthia gigaspora (*P. halima*)	CMG 68	MT235712	MT235753	MT235736						
Paralulworthia gigaspora (*P. halima*)	CMG 69	MT235713	MT235754	MT235737						
Paralulworthia gigaspora (*P. halima*)	MUT 1483	MZ357770	MZ357749	MZ357727	MZ407529	MZ365283	MZ357232	MZ407553		

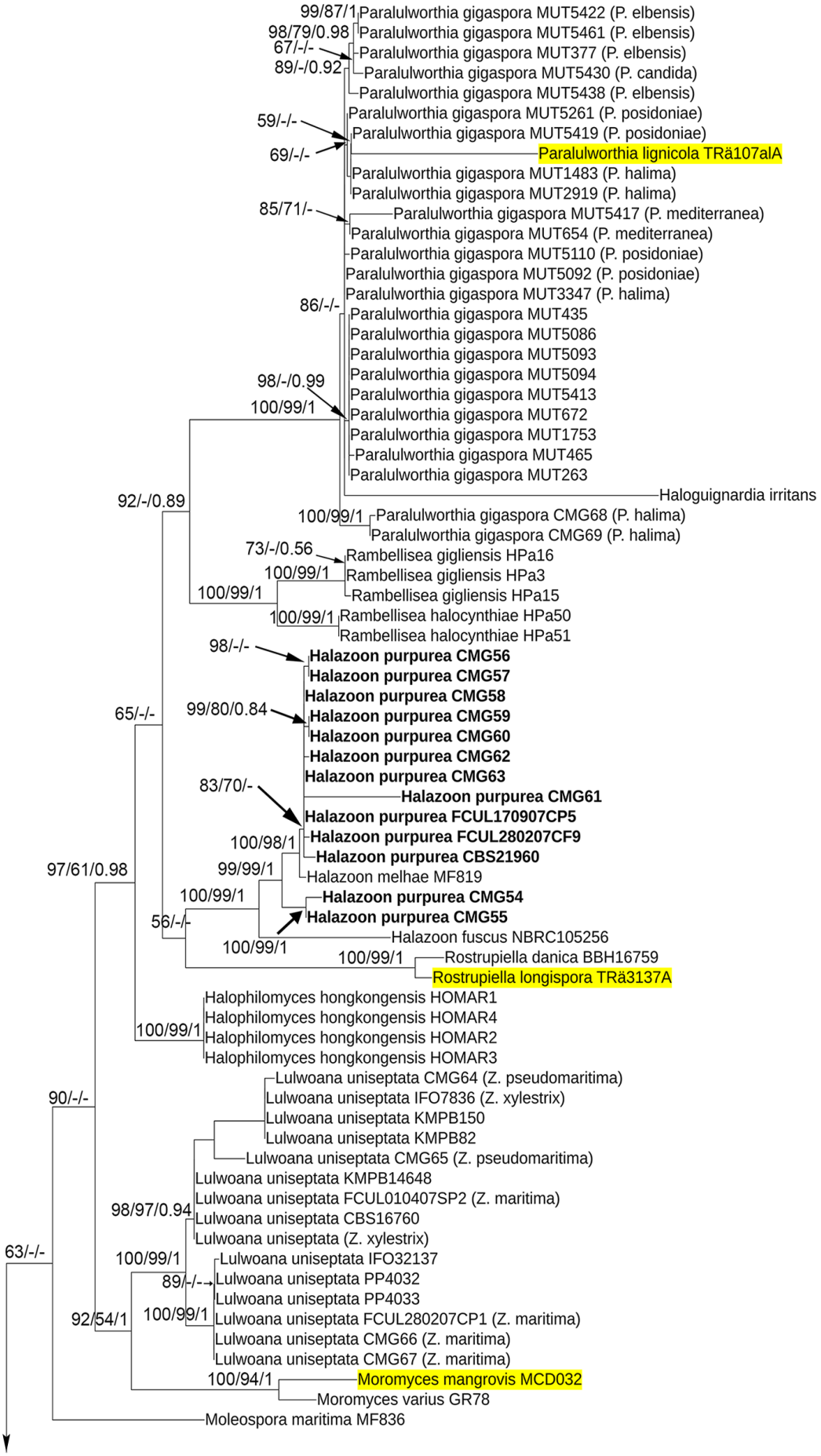
Table 2 Continued

Taxa	Isolate no.	18S rDNA	28S rDNA	ITS rDNA	TEF1-α	RPB1	RPB2	TUB2	MCM7	mitochondrial 16S rDNA
Paralulworthia gigaspora (*P. halima*)	MUT 2919	MZ357756	MZ357735	MZ357713	MZ407519	MZ365272	MZ357218	MZ407539		
Paralulworthia gigaspora (*P. halima*)	MUT 3347	MZ357771	MZ357750	MZ357728	MZ407530	MZ365284	MZ357233	MZ407554		
Paralulworthia gigaspora (*P. mediterranea*)	MUT 5080	MZ357757	MZ357736	MZ357714	MZ407520	MZ365273	MZ357219	MZ407540		
Paralulworthia gigaspora (*P. mediterranea*)	MUT 5417	NG_078761	MZ357743	NR_175738		MZ365280	MZ357226	MZ407547		
Paralulworthia gigaspora (*P. mediterranea*)	MUT 654	MZ357754	MZ357733	MZ357711	MZ407517		MZ357216	MZ407537		
Paralulworthia gigaspora (*P. posidoniae*)	MUT 5092	MZ357760	MZ357739	MZ357717	MZ407523	MZ365276	MZ357222	MZ407543		
Paralulworthia gigaspora (*P. posidoniae*)	MUT 5110	MZ357763	MZ357742	MZ357720		MZ365279	MZ357225	MZ407546		
Paralulworthia gigaspora (*P. posidoniae*)	MUT 5261	MN649249 NG_070319	MN649253	NR_169704	MZ407535		MZ357238	MZ407559		
Paralulworthia gigaspora (*P. posidoniae*)	MUT 5419	MZ357765	MZ357744	MZ357722		MZ365281	MZ357227	MZ407548		
Paralulworthia lignicola	TRä107alA	OP680780	OP683565	OP683565	OP715911	OP715903	OP715907		OP715898	
Paramoleospora guttulata	CGMCC 3.22494	NG_242955	NG_243259							
Paramoleospora guttulata	CGMCC 3.22495	OQ758190	OQ758157							
Pisorisporium cymbiforme	PRM 924377	KM588901	KM588904 NG_060135				KM588907			
Pontogeneia microdictyi	JK5748	EU863582								
Rambellisea gigliensis	Hpa3	OR371466	OR369726							
Rambellisea gigliensis	HPa15	OR371482	OR369725							
Rambellisea gigliensis	HPa16	OR371483	OR371456							
Rambellisea halocynthiae	HPa50	OR371485	OR371457							

Table 2 Continued

Taxa	Isolate no.	18S rDNA	28S rDNA	ITS rDNA	TEF1-α	RPB1	RPB2	TUB2	MCM7	mitochondrial 16S rDNA
Rambellisea halocynthiae	HPa51	OR371484	OR371461							
Rostrupiella danica	BBH16759		DQ394094							
Rostrupiella longispora	TRä3137A	OP680781	OP683566	OP683566						
Sammeyersia grandispora	JK4686 (AFTOL_ID_424 and 747)	DQ522855	DQ522856		DQ497608		DQ518181			FJ190595
Sammeyersia grandispora	JK5168A	AY879012	AY878969							
Sammeyersia grandispora	NTOU3845	OP908045	OP908052		OP934059		OP934058		OP934056	
Sammeyersia grandispora	JK5255A	AY879013	AY878970							
Sammeyersia grandispora	Kohlmeyer 4686.1	AF047582	AF047583							
Sammeyersia grandispora	MCD092	OR805512	OR816037							
Sammeyersia grandispora	NTOU3841	KY026044	KY026048							
Sammeyersia grandispora	NTOU3847	KY026046	KY026049							
Sammeyersia thailandica	MCD033		OP884600							
Sammeyersia yanbuensis	LN01	OR805511	OR816036							
Sammeyersia yanbuensis	SUMCC H-11020		OP646429							
Sammeyersia yanbuensis (as *S. grandispora*)	NTOU3849	KY026047	KY026050							

Abbreviations: ITS: internal transcribed spacer regions, 28S: 28S Ribosomal RNA, 18S: 18S Ribosomal RNA, TEF1-α: translation elongation factor 1-alpha, RPB1: RNA polymerase largest subunit I, and RPB2: RNA polymerase largest subunit II, TUB2: β-tubulin, MCM7: Mini-chromosome maintenance complex component 7.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Paralulworthia gigaspora MUT5422 (P. elbensis)
98/79/0.98
Paralulworthia gigaspora MUT5461 (P. elbensis)
67/-/-
Paralulworthia gigaspora MUT377 (P. elbensis)
89/-/0.92
Paralulworthia gigaspora MUT5430 (P. candida)
Paralulworthia gigaspora MUT5438 (P. elbensis)
59/-/-
Paralulworthia gigaspora MUT5261 (P. posidoniae)
Paralulworthia gigaspora MUT5419 (P. posidoniae)
69/-/-
Paralulworthia lignicola TRä107alA
Paralulworthia gigaspora MUT1483 (P. halima)
Paralulworthia gigaspora MUT2919 (P. halima)
85/71/-
Paralulworthia gigaspora MUT5417 (P. mediterranea)
Paralulworthia gigaspora MUT654 (P. mediterranea)
Paralulworthia gigaspora MUT5110 (P. posidoniae)
Paralulworthia gigaspora MUT5092 (P. posidoniae)
Paralulworthia gigaspora MUT3347 (P. halima)
86/-/-
Paralulworthia gigaspora MUT435
Paralulworthia gigaspora MUT5086
Paralulworthia gigaspora MUT5093
Paralulworthia gigaspora MUT5094
98/-/0.99
Paralulworthia gigaspora MUT5413
100/99/1
Paralulworthia gigaspora MUT672
Paralulworthia gigaspora MUT1753
Paralulworthia gigaspora MUT465
Paralulworthia gigaspora MUT263
Haloguignardia irritans
92/-/0.89
100/99/1
Paralulworthia gigaspora CMG68 (P. halima)
Paralulworthia gigaspora CMG69 (P. halima)
73/-/0.56
Rambellisea gigliensis HPa16
100/99/1
Rambellisea gigliensis HPa3
100/99/1
Rambellisea gigliensis HPa15
100/99/1
Rambellisea halocynthiae HPa50
Rambellisea halocynthiae HPa51
98/-/-
Halazoon purpurea CMG56
Halazoon purpurea CMG57
Halazoon purpurea CMG58
65/-/-
99/80/0.84
Halazoon purpurea CMG59
Halazoon purpurea CMG60
Halazoon purpurea CMG62
Halazoon purpurea CMG63
83/70/-
Halazoon purpurea CMG61
Halazoon purpurea FCUL170907CP5
100/98/1
Halazoon purpurea FCUL280207CF9
Halazoon purpurea CBS21960
97/61/0.98
99/99/1
Halazoon melhae MF819
100/99/1
Halazoon purpurea CMG54
56/-/-
Halazoon purpurea CMG55
Halazoon fuscus NBRC105256
100/99/1
100/99/1
Rostrupiella danica BBH16759
Rostrupiella longispora TRä3137A
Halophilomyces hongkongensis HOMAR1
Halophilomyces hongkongensis HOMAR4
100/99/1
Halophilomyces hongkongensis HOMAR2
Halophilomyces hongkongensis HOMAR3
Lulwoana uniseptata CMG64 (Z. pseudomaritima)
90/-/-
Lulwoana uniseptata IFO7836 (Z. xylestrix)
Lulwoana uniseptata KMPB150
Lulwoana uniseptata KMPB82
Lulwoana uniseptata CMG65 (Z. pseudomaritima)
Lulwoana uniseptata KMPB14648
Lulwoana uniseptata FCUL010407SP2 (Z. maritima)
98/97/0.94
Lulwoana uniseptata CBS16760
Lulwoana uniseptata (Z. xylestrix)
63/-/-
100/99/1
Lulwoana uniseptata IFO32137
89/-/-
Lulwoana uniseptata PP4032
Lulwoana uniseptata PP4033
92/54/1
100/99/1
Lulwoana uniseptata FCUL280207CP1 (Z. maritima)
Lulwoana uniseptata CMG66 (Z. maritima)
Lulwoana uniseptata CMG67 (Z. maritima)
100/94/1
Moromyces mangrovis MCD032
Moromyces varius GR78
Moleospora maritima MF836

Figure 1 – Maximum likelihood tree of taxa of the *Lulworthiales* based on 18S and 28S rDNA sequences. New species are highlighted in yellow, and new combinations are in bold. The numbers at the nodes represent maximum likelihood bootstrap (>50), maximum parsimony bootstrap (>50) and posterior probability (>0.5), respectively. The scale bar shows mean expected rates of substitution per site. Tree nodes in black indicate the *Lulworthia sensu stricto* clade. The branch of *Spathulospora* was shortened by one-third.

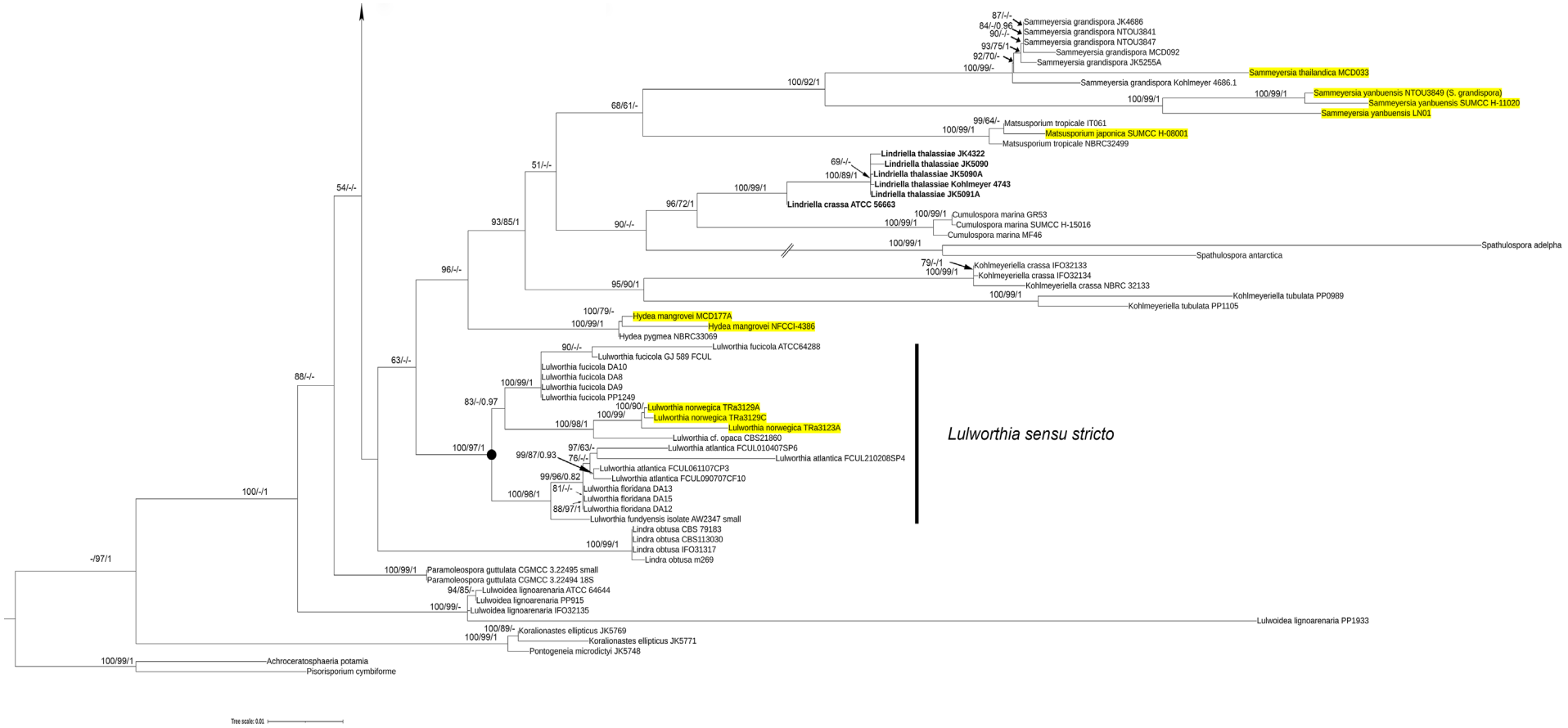

Figure 1 – Continued.

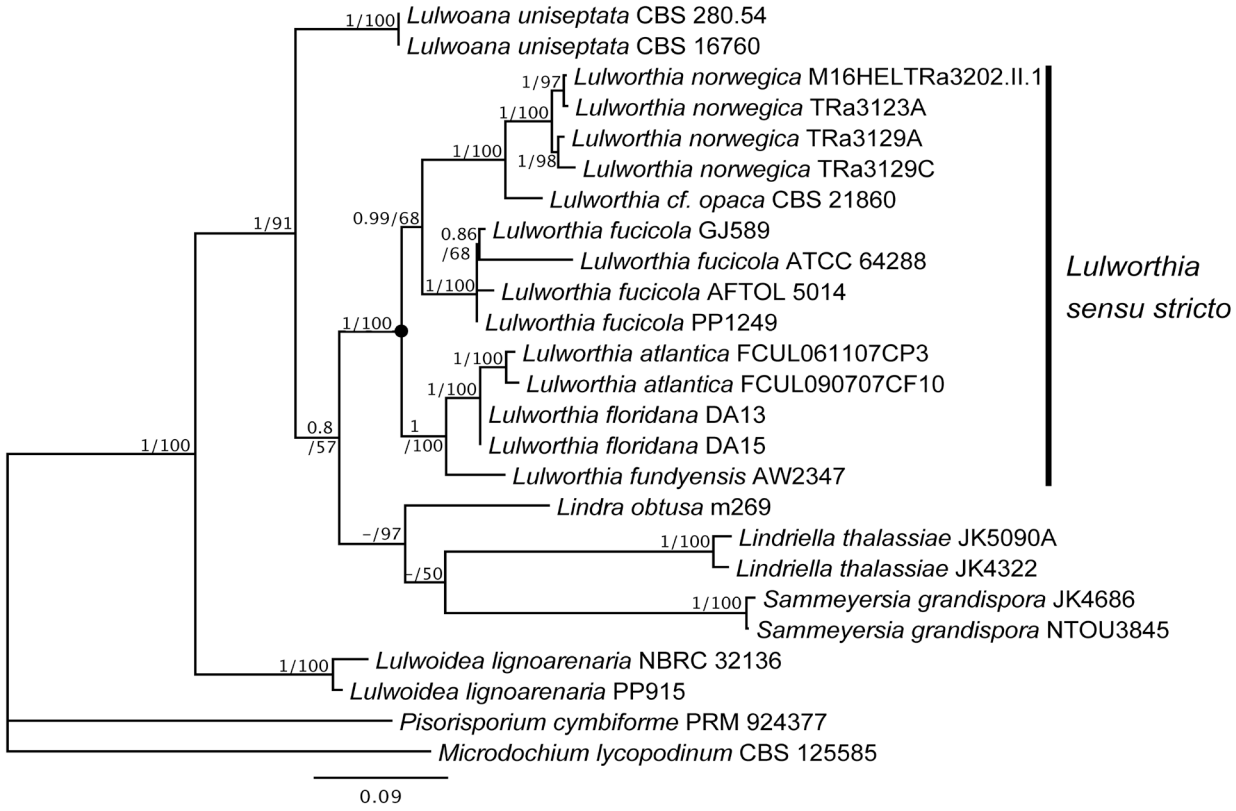

Figure 2 – Maximum likelihood tree of *Lulworthia sensu stricto* based on 18S, ITS, 28S, TEF1α, TUB2, RPB1, RPB2, MCM7 and mtSSU sequences using *Microdochium lycopodinum* (*Amphisphaeriaceae*) and *Pisorisporium cymbiforme* (*Pisorisporiaceae*) as outgroup taxa. The numbers at the nodes represent posterior probability and maximum likelihood bootstrap support values, respectively. The scale bar shows mean expected rates of substitution per site. Bayesian and ML analysis produced trees with identical topography and for this reason, only the ML tree is shown. Tree nodes in black indicate the *Lulworthia sensu stricto* clade.

The concatenated alignment of the *Lulworthiales sensu stricto* analysis (Fig. 2) consisted of 25 isolates and was 10394 characters long. Following gene partitions, evolutionary models and parameters were used for the Bayesian analysis: 18S, 28S, and TEF1α in partition 1 with GTR+F+I+G4, ITS1 and ITS2 in partition 2 with SYM+FQ+G4, 5.8S in partition 3 with K2P+FQ, RPB1, RBP2 and MCM7 in partition 4 with GTR+F+G4, TUB2 in partition 5 with HKY+F+G4 and mtSSU in partition 6 with HKY+F. All parameters except topology and length were unlinked between partitions. The analysis was run until the average standard deviation of split frequencies fell below 0.01 (after 240,000 generations). Burn-in for tree generation and convergence analysis was set to 50%. The ML analysis was run using RAxML v8.2.11 within Geneious. The alignment was split into five partitions, partition 1 contained 18S, 5.8S, 28S and TEF1α, partition 2 contained ITS 1 and 2, partition 3 contained RPB1, RPB2 and MCM7, partition 4 contained TUB2, partition 5 contained mtSSU. All partitions used GTR+G as the evolutionary model. For the analysis, 2000 rapid bootstrap inferences were made, followed by a thorough ML search.

The concatenated alignment for the *Paralulworthia* tree shown in Fig. 3 had 62 isolates included and was 9421 characters long. Following gene partitions, evolutionary models and parameters were used for the Bayesian analysis: 18S, 5.8S and 28S in partition 1 with GTR+F+I+G4 model, ITS1 and 2 in partition 2 with SYM+G4 model, TEF1α in partition 3 with GTR+F+G4 model and RPB1, RPB2, TUB2 and MCM7 in partition 4 with GTR+F+G4 model. All parameters except topology and branch lengths were unlinked. The BI analysis was performed until the average standard deviation in split frequencies was below 0.01 (occurred after 2,590 000 generations). ML analysis was run for 2000 bootstrap replicates and searched for the best-scoring ML tree using the same

partition as in the BI analysis with the model GTR+G. The trees were compared and support values from both were added to identical branches of the Bayesian tree. SSU had three regions where introns were present in some sequences, introns were not coded as presence/absence data but included as nucleotide data. RPB1, RPB2 (3' end) and TUB2 contained introns present in all sequences used.

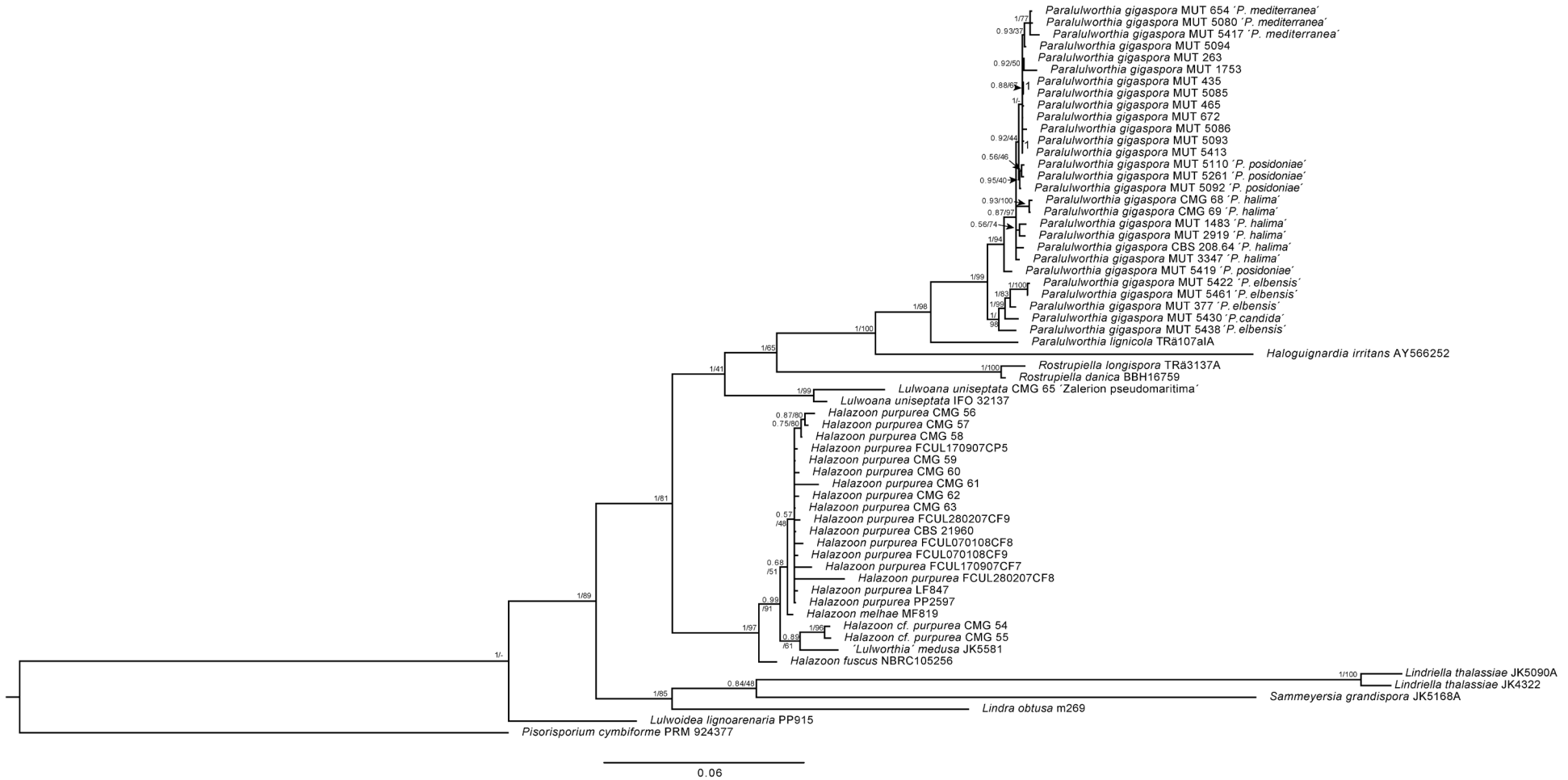

Figure 3 – Bayesian tree of the *Paralulworthia* clade including data from 18S, ITS, 28S, TEF1α, TUB2, RPB1, RPB2, MCM7 and mtSSU sequences using *Pisorisporium cymbiforme* (*Pisorisporiaceae*, *Sordariomycetes*) as an outgroup. The numbers at the nodes represent posterior probability and maximum likelihood bootstrap support values, respectively. The scale bar shows estimated substitutions per site. Bayesian and ML analysis produced trees with similar topography and for this reason, only the Bayesian tree is shown.

RESULTS

Phylogeny

The maximum likelihood tree shown in Fig. 1 was constructed based on partial 18S and 28S rDNA sequences of the *Lulworthiaceae*. The following groupings were observed: (1) *Lulworthia sensu stricto* was composed of *L. fucicola*, *L. opaca, L. atlantica*, *L. floridana, L. fundyensis* and *L. norwegica* sp. nov., (2) *Paralulworthia* was a polyphyletic genus while *Haloguignardia irritans* and the new isolate TRä107aIA grouped within this clade (*Paralulworthia lignicola* sp. nov.); the genus *Rambellisea* formed a sister clade to *Paralulworthia* (Braconcini et al. 2024), (3) *Lulworthia purpurea* grouped with *Halazoon fuscus* and *H. melhae* and so *L. purpurea* is transferred to *Halazoon*, (4) the isolate TRä3137A grouped with *Rostrupiella danica*, but morphology of TRä3137A is different from *R. danica* and so *R. longispora* sp. nov. is described, (5) the isolate MFLUCC 17-0392 grouped with *Moromyces varius* but morphologically MFLUCC 17-0392 was different from *M. varius* and so *M. mangrovis* sp. nov. is described, (6) *Lulwoana uniseptata, Zalerion maritima, Z. pseudomaritima* and *Z. xylestrix* formed a monophyletic group, (7) *Lindra obtusa* did not form a monophyletic group with *L. crassa* and *L. thalassiae*, and *Lindriella* gen. nov. is described for the latter two species and *L. hawaiiensis*, (8) *Lindriella* formed a sister clade to *Cumulospora* which consisted of three *C. marina* isolates, (9) *Hydea* consisted of *H. pygmea* and *H. mangrovei* sp. nov. while *H. mangrovei* is morphologically different from *H. pygmea,* (10) *Kohlmeyeriella crassa* and *Kohlmeyeriella tubulata* formed a well-supported clade, (11) the isolate SUMCC H-08001 formed a monophyletic clade with *Matsusporium tropicale*; morphologically they are different and so *M. japonica* sp. nov. is described, (12) *Paramoleospora guttulata* formed a sister clade to *Moleospora maritima*, (13) the isolates LN01, MCD033 and SUMCC H-11020 formed part of the *Sammeyersia* clade but they were not conspecific with *S. grandispora*, and *S. yanbuensis* sp. nov. and *S. thailandica* sp. nov. are described, (14) *Spathulospora* (*S. adelpha* and *S. antarctica*) formed a sister clade with *Cumulospora marina* with a weak support, and (15) isolates of *Koralionastes ellipticus* and *Pontogeneia microdictyi* formed a separate clade to the taxa described above.

These placements reflect the earlier studies, with *Spathulospora* grouping with the *Sammeyersia* clade (Campbell et al. 2005) and *Koralionastes ellipticus and Pontogeneia microdictyi* forming a separate but monophyletic clade with the rest of the *Lulworthiales* genera such as *Kohlmeyeriella*, *Lulworthia*, *Lulwoana*, *Lulwoidea*, *Lindra*, etc. (Campbell et al. 2009), thus rendering the orders and families *Koralionastetales* (*Koralionastetaceae*) and *Spathulosporales* (*Spathulosporaceae*) phylogenetically redundant. However, morphologically and ecologically there are important differences as detailed by Campbell et al. (2005, 2009). Further collections of these elusive and poorly known genera (*Koralionastes*, *Pontogeneia*, *Spathulospora*) are required to establish their relationships within the *Lulworthiomycetidae*.

Key to genera of *Lulworthiomycetidae*

1. Hyphomycetes asexual morphs	2
1. Sexual morphs with ellipsoid to fusiform to filiform ascospores	9
2. Conidia hyaline, long	*Lindra*
2. Conidia brown	3
3. Conidia globose with radiating appendages	*Orbimyces*
3. Conidia lacking appendages	4
4. Conidia chlamydospores	5
4. Conidia helicoid	6
4. Conidia forming a ball of cells, muriform	9
4. Conidia 2 types: chlamydospores and coiled, (sub)globose and with 1-4 septa	*Halophilomyces*
5. Isolated from seagrasses/wood	*Paralulworthia*
5. Isolated from tunicates	*Rambellisea*

6. Conidia with large apical cells, ½-1 coiled, 3-4 septate *Hydea*
6. Conidia same width in the coil 7
7. Conidia on long stalks, 1-3 coiled *Matsusporium*
7. Conidia lacking a stalk 8
8. Conidia ½-2½ loosely coiled, *Halazoon*
8. Conidia 1-2 coiled, *Zalerion* anamorph *Lulwoana*
9. Conidia coiled becoming a ball of cells, 5-10 cells, *Cumulospora*
9. Conidia ball of cells, up to 40 cells, width 20 µm diam. *Moromyces*
9. Conidia, massive with more than 50 cells, 14 µm diam. *Moleospora*
9. Conidia, ellipsoidal to ovoid aseptate, 12–21 × 7.5–14 µm *Paramoleospora*
10. Ascomata with bell-like structure within the centrum *Rostrupiella*
10. Ascomata lacking the bell-like structure 11
11. Ascospores aseptate… 12
11. Ascospores septate... 18
12. Ascospores filiform, without appendages or chambers *Lindriella*
12. Ascospores fusiform, ellipsoidal, with appendages or chambers 13
12. Ascospores filiform, with appendages or chambers 15
13. Ascospore appendages tubular longer than 35 µm *Kohlmeyeriella*
13. Ascospore appendages apiculate or conical chambers, less than 35 µm 14
14 Ascomata superficial, with sterile hairs, parasitic on red algae S*pathulospora*
14. Ascomata immersed in a gall, lacking sterile hairs, on brown algae *Haloguignardia*
15. Ascospores filiform, lacking asexual morph: 16
15. Ascospores filiform, with asexual morphs 17
16. Ascospores 90-300 µm *Lulworthia*
16. Ascospores over 300 µm *Sammeyersia*
17. Ascospores 320-385 · 4-5 µm, apical chamber 5–7 × 2.5–3 µm *Cumulospora*
17. Ascospores 190-292 · 3-4 µm, apical chamber 10–16–(26) µm *Halazoon*
17. Asexual morph: with chlamydospores *Paralulworthia*
18. Ascospores 1-septate, with apical chambers *Lulwoana*
18. Ascospores many times septate 19
19. Ascospore with or without globose apical appendages *Lindra*
19. Ascospores lacking apical appendages 20
20. Ascospores filiform *Lulwoidea*
20. Ascospores ellipsoidal to oval, thick-walled, on coral rock, associated with crustose sponges *Koralionastes*
20. Ascospores filiform, rarely ellipsoidal, hyaline, on marine algae *Pontogeneia*

Account of *Lulworthiales* taxa

Genera are listed in alphabetical order after the type genus *Lulworthia*.

Lulworthiomycetidae Dayar., E.B.G. Jones & K.D. Hyde, Fungal Divers. 72: 208 (2015)

Index Fungorum number: IF551131

Lulworthia G.K. Sutherl., Trans. Br. mycol. Soc. 5(2): 259 (1916) [1915]

Index Fungorum number: IF2953

Saprobic on algae, drift, trapped and submerged wood, rope and polyurethane panels. Sexual morph: *Ascomata* immersed to superficial, variously shaped, colour, and length of the neck, membranous to subcarbonaceous. *Paraphyses* lacking. *Asci* deliquescent, 8-spored, clavate to cylindrical, lacking an apical apparatus. *Ascospores* filiform, hyaline, narrow, 0-septate, with terminal end chambers/appendages releasing a drop of mucilage when in water. Asexual morph: *Chlamydospores* formed hyaline chains, globose to subglobose with thick walls.

Type species – *Lulworthia fucicola* G.K. Sutherl., Trans. Br. mycol. Soc. 5(2): 259 (1916) [1915]

Notes – *Lulworthia* species have been recorded from various marine habitats and is one of the largest genera among marine fungi (Kohlmeyer et al. 2000). Sutherland (1916) introduced the genus *Lulworthia* to accommodate the species *L. fucicola* found on the brown seaweed, bladder wrack at Lulworth Cove on the coast of Dorset, UK, but no type material was deposited for this taxon. Campbell (2005) designated a neotype as the Type species of *Lulworthia* (*L. fucicola*) from a collection of wood made in Chile by C.A. Shearer in 1984 (Shearer & Burgos 1987). The genus *Lulworthia* has been revisited over many years (Kohlmeyer 1972, Kohlmeyer & Kohlmeyer 1979, Koch & Jones 1984, Schaumann et al. 1986). Johnson and Sparrow (1961) listed 12 *Lulworthia* species, which were synonymized to *L. medusa* by Cavaliere and Johnson (1966). Three species were accepted by Kohlmeyer (1972) and Koch and Jones (1984) recognized six species. Eleven accepted species were included in *Lulworthia* with several other taxa by Kohlmeyer et al. (2000). However, their morphological differences are not sufficient to distinguish the species (Kohlmeyer et al. 2000).

As a result of 18S and 28S rDNA sequence analysis, several transfers have been recommended, such as, *Lulworthia crassa* to *Kohlmeyeriella*, *Lulworthia lignoarenaria* to the new genus *Lulwoidea* and *Lulworthia uniseptata* to *Lulwoana* (Campbell et al. 2005). Jones et al. (2015) opined that only *L. fucicola* can be accepted in *Lulworthia sensu stricto*, 11 species were referred to *Lulworthia sensu lato* until further taxa are collected and sequenced. Abdel-Wahab et al. (2017) recently introduced a novel genus *Sammeyersia* to accommodate *L. grandispora*, while Azevedo et al. (2017) introduced a novel species, *Lulworthia atlantica*, and *L. fundyensis* was described by Taylor et al. (in Crous et al. 2022).

Sequences available for the genus include 18S, 28S, ITS rDNA and protein-coding sequences for certain species introduced recently. The genus has been subject to multilocus phylogenetic studies but still many genera remain unresolved. Despite the lack of agreement that the lignicolous short-spored collections are *L. fucicola*, and rare collections on brown seaweeds are the same, *Lulworthia* is an accepted genus with *L. fucicola* as the Type species. Currently six species with available sequence data are accepted based on the phylogenetic analyses of 18S and 28S rDNA (Fig. 1) and of 18S, ITS, 28S, TEF1α, TUB2, RPB1, RPB2, MCM7 and mtSSU (Figs. 2–3): *L. atlantica, L. fucicola*, *L. floridana*, *L. fundyensis*, *L. opaca* and *L. norwegica*. *Lulworthia medusa* is kept in *Lulworthia* although the only isolate with 18S and 28S rDNA grouped with *Halazoon* (Fig. 3), until further isolates are available for analysis to confirm its placement. There is still unclear resolution of *L. fucicola* as all isolates included are from wood and two sequences were on a long branch, while recent collections formed a sister group. The multilocus analyses with four *L. fucicola* isolates included an ITS sequence for the isolate GJ589_FCUL and RPB2 sequence for the isolate AFTOL 5014, in addition to 18S and 28S sequences. Here, *L. fucicola* appeared monophyletic, but clearly more sequence data from morphologically identified isolates is needed to verify this. It is worth noting that the isolate AFTOL 5014, which was originally identified as *Zalerion maritima* (=*Lulwoana uniseptata*), was phylogenetically related to and may represent *Lulworthia fucicola*. Two new species are also included: *Lulworthia fundyensis*, collected in Nova Scotia, Canada and *Lulworthia norwegica* (this paper). Further collections and sequences are required to determine if the taxa listed as *Lulworthia sensu lato* belong in the genus (Jones et al. 2015): *L. bulgariae, L. calcicola, L. curalii, L. halima, L. kniepii, L. lindroidea* and *L. longirostris.*

Lulworthia atlantica E. Azevedo, Caeiro & Barata, Mycologia, 109(2): 292 (2017).

Index Fungorum number: IF812640

Etymology – referring to the Atlantic Ocean where the fungus was collected.

Holotype – LISU 254159

Saprobic on *Fagus sylvatica* bait. Sexual morph: *Ascomata* 100–450×35.5–470 µm (n=33); solitary to gregarious, superficial or immersed, dark brown to black, globose or subglobose to cylindrical, coriaceous, ostiolate, with long neck 23.5–945 × 11.5–35.5 µm (n=33). *Peridium* 12.5–

21.5 µm, thick, two layered, the inner layer formed of oblong cells and outer layer of cells of *textura angularis. Asci* 41.5–155×12.5–22.5 µm (n=22), 8-spored, cylindrical, unitunicate, early delisquescing. *Ascospores* 150–270×2.5–5.0 µm (mean and SE = 212±1.9×3.5±0.04 µm, n=236), hyaline, filiform, aseptate, with apical chambers 6–25×2.5–5 µm (mean and SE=14.7±0.4×3.5±0.07 µm, n=268), filled with mucus released through by an apical pore. Asexual morph: Undetermined.

Culture characters – single spore colonies on 50% seawater CMA growing 5 cm diameter after five days at room temperature, green to light brown; velvety, planar, without pigment diffusion into medium; after 1-month incubation chains of chlamydospores globose to subglobose. Immature ascomata were observed after three months of incubation at room temperature, in light or dark condition in different media: cornmeal agar, malt agar, water agar with pieces of *Fagus sylvatica* or in moist chambers with small pieces of *Fagus sylvatica*.

Type material – Portugal, West Coast, Lisbon, Cascais marina (38º40′N, 09º25′W) from *Fagus sylvatica* bait number 090707CF10, submerged 2 meters deep, for seven months (20 December 2006, re-collected 09 July 2007), holotype LISU254159; ex. Type cultures CBS 139632, FCUL 090707CF10.

Other material observed – *Fagus sylvatica* and *Pinus pinaster* baits submerged in Cascais marina (38º40′N, 09º25′W) and Sesimbra marina (38º26′N, 09º06′W), located in the west coast of Portugal (Azevedo et al. 2017).

Distribution – West coast of Portugal.

Notes – This species was described based on phylogenetic analyses (Bayesian and maximum likelihood analyses) comprising sequences of the 18S, 28S, and ITS regions (ITS1+ITS2+5.8S gene) of the nuclear ribosomal cistron, all sequences clustering in a highly supported clade, apart from the other sequences of *Lulworthiales* available in public databases (Azevedo et al. 2017). In our analysis, a highly supported clade group *L. atlantica* with *L. floridana*, *L. fundyensis* is placed in a sister clade (Figs. 1–2).

Lulworthia floridana Meyers Mycologia 49: 515 (1957).

Index Fungorum number: IF299894

Saprobic on woody plants. Sexual morph: Ascomata superficial on the wood, light brown to black, 187–218×173–210 µm, necks short to long 280–720×28–30 µm, paraphyses lacking, asci cylindrical, 8-spored, unitunicate, deliquescing early, ascospores 230–266–320×3.6–4.2–5.7 µm filiform, hyaline, aseptate, with an apical end chamber 7×14 µm. Asexual morph: Undetermined.

Type material **–** In seawater on wood of *Pinus palustris*: Caribbean Sea and Massachusetts

Notes – British measurements are: ascomata 140–280×28–250, necks 28–1960×26–50 µm, ascospores 180–260×3.5 µm and apical-chamber 8–20 µm (Jones 1962). This species occurred on a wide range of substrata: wood, driftwood, wood panels (balsa, *Fagus sylvatica*, *Pinus* spp., *Pseudosuga douglasii*, *P. menzisii*), cellulose tape, manila cordage, rhizomes of *Ruppia maritima*, *Spartina alterniflora*. It grew and sporulated well in culture and used in investigations to determine the degradation of lignocellulose (Meyers & Reynolds 1959a), perithecial development (Meyers & Reynolds 1959b, Meyers 1966), and fungal succession (Jones 1963b). *Lulworthia floridana* was an early colonizer (12-18 weeks) of beech and Scots pine test panels exposed at six test sites in the UK, and the most common after *Halazoon purpurea* (Jones 1963a). On incubated wood, *L. floridana* formed long and branched necks to the perithecia (Jones 1962).

In our phylogenetic analyses, *L. floridana* was placed in the genus *Lulworthia* (*sensu stricto*) together with the Type species of *Lulworthia, L. fucicola*. It was most closely related to *L. atlantica*, both species also clustering with high support, with *L. fundyensis* (Figs. 1–2).

Material examined – Many collections in the UK on test panels submerged in the sea at Langstone harbour (Portsmouth), Plymouth, Southampton and Shoreham harbour (1958–1960) (Jones 1963b). Denmark: Vedbaek, isolates DA12, 13, 15, BIOTEC.

Distribution – A widely distributed species in the Atlantic, Pacific and Indian Oceans (Kohlmeyer & Kohlmeyer 1979).

Lulworthia fucicola G.K. Sutherl., Trans. Br. mycol. Soc. 5(2): 259 (1916) [1915] Figs. 4,5

Index Fungorum number: IF215582

Saprobic on wood, *parasitic* (perthophytic?) on brown seaweeds. Sexual morph: *Ascomata* 440–762×123–155 µm, immersed to superficial, globose, cylindrical, membranous, black, ostiolate. *Paraphyses* absent. *Asci* 90–125×14–20 µm, clavate or fusiform, deliquescent, 8-spored, lacking an apical apparatus. *Ascospores* 65–105×3–5.5 µm, hyaline, with a conical end chamber/appendage 6–9×2 µm, releasing a drop of mucilage when in seawater. Culture characters on cornmeal agar (CMA) made with seawater (50%): single spore colony growing regularly with 30 to 50 mm in diameter after 15 days at room temperature (about 20°C), velvety, grayish green, flat without pigment diffusion into medium, reverse dark green (Fig. 5). Asexual morph: Undetermined.

Material examined – GJ 589_FCUL, on a piece of driftwood, Hayling Island 50°47'01" N, 0°58'07" W, United Kingdom, collected by E.B.G. Jones, 7 February 2019. K(M) 116777 on beech wood test block, Langstone Harbour, Portsmouth, E.B.G. Jones, other fungi present *Halazoon purpurea, Halosphaeria appendiculata, Zalerion maritimum* (*=Lulwoana uniseptata*).

Notes – Initially collected on *Fucus vesiculosus* by Sutherland (1916) but subsequently reported from wood (Kohlmeyer & Kohlmeyer 1979), on drift stems (Figueira & Barata 2007). Not frequently encountered on seaweeds.

Distribution – Canada, Denmark, Germany, Portugal, UK (England, Scotland, Wales), USA (Massachusetts, Washington).

Lulworthia fundyensis V.A. Taylor, S.J. Adams, B.M. Robicheau & A.K. Walker, Fungal Planet 331: 1417 (2022)

Index Fungorum number: IF1465136

Saprobic on wood. Sexual morph: Undetermined. No measurements recorded for ascomata, asci and ascospores in Taylor et al. (2022). Species known from an isolated culture. Asexual morph: *Chlamydospores* formed hyaline chains, globose to subglobose with thick walls, measuring (7.18–) 9.09–14.30 (–18.55) µm length and (6.61–) 8.01–12.42 (–15.18) µm width (av.=11.23×10.27 µm, S.D. 1.98, 1.71, n1=100, n2=100).

Type material – Canada, Nova Scotia, Cumberland County, Edgett's Beach, N45°27'23.7" W64°51'10.7", dried perithecia from culture obtained from direct plating of recently exposed buried intertidal wood onto 50 % seawater CMA, 19 June 2017, S.J. Adams, E. Adams and S. Winters (holotype DAOMC 251940, ex-type culture ACAD21000F; ITS, LSU and SSU nrDNA sequences).

Notes – This species is based on a molecular dataset comprising 18S, 28S and ITS rDNA sequences of the isolated culture ACAD21000F which grouped with *Lulworthia atlantica* with high support (Taylor et al. in Crous et al. 2022). In our analysis, it also grouped with high support in a sister clade comprising *L. atlantica* and *L. floridana* in a well-supported clade (Figs. 1–2).

Lulworthia medusa (Ellis & Everh.) Cribb & J.W. Cribb, Pap. Dept. Bot. (formerly Biol.) Univ. Qd. 3: 80 (1955)

Index Fungorum number: IF299901

Basionym – *Ophiobolus medusa* Ellis & Everh., J. Mycol. 1 (12): 150 (1885)

Synonymy –

Halophiobolus medusa (Ellis & Everh.) Linder, Farlowia 1(3): 419 (1944) [1943-1944]

Linocarpon medusa (Ellis & Everh.) Petr., Sydowia 6(5-6): 388 (1952)

Lulworthia grandispora var. *apiculata* T.W. Johnson, Mycologia 50(2): 159 (1958)

Lulworthia medusa var. *apiculata* (T.W. Johnson) T. Booth, Can. J. Bot. 61(2): 500 (1983)

Lulworthia medusa var. *biscaynia* Meyers, Mycologia 49(4): 516 (1957)

Holotype – Old stems or culms of *Spartina* lying on the beach. Cape May, New Jersey, summer 1984, coll. C. Treat (NY 914502, 927803, 927804, 927806). Isotype – NY 927805

Molecular data available – SSU, LSU rDNA genes

Saprobic on *Spartina* culms and leaves. Sexual morph: *Ascomata* subimmersed or immersed, becoming black, 333–500 µm in diameter, with punctiform, papillate ostiole, short ostiole neck, occasionally up to 1000 µm, *paraphyses* lacking. *Asci* more than 400 µm long, 12–15 µm wide, 8-spored, unitunicate, deliquescing early. *Ascospores* 350–442–526×4.0–4.4–4.8 µm, filiform, hyaline, aseptate, with apical end chambers, 7–8.4 µm, containing mucilage. Asexual morph: Undetermined.

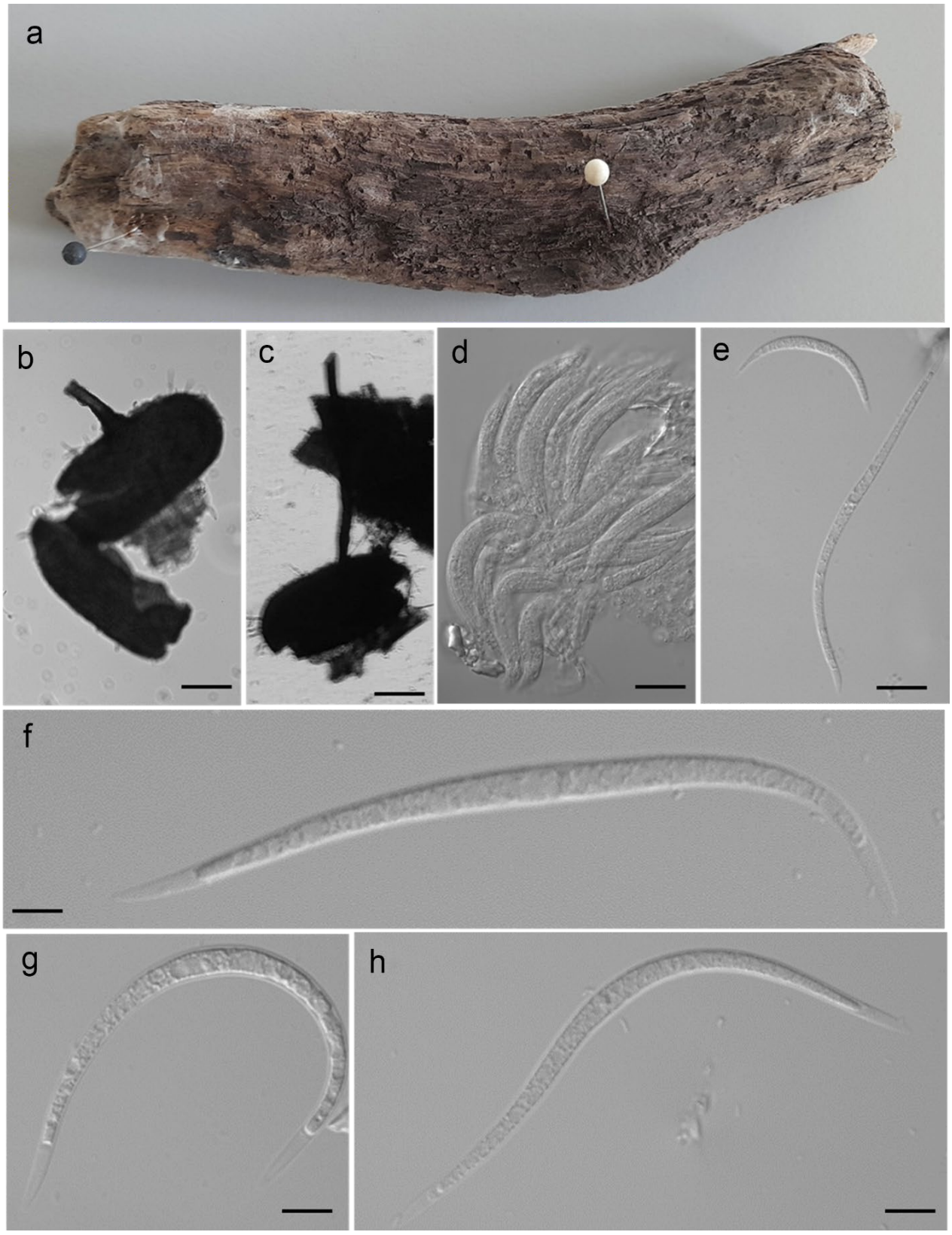

Figure 4 – *Lulworthia fucicola* GJ 589_FCUL. a Driftwood. b–c Ascomata. d. Asci. e–h Filiform ascospores with end chambers. Scale Bar: B–C =30 µm, D–H = 10 µm.

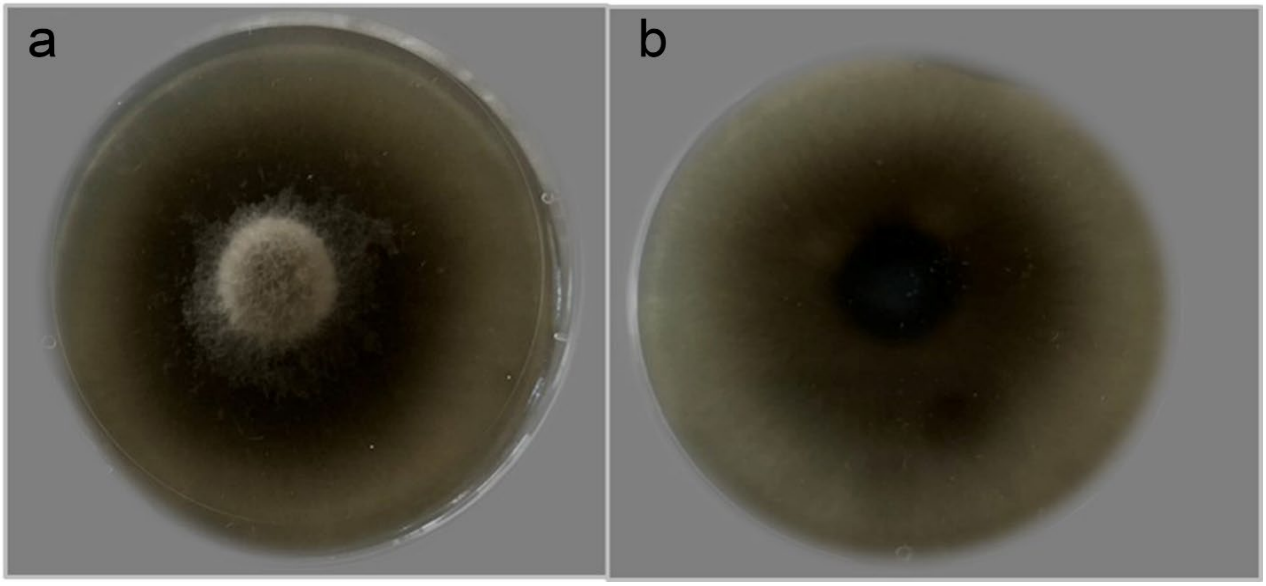

Figure 5 – *Lulworthia fucicola* GJ 589_FCUL. a–b Colonies on cornmeal agar after 15 days at room temperature (obverse and reverse).

Notes – There is only one sequenced isolate of this long-spored *Lulworthia* species without any morphological description published (JK5581, IMS) and there are uncertainties related to the host range of the taxon. Lloyd and Wilson (1962) described the species abundantly fruiting on *Spartina townsendii*, whereas Kohlmeyer and Kohlmeyer (1979) gave *Agropyron pungens*, *Spartina alterniflora*, *S. cynosuroides* and *S. townsendii*, *Zostera marina*, *Tamarix aphylla*, driftwood, intertidal wood and test panels of different tree species as substrates of occurrence. Later examination of the type specimen by Kohlmeyer and Volkmann-Kohlmeyer (1993) concluded in a note attached to the digitalized specimen that the substrate was a leaf, but not necessarily *Spartina* (sweetgum.nybg.org, Kohlmeyer et al. 2000). Kohlmeyer et al. (2000) suggested that the epithet *medusa* should be applied only to *Lulworthia* species matching the morphological description, especially the long ascospores, and occurring on *Spartina*.

Based on our multigene analyses, including protein coding genes and using 18S and 28S sequences from the specimen JK5581 (Fig. 3), *Lulworthia medusa* should be placed in the genus *Halazoon*. However, we refrain to make a new combination until additional isolates with morphology and multiple loci sequenced becomes available to study. *Lulworthia medusa* is nested within the clade containing *Halazoon fuscus*, *H. purpurea* and *H. melhae*. It clusters in a subclade with two non-sporulating isolates from driftwood in Portugal (CMG 54 and CMG 55) that were named *Lulworthia cf. purpurea*, although they seem to be non-conspecific with *H. purpurea* (Gonçalves et al. 2021). *Lulworthia medusa* isolate JK5581 is clearly different from CMG 54 and CMG 55 based on the multigene tree, although the node splitting these two taxa is not supported, likely due to sparse sequence data available for these isolates (Table 2).

Material examined – the digitalized type specimen available at www.sweetgum.nybg.org and taxonomic description provided by Lloyd and Wilson (1962).

Culturing and perithecial development – The species grow and sporulates well in culture with fruiting bodies forming after 6-7 months of incubation on seawater-based agar (Lloyd & Wilson 1962). Ascospores germinate within 48h of discharge. Perithecial development is thoroughly described in Lloyd and Wilson (1962).

Distribution – A widely distributed species in the Atlantic, Pacific and Indian Oceans, Baltic Sea, Mediterranean Sea (Kohlmeyer & Kohlmeyer 1979).

Lulworthia norwegica Rämä & Hagestad, sp. nov. Fig. 6

Index Fungorum number: IF900119

Etymology – referring to the geographical origin of this species.

Holotype – Arctic University Museum of Norway (TROM-F26838).

Saprobic on submerged wood. Sexual morph: *Ascomata* gregarious, superficial – embedded in the substrate, brown-blackish with thin melanized walls, carbonaceous, easily rupturing, ellipsoid to ovoid, often asymmetric and pointed at the ostiolated end, 270–362 (median) –444 µm long (without ostiole neck), 106–138–176 µm wide with the long axis parallel to wood fiber orientation, ostiolate. Ascoma wall 2-layered, 11–27 µm thick, inner melanized layer 6–15 µm consisting of 2-3 layers of flattened prismatic cells, outer layer 5–14 µm and consisting of interlaced hyaline hyphae that form a loose hairy covering surrounding the whole ascoma. No paraphyses or catenophyses. Necks cylindrical, slightly flattened, brown, paler than rest of the ascoma, especially in the apical part, 150 to 770 µm long, 29–33 µm in diam. in upper part, 25–43 µm in basal part, inner diam. 10–18 µm in basal part. Lacking bladder-like cells. *Asci* 8-spored, cylindrical with pointed ends, thin-walled, early deliquescing, without an apical apparatus 120–135 µm× 10–16 µm. *Ascospores* 90–149 (median) –187 µm×3.4–4.6–5.7 µm, hyaline, filiform, curved–twisted, tapering towards both ends, aseptate, with an apical cone-shaped end-chamber, 5.2–7.2–10.4 µm in length, filled with mucus. Ascospore tips swell before germination. Asexual morph: Undetermined.

Type material – Norway, Arctic Ocean, White Island (station M16HEL1360), 80.08007713 N 31.20546539 E, a piece of timber floating in the ocean (*Pinus* sp., diameter 26 cm, length 3.5 meters, decay class 2 at scale from 1 to 5), leg. Teppo Rämä 9.8.2016, M16HELTRa3202 (axenic culture isolates M16HELTRa3202II and M16HELTRa3202IV established from a spore suspension of the specimen). The type materials are preserved in the collections of the Arctic University Museum of Norway (TROM-F26838).

Other material examined – Norway, Arctic Ocean, Svalbard, Spitsbergen, Sassenfjorden (station M11HEL0142), 78.3575000 N 16.4466667 E, a piece of wooden board (diameter 1 cm, length 10 cm, decay class 4 at scale of 1 to 5, where 5 is most decayed) trawled from sea bottom at a depth of 74 m with an Agassiz trawl, leg. Teppo Rämä 30.9.2011, TRä3123A (axenic culture isolate 3123AIV established from a spore suspension of the specimen); TROM-F26836. Norway, Arctic Ocean, Svalbard, Hinlopenrenna (station M11HEL0159); 80.2894444 N 16.1200000 E, a piece of unidentified timber (diameter 19 cm, length 1.4 m, decay class 2 at scale of 1 to 5) trawled from sea bottom at a depth of 295 m with an Agassiz trawl, together with *Remispora stellata, Ceriosporopsis halima* and *Nais inornata*. leg. Teppo Rämä 4.10.2011, TRä3129C (axenic culture isolate 3129CIV1.2 established from a spore suspension of the specimen) =TROM-F26839.

Notes – *Lulworthia norwegica* has a long ostiole neck, like *L. opaca* and shows a resemblance to this species in cell wall thickness and structure. Ascoma and ascospore sizes are overlapping between these two species. Ascoma of *L. norwegica* are longer and narrower than *L. opaca* that are 198–264 µm long and 148–214 µm wide. Spore length is similar with *L. opaca* having in general longer and thinner spores (155–200×3–4 µm, Campbell et al. 2005, Koch et al. 2007). *Lulworthia norwegica* is found fruiting in truly Arctic waters, whereas *L. opaca* is a temperate water species.

Lulworthia norwegica is found on submerged wood at the sea-bottom or driftwood in the Arctic (but a culture isolate, 020cIV1.1, was isolated from temperate waters in mainland Norway (Tromsø, Skarsfjord from 50 cm below sub-tidal line). The habitat of *L. norwegica*, long ostiole neck (Fig. 6) and ascomata deeply submerged in the wood, suggests that the fungus can grow in wood in anoxic sediments.

Phylogenetically, based on nuclear rRNA sequences of 18S and 28S genes, ITS region (including 5.8S gene) and protein coding genes (TEF1α, RPB1, RPB2 and MCM7) *Lulworthia norwegica* is placed in the genus *Lulworthia* (*sensu stricto*) together with the type species of *Lulworthia, L. fucicola*. It is a distinct species and most closely related to *Lulworthia opaca* that forms a sister taxon to *L. norwegica*.

Lulworthia opaca (Linder) Cribb & J.W. Cribb, Pap. Dept. Bot. (formerly Biol.) Univ. Qd. 3: 79 (1955)

Basionym – *Halophiobolus opacus* Linder, Farlowia 1(3): 417 (1944)

Index Fungorum number: IF299902

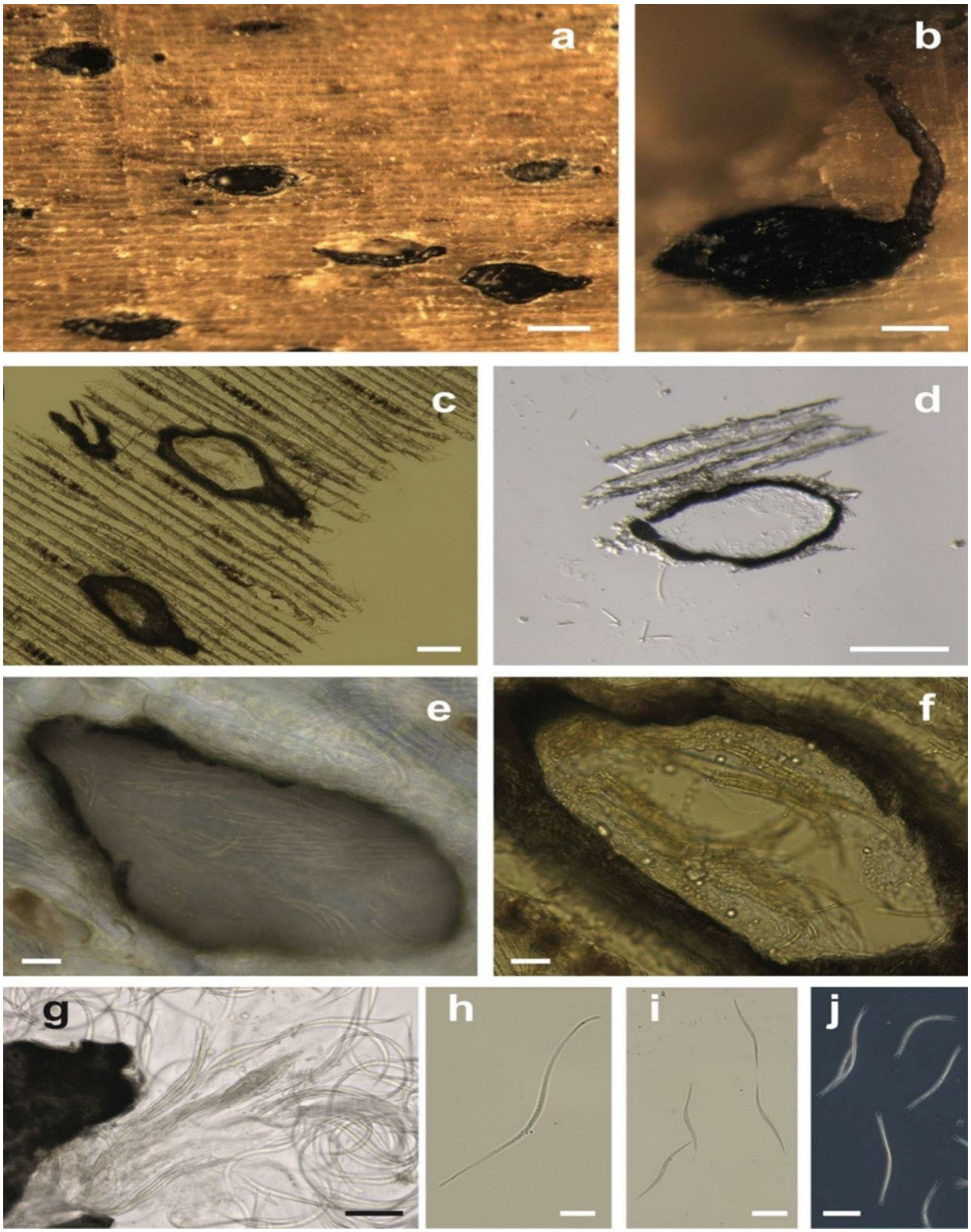

Figure 6 – *Lulworthia norwegica* (holotype TROM-F26838). a Horizontal section of wood revealing ascomata of different shapes. b A single ascoma in wood. c Two ascomata parallel to the long axis of wood cells showing the general appearance and location of ostioles at the other end of ascomata, in Lugol's solution. d A section along the long axis of an ascoma showing the

pseudoparenchymatic tissue inside. e A longitudinal section of an ascoma showing the melanized cell wall layer and the outer layer with interlaced hyphae. f A longitudinal section showing ascoma contents with asci, germinating spores with swollen tips and structure of the cell wall, in Lugol´s solution. g Deliquescing asci and spores bursting out from a ruptured ascoma. h–j Ascospores. (j phase contrast). Scale bars: a = 500 µm, b–d = 100 µm, e–h = 20 µm, i–j = 50 µm.

Saprobic on wood. Sexual morph: *Ascomata* 198–264×148–214 µm, superficial or immersed, subglobose to ovoid or, when immersed in the substratum frequently cylindric–ellipsoid, black, ostiolate. Ostiole neck cylindrical or somewhat tapering, elongate ostiole arising from one end of the ascoma, neck up to 300×28–33 µm. Walls of the perithecium 11.5–16.5– (21.5) µm thick, the inner layer composed of thin-walled subhyaline to light fuscous cells, the middle layer thick, pseudoparenchymatous and deep fuscous to black and opaque, the outer layer of rather closely interlaced and somewhat bullate hyphae which give rise to more slender dark hyphae that either ramify in the substratum or form a loose hairy covering. *Paraphyses* absent. *Asci* cylindric–clavate and curved when young, deliquescent, 8-spored, lacking an apical apparatus. *Ascospores* 155–200×3–4 µm, hyaline, aseptate and multivacuolated until germination when they become 4–7 septate, with conoid end chambers that are 7.5–8.5 µm long. Asexual morph: *Saprobic* on wood and on artificial medium, producing chains of cells on artificial medium that may attain the length of 350–400 µm, the individual cells reaching a length of (11.5–)16.5–21.5 µm×(8–)13–16.5 µm with the central cells larger than the terminal. Occasionally the chains of cells are furcated at the base, rarely branched above, cells first hyaline, become brownish with age. These chains of cells have their counterpart as intercalary chains of varying length and in the natural substratum as single bladder-like cells or as short chains of two to five cells which are usually globose but when their diameter reaches the limit of size set by the diameter of the lumen of the tracheids, become elongate and ellipsoidal (after Barghoorn & Linder 1944, Cribb & Cribb 1955, Campbell et al. 2005, Koch et al. 2007).

Original description by Barghoorn and Linder (1944) of the type specimen collected in Massachusetts, Provincetown, on piling two feet above low tide level, July 24, 1942, E.S. Barghoorn. Additional comments to the morphology have been made by Meyers (1957) and Johnson (1958) who considered *L. opaca* and *L. longirostris* as synonyms of *L. salina.*

Notes – *Lulworthia opaca* is a temperate water species that has morphological resemblance to *Rostrupiella danica* and *Lulworthia medusa*. The type specimen was studied by Campbell et al. (2005), and Koch et al. (2007). It contains no measurable asci. Contrary to the original description and Campbell et al. (2005), there were no bladder cells found in the wood as examined by Koch et al. (2007) who described *R. danica* based on *L. opaca*-like material from Denmark. Another species occasionally treated together with *L. opaca* is *L. medusa* (Tibell 2016). However, in Campbell et al. (2005), *L. opaca* and *L. medusa* were treated as separate species, and both were sequenced: *L. medusa* was represented by JK5881 specimen and *L. opaca* by the culture CBS 21860. The culture was established from a collection made in Washington State and called *Lulworthia* cf. *opaca*, whereas the type specimen of *L. opaca* was collected in Massachusetts on piling two feet above low tide level in 1942 (Barghoorn & Linder 1944). The morphology of these isolates was in agreement, except that the type specimen had chlamydospores, whereas they were lacking in the Washington isolate (Campbell et al. 2005). We treat *L. opaca* and *L. medusa* as separate species in this study. They clearly group in different clades with *L. medusa* being associated with *Halazoon purpurea* and the isolates CMG54 and CMG55 separated from *Lulworthia sensu stricto,* while *L. opaca* (isolate CBS 21860) grouped in *Lulworthia sensu stricto* as a sister to *L. norwegica* described in this paper.

Distribution and substrates – Denmark, Sweden, UK (England, Scotland, Wales), USA (Massachusetts, North Carolina, Washington). Kohlmeyer and Kohlmeyer (1979) lists the name *L. opaca* additionally being reported from Canada, Germany, USA (California (Salton Sea), Florida, Texas, Virginia) and being associated with intertidal wood and rope, driftwood and test panels, litter of two grass (Poaceae) species, *Laminaria saccharina* and sediment.

Cumulospora I. Schmidt, Mycotaxon 24: 420 (1985)

Index Fungorum number: IF25713

Saprobic on submerged marine substrates. Sexual morph: *Ascomata* superficial, membranous to coriaceous, light-brown to orange-brown in colour. *Peridium* two-layered, outer layer orange-brown, inner layer hyaline to yellow-brown. *Paraphyses* absent. *Asci* 8-spored, fusiform, unitunicate, thin-walled, early deliquescing. *Ascospores* filamentous, curved, hyaline, tapering at each end into an elongate, conical process or apical chamber. Asexual morph: *Hyphae* septate, branched, light-brown, superficial or immersed. *Conidiophores* present or obsolete, micronematous. *Conidiogenesis* is holoblastic. *Conidia* terminal or lateral, consist of mass of cells, gray to brown, outer cells are larger than internal conidial cells.

Notes – Schmidt (1974) introduced the genus *Vesicularia*, a name already occupied and therefore proposed *Cumulospora* (Schmidt 1985) for collections made on submerged stems of *Phragmites australis*, in the Baltic Sea, Germany. Subsequently, Abdullah et al. (1989) described the same taxon as *Basramyces*, also from *Phr. australis* collected from southern marshes of Iraq and was synonymized under *Cumulospora* (Abdel-Wahab et al. 2010). In this monograph we describe and illustrate the sexual morph of the species.

No sequences are available for the type species. A molecular study based on 18S and 28S rDNA placed two isolates from Egypt and Thailand (MF46 and GR53, respectively) in a well-supported clade with *Lindra* species (Abdel-Wahab et al. 2010).

Type species – *Cumulospora marina* I. Schmidt

Cumulospora marina I. Schmidt, Mycotaxon 24: 421 (1985) Figs. 7–8

Basionym – *Vesicularia marina* I. Schmidt, Natur. Naturschutz Mecklenberg 12:117,1974.

Synonym – *Basramyces marinus* Abullah, Abdulkadder and Goos, Intern. J. Mycol. and Lichenol. 4:181–186, 1989.

Index Fungorum number: IF104154

Saprobic on submerged decaying mangrove wood in the intertidal zone. Sexual morph: *Ascomata* 160–205 µm in diameter, superficial, membranous to coriaceous, light-brown to orange-brown in colour. *Peridium* 28–32 µm thick, two-layered, outer layer 11–15 µm, orange-brown, consists of 3–4 layers of polygonal melanized cells, inner layer 16–20 µm, hyaline to yellow-brown, consists of 4–6 layers of polygonal, flattened, thick-walled cells. *Paraphyses* absent. *Asci* 225–240×15–17 µm, 8-spored, fusiform, unitunicate, thin-walled, early deliquescing. *Ascospores* 320–385×4–5 µm (=340×4.2 µm, n=50), filamentous, curved, hyaline, tapering at each end into an elongate, conical process or apical chamber (5–7×2.5–3 µm). Asexual morph: *Hyphae* 1.8–3 µm, immersed to superficial, branched, septate, light-brown. *Conidiophores* micronematous, light-brown, unbranched. *Conidiogenous cells* holoblastic. *Conidia* 33–67 µm in diam., scattered or gregarious, superficial, globose to subglobose, brown to dark-brown, composed of spherical compact cells, ranging from 3 to 15 cells per conidium. *Apical cells* 15–24 µm in diam., dark-brown. *Basal cells* 3–10 µm in diam., light-brown in colour.

Material examined – Saudi Arabia, Red Sea, El-Leith mangroves, 100 km north of Al-Leith City near Al-Qattan Resort, intertidal wood of *Avicennia marina*, 7 April 2015, M.A. Abdel-Wahab (SUMCC H-11020, holotype).

Notes – Phylogenetic analyses of the combined 18S and 28S rDNA placed the sequence of the lulworthia-like taxon with the two isolates of *Cumulospora marina* (isolates: MF46, GR53) in a well-supported clade, sister of the *Lindriella* gen. nov. clade. *Cumulospora marina* has been variously collected from temperate to tropical locations (Schmidt 1974, Abdullah et al. 1989, Abdel-Wahab et al. 2010). Chatmala et al. (2004) recorded a sheath-like structure around the conidia. This is the first record for a sexual morph for the genus *Cumulospora*.

Distribution – Germany, Iraq, Saudi Arabia.

Halazoon Abdel-Aziz, Abdel-Wahab & Nagah., in Abdel-Wahab, K.L. Pang, Nagahama, Abdel-Aziz & E.B.G. Jones, Mycol. Progr. 9: 545 (2010)

Index Fungorum number: IF543113

Saprobic on driftwood in the intertidal zone in marine habitats. Sexual morph: *Ascomata* elongate cylindrical, centric or eccentric, rarely globose, immersed, becoming superficial, membranous, thin-walled, pale brown, becoming purple-brown, ostiolate. *Neck* long. *Peridium* thin-walled, membranous, narrow, comprising 2–3 layers of cells. *Paraphyses* lacking. *Asci* clavate, early deliquescing. *Ascospores* filiform, one-celled, hyaline, with conical polar end chambers at each end (appendages) containing mucilage. Asexual morph: *Conidiophores* present or obsolete, micronematous, hyaline to yellow-brown in colour, cylindrical, septate. *Conidiogenesis* monoblastic or holoblastic. *Conidia* terminal or lateral, forming single coil or branched to form two to three coils, coiled in two or three dimensions, semi-contorted to several coils; conidial cells increase in size and pigmentation from base to apex.

Notes – Initially an asexual genus of *Lulworthiaceae* that was established by Abdel-Wahab et al. (2010) with the type species, *H. melhae.* Molecular study based on 18S and 28S rDNA placed *H. melhae* along with *Cirrenalia fusca* in a well-supported clade within *Lulworthiaceae* with *Halazoon purpurea* (=*Lulworthia* c.f. *purpurea*) (Fig. 1).

Type species – *Halazoon melhae* Abdel-Aziz, Abdel-Wahab & Nagah.

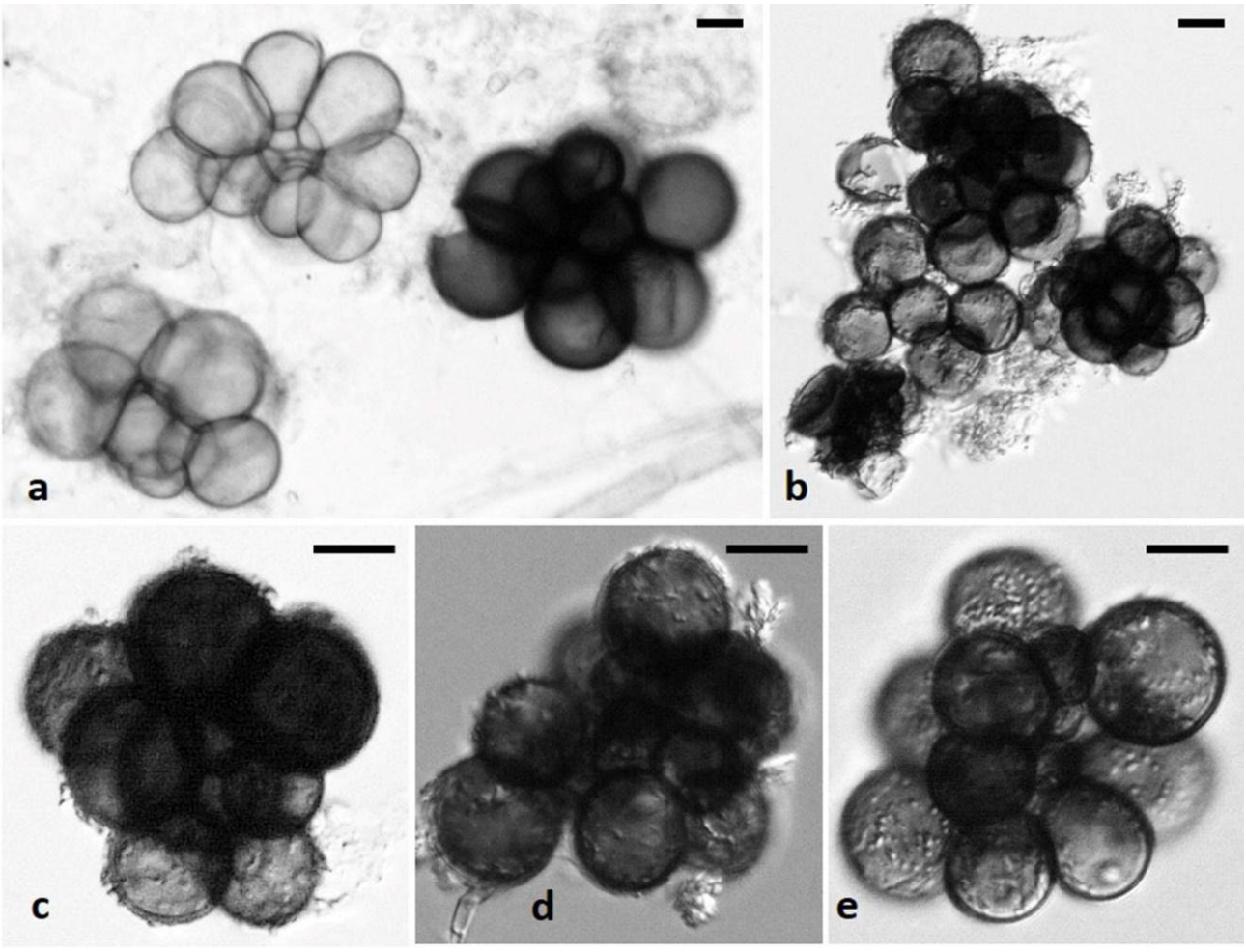

Figure 7 – *Cumulospora marina* (asexual morph). a–e Variously shaped conidia at different stages of maturity. Scale bars: a–e = 10 μm.

Halazoon fuscus (I. Schmidt) Abdel-Wahab, K.L. Pang, Nagah., Abdel-Aziz & E.B.G. Jones, Mycol. Progr. 9 (4): 547 (2010) Fig. 9

Index Fungorum number: IF543114

Saprobic on submerged marine substrates. Sexual morph: Undetermined. Asexual morph: *Hyphae* 2.5–3.5 μm in diameter, septate, ramose, superficial or immersed in the substrate, yellow or

brown. *Conidiophores* up to 23 µm long, ca. 2 µm in diameter, cylindrical, one- or two-septate, simple, sometimes obsolete, yellow or brown. *Conidiogenous cells* monoblastic, integrated, terminal, determinate. *Conidia* acrogenous, solitary, regularly or irregularly helicoid, conidia semicontorted to 1.5 times contorted, 2–4 septate, constricted at the septa, brown to dark-brown (never reddish); cells increasing in diameter and pigmentation from base to apex, distinctly dissimilar; spirals 20–36 µm high, 20–30 µm in diameter; terminal cell 13–33 µm high, 11–22.5 µm in diameter, reniform or ellipsoidal, fuscous; basal cells obtusely conical; central cells irregularly ellipsoidal or subglobose.

Material examined – Japan, Sarushima Island, on decaying driftwood, 28 April 2008, M.A. Abdel-Wahab, NBRC 105256.

Notes – Phylogenetic analyses based on 18S and 28S rDNA placed *Halazoon fuscus* within *Lulworthiaceae* in a sister clade to *Halazoon melhae* and *H. purpurea* (Fig. 1). *Halazoon melhae* and *Halazoon fuscus* share some morphological features, especially initial conidial development. However, it does not form the ball of coiled cells as in *H. melhae.* The apical cell in *H. fuscus* resembles that of *Cirrenalia* (=*Hydea*) *pygmea* but lacks the dark pigmentation of the latter.

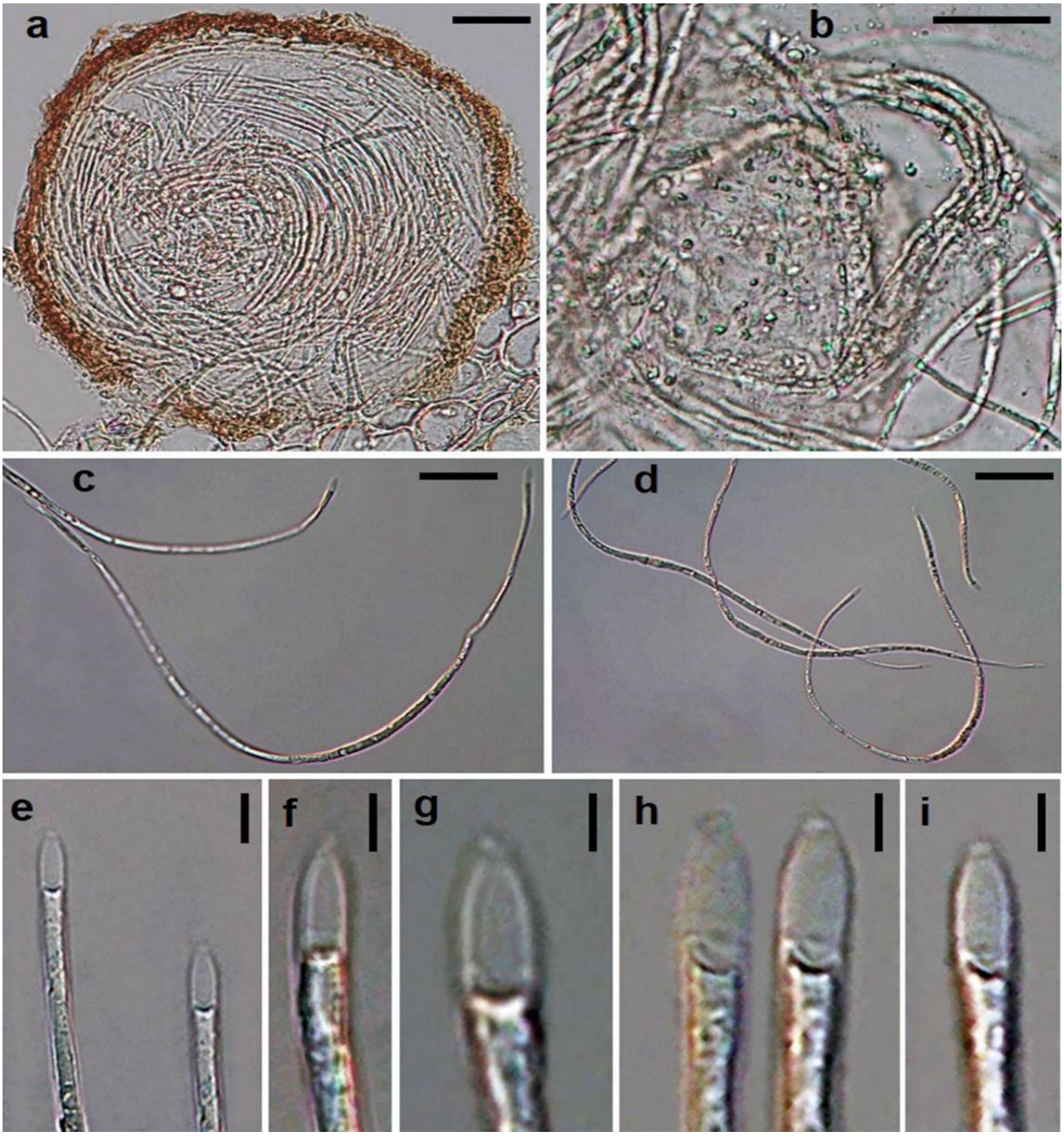

Figure 8 – *Cumulospora marina* (sexual morph). a Vertical section of the ascoma. b Deliquesced asci. c–d Variously shaped ascospores. e–i Apical chambers. Scale bars: a–d = 40 µm, e = 10 µm, f – i = 5 µm.

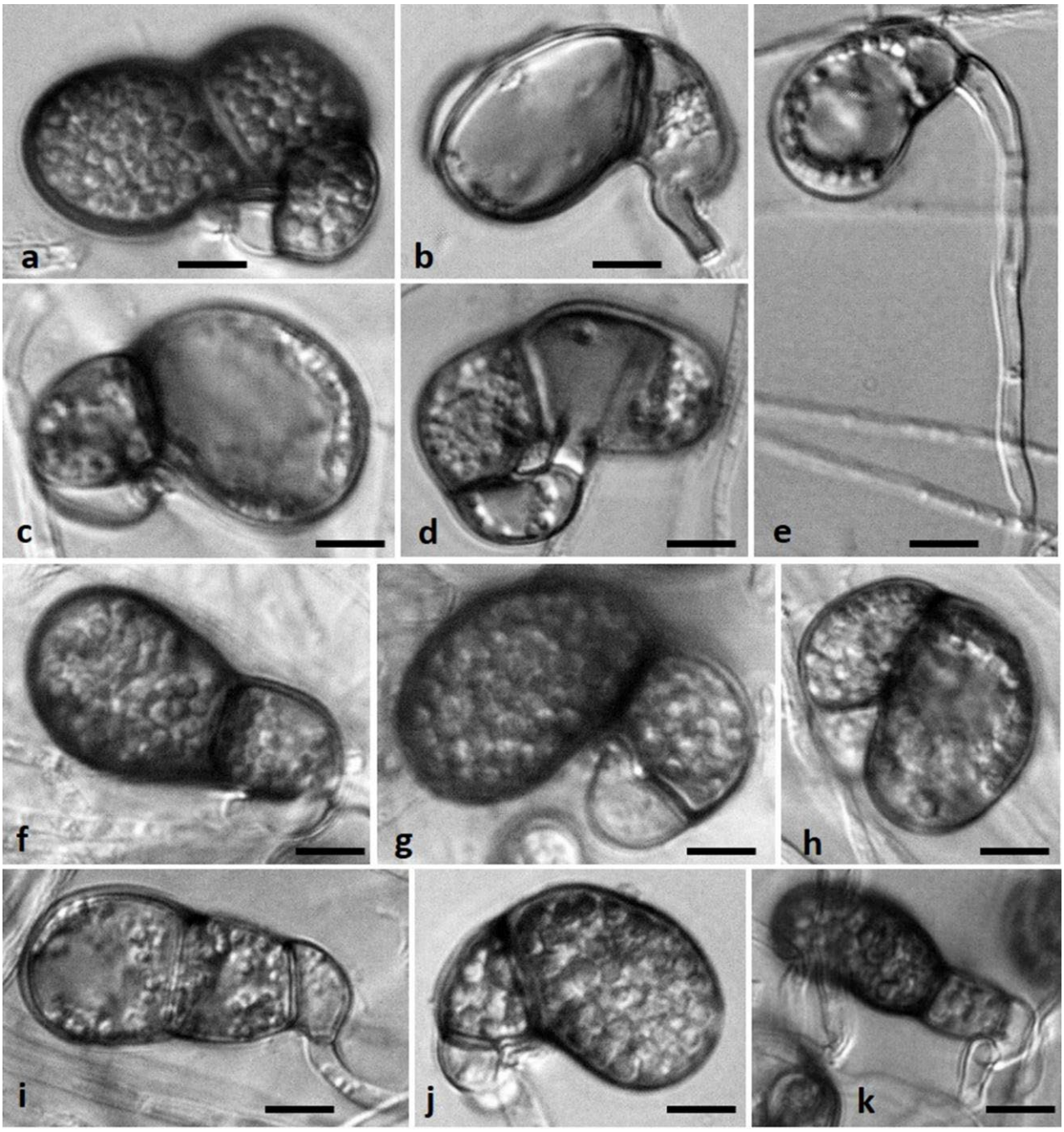

Figure 9 – *Halazoon fuscus*. a–k Variously shaped mature conidia. Scale bars = 10 µm.

Halazoon melhae Abdel-Aziz, Abdel-Wahab & Nagah., in Abdel-Wahab, K.L. Pang, Nagahama, Abdel-Aziz & E.B.G. Jones, Mycol. Progr. 9: 546 (2010)

Synonymy – *Cirrenalia fusca* I. Schmidt, Mycotaxon 24: 419 (1985)

Index Fungorum number: IF543114

Saprobic on decaying drift stems of *Phragmites australis.* Sexual morph: Undetermined. Asexual morph: *Hyphae* 2.5–4 µm in diameter, septate, branched, hyaline. *Conidiophores* present or obsolete, when present are 30–50 µm long, 3–5 µm in diameter, micronematous, 0–3 septate, hyaline, cylindrical. *Conidiogenesis* holoblastic. *Conidia* 35–125×23–58 µm ($\bar{x}$=69×38.1 µm,

n=20), terminal or lateral, forming single coil or branched to form two to three coils, coiled in two or three dimensions, semi-contorted to 6 coils, conidial filament 7–15 µm in diameter, 6- to 26-septate, constricted at the septa, reddish brown in colour, conidial filament diameter and pigmentation generally increase from base to apex. *Apical* cell 8–38×5–15 µm, subglobose, curved to reniform in shape with truncate base, reddish brown; median cells 10–25×5–11 µm, clavate, cylindrical, subglobose, curved or helicoid, yellow-brown to brown.

Material examined – Egypt, Port Said, Mediterranean Sea coast, 31°30′N, 32°22′E, on decaying drift stems of *Phragmites australis* June 2006, M.A. Abdel-Wahab and F. A. Abdel-Aziz, IMI 397964, holotype.

Notes – *Halazoon melhae* is different from the closely similar asexual stage of *Lulwoana uniseptata* (=*Zalerion maritimum*) in having larger conidia (35–125×23–58 µm vs. 14–35 µm for *H. melhae* and *L. uniseptata*, respectively), more coils (1/2–6 coils vs. 1–3 coils in *H. melhae* and *L. uniseptata,* respectively) and reddish brown in the former and dark-brown to black in the latter. Conidial cells in *H. melhae* increase in size and pigmentation from base to apex but in *L. uniseptata* all cells are dark-brown to fuscous and the same width. The conspecificity of the *Lulwoana uniseptata* teleomorph and anamorph stage is confirmed by culture studies and rDNA sequences (Nakagiri 1984, Campbell et al. 2005).

Distribution – Egypt.

Halazoon purpurea (I.M. Wilson) Dayar., K.L. Pang, E. Azevedo, M.F. Caeiro, Hagestad, Rämä & E.B.G. Jones, comb. nov. Fig. 10

Basionym – *Halophiobolus purpureus* I.M. Wilson 1956

Synonym – *Lulworthia purpurea* (I.M. Wilson) T.W. Johnson, Mycologia 50(2): 154 (1958)

Index Fungorum number: IF299903

Saprobic on drift and trapped wood, wood panels, rope, polyurethane panels. Sexual morph: *Ascomata* 126–339×98–224 µm, elongate, cylindrical, centric or eccentric, rarely globose, immersed, becoming superficial, membranous, thin-walled, pale brown, becoming purple, ostiolate. *Neck* long, curved, up to 628 µm long, 15–27 µm wide. *Peridium* thin-walled, membranous, narrow, comprising 2–3 layers of cells, 8–12– (20) µm, inner two layers hyaline, flattened, outer layer of cells flattened with purple-brown pigment. *Paraphyses* lacking. *Asci* elongated, clavate, 8-spored, deliquescing. *Ascospores* 190–257(–292) ×3–4 µm, filiform, one-celled, hyaline, with conical polar end chambers at each end (appendages) 10–16– (26) µm, containing mucilage which is released as a drop, attaching ascospores to surfaces. Asexual morph: Undetermined.

Material examined – United Kingdom, IMI 68135, on wood, Aberystwyth: type material at Kew. Also, many collections on submerged wood in Langstone harbour, Portsmouth, UK, and deposited at Kew: IMI 16586 (slide), IMI 81688, IMI 81691, IMI 81690.

Notes – Johnson (1958) transferred all *Halophiobolus* species introduced by Barghoorn and Linder (1944) to *Lulworthia*, an earlier name proposed by Sutherland (1916), and this also included *Halophiobolus purpureus* described by Wilson (1956) on material collected on wood and rope at Aberystwyth (Wales). No sequences of the type material exist, but many 28S rDNA sequences are listed in Table 2 from multiple sources. In our phylogenetic analysis of the genus *Lulworthia, L. purpurea* is distantly placed from the type species *Lulworthia fucicola* but is congeneric with *Halazoon melhae* (Fig. 1). A new combination is therefore proposed for *Lulworthia purpurea* as *Halazoon purpurea*. It is an early colonizer of submerged wood, and this confirmed by Jones (1963b) when it was found to colonize *Fagus sylvatica* test blocks within 18 weeks of submergence. *Pinus sylvestris* test blocks were colonized after 24-week submergence in Langstone harbour, Portsmouth. This fungus was recorded on a *Fagus sylvatica* bait within 10 weeks of submergence in Cascais marina, Portugal (Azevedo et al. 2017). This is a common ascomycete on submerged test blocks, present at the six test sites around the UK (Jones 1963b). However, it was not recovered from test blocks submerged at three rafts in Yealm Estuary, Newton Ferrers, Devon (Byrne & Jones 1974). Likewise, it was not found on driftwood associated with sand from Danish sand dunes (Rees et al. 1979).

Halazoon purpurea grew well in culture and sporulates on 0.1% yeasts extract seawater agar with added wood. It also causes severe soft rot decay of wood with high weight loss. In culture ascomata with 2–5 necks were quite common (Jones 1963a)

Distribution – Australia, France, India, Ivory Coast, New Zealand, Norway, Malaysia, Portugal, South Africa, South Yemen, UK (England, Scotland, Wales), USA (North Carolina).

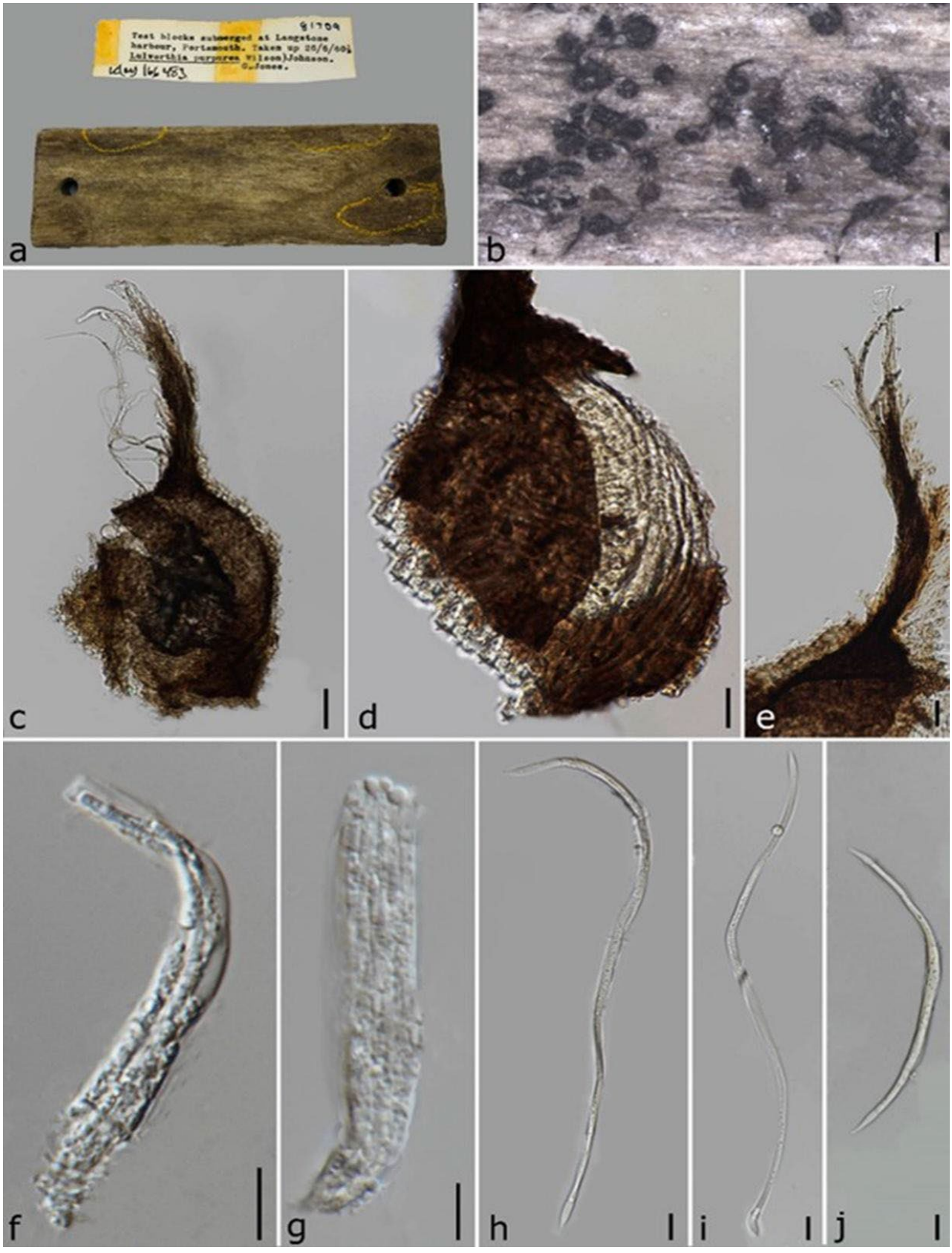

Figure 10 – *Halazoon purpurea* comb. nov. (IMI 68135) a Herbarium material. b Appearance of ascomata on host substrate. c Perithecium. d Section through perithecium. e Neck. f–g Asci. h–j Ascospores with appendages. Scale bars: b = 50 µm, c–d = 4 µm, e = 20 µm, f–j = 10 µm.

Haloguignardia Cribb & J.W. Cribb, Pap. Dept. Bot. (formerly Biol.) Univ. Qd. 3: 97 (1956)

Index Fungorum number: IF2205

Parasitic forming galls on marine algae (Phaeophyta). Sexual morph: *Ascomata* perithecial, subglobose or ellipsoidal, immersed in gall tissue, ostiolate, short papillate, coriaceous, hyaline, periphysate. *Paraphyses* absent. *Asci* 8-spored ellipsoidal, clavate or cylindrical, unitunicate, thin-walled early deliquescing. *Ascospores* ellipsoidal to fusiform, aseptate, hyaline, conical end, chambered or with a mucilaginous appendage. Asexual morph: *Spermogonia* on separate algal galls, ostiolate, periphysate, short papillate, spermatia ellipsoidal, aseptate, hyaline.

Notes – *Haloguignardia* was introduced by Cribb and Cribb (1956), from marine algae with members of the genus collected exclusively from the marine environment (Cribb & Cribb 1956, Alongi et al. 1999). The genus resembles *Guignardia* but differs in forming distinct galls on marine brown algae of the order Fucales, by the early deliquescent asci, and by the unique spore apices which are hyaline, acute, and deciduous or non-deciduous, and into each of which there projects a small peg-like projection from the main body of the spore (Cribb & Cribb 1956, Alongi et al. 1999). Two species previously referred to the genus, *Guignardia irritans* and *G. tumefaciens*, were transferred to *Haloguignardia* by Cribb and Cribb (1956). This genus comprises six species namely, *H. cystoseirae*, *H. decidua*, *H. irritans*, *H. longispora, H. oceanica* and *H. tumefaciens*. Inderbitzin et al. (2004) showed that the genera *Spathulospora* and *Haloguignardia* had affinities within the *Lulworthiales*.

Sequence data are only available for *H. irritans*. *Haloguignardia* species need to be recollected, isolated and sequenced to better understand their phylogenetic relationships. Currently, only an 18S sequence is available for this species which grouped within the clade of *Paralulworthia*. Therefore, a wider range of genes may resolve its taxonomical placement.

Ultrastructural studies of the apical chambers/appendages are required to compare with those of *Lulworthia* species to better understand the release of mucilage from the appendages and their function (Jones 1994, Yusoff et al. 1995). Kohlmeyer and Kohlmeyer (1979) illustrated the ascospore of *Haloguignardia oceanica* with a pointed end chamber, which was subsequently lost, but it is not clear if this deliquesces or mucilage is released from the end chamber.

Type species – *Haloguignardia decidua* Cribb & J.W. Cribb

Haloguignardia decidua Cribb & J.W. Cribb, Pap. Dept. Bot. (formerly Biol.) Univ. Qd. 3: 97 (1956)

Index Fungorum number: IF298091

Saprobic on brown algae. Sexual morph: *Ascomata* perithecial, embedded in host, 170–420 µm in diam., gregarious, black, globose to subglobose, ostiolate. *Asci* 52–70×20–32.5 µm, 8-spored, unitunicate, cylindrical, deliquescent. *Ascospores* 50–64×6.4–7.5 µm ($\bar{x}$=62×7 µm, n=30), hyaline, elongate ellipsoidal to fusiform, tapering at the apices, aseptate, straight, appendaged. Asexual morph: *Spermogonia* on separate algal galls, ostiolate, periphysate, short papillate, spermatia ellipsoidal, aseptate, hyaline.

Material examined – Australia, Queensland, *Sargassum* sp., 20 Aug. 1953, A. B. Cribb, H.L.B. 937, holotype

Notes – *Haloguignardia decidua* can be found on both “stem” and “leaf” of the host forming irregular galls (Cribb & Cribb 1956). Kohlmeyer and Kohlmeyer (1979) reported *H. decidua* from *Sargassum daemelii* and *Sargassum* sp. from Australia (Queensland, New South Wales). No recent collections are reported, so little is known of its geographical distribution.

Halophilomyces X. Wang, L. Pecoraro & H.B. Liu, J. Fungi 10 (7, no. 474): 10 (2024) **emend. K.L. Pang & E.B.G. Jones**

Index Fungorum number: IF854689

Endophytic in roots of *Halophila ovalis*. Sexual morph: Undetermined. Asexual morph: *Hyphae* septate, hyaline, olivaceous or brown, abundant loop structures. *Chlamydospores* in chains, cells ellipsoidal, brown or olivaceous. *Conidia* pleurogenous, solitary, single-celled or with 1–3 (4) septa, coiled, constricted at the septa, dark olivaceous or brown; conidial cells globose to subglobose, generally increasing in size from base to apex.

Type species – *Halophilomyces hongkongensis* Xiao Wang, L. Pecoraro & H.B. Liu, in Wang, Pecoraro, Chen, Tang, Lee, Chen & Liu, Journal of Fungi 10(7, no. 474): 10 (2024)

Notes – *Halophilomyces* was described as an endophyte of roots of *Halophila ovalis*. The original generic diagnosis of *Halophilomyces* was poorly defined and thus, it was emended in this monograph to include the key morphological characteristics of the genus.

Halophilomyces hongkongensis X. Wang, L. Pecoraro & H.B. Liu, in Wang, Pecoraro, Chen, Tang, Lee, Chen & Liu, Journal of Fungi 10(7, no. 474): 10 (2024)

Index Fungorum number: IF854690

Endophytic in roots of *Halophila ovalis*. Sexual morph: Undetermined. Asexual morph: *Hyphae* 1.9–5.3 µm wide, septate, hyaline, olivaceous or brown, abundant loop structures. *Chlamydospores* in chains, cells ellipsoidal, brown or olivaceous. *Conidia* pleurogenous, solitary, coiled, 24.5–53.8 µm in diameter, 1–3 (4) septa, constricted at the septa, dark olivaceous or brown; conidial cells globose to subglobose, generally increasing in size from base to apex: apical cell 14.1–24.8 µm, basal cell 9.1–21.5 µm. Single-celled conidia (9.5–29 µm) also common.

Material examined – Hong Kong SAR, South China Sea, Lantau Island, intertidal zone, from seagrass *Halophila ovalis* rhizomes, 10 March 2023, X. Wang (HOMAR2, ex-type living culture).

Notes – In the 18S and 28S tree, isolates of *H. hongkongensis* formed a clade and was in a bigger clade comprising two unknown Lulworthiaceae sp., *Halazoon* spp. and *Paralulworthia* spp. while in the ITS tree, they formed a well-supported clade with *Halazoon purpurea* isolates (Wang et al. 2024). Morphologically, *H. hongkongensis* is similar to *Halazoon fusca* and *H. melhae* in having coiled, dark-coloured, multiseptate conidia with cells increased in size towards the end (Abdel-Wahab et al. 2010).

Hydea K.L. Pang & E.B.G. Jones, in Abdel-Wahab et al., Mycol. Progr. 9(4): 549 (2010)

Index Fungorum number: IF2205

Saprobic on wood. *Hyphae* septate, ramose, fuscous. Sexual morph: Undetermined. Asexual morph: *Conidiophores* obsolete. *Conidia* acrogenous, solitary, helicoid, 1/2–1 time contorted, 3-to 4-septate, black or fuscous, not or slightly constricted at the septa, cells increasing in diameter and pigmentation from the base to the apex.

Notes – Abdel-Wahab et al. (2010) introduced *Hydea* to accommodate *Cirrenalia pygmea,* a monotypic genus typified by *Hydea pygmea*. *Hydea* species are characterised by 1/2–1 time contorted, 3-to 4-septate, dark-coloured conidia that are not or slightly constricted at the septa, cells increasing in size and pigmentation from the base to the apex. *Cirrenalia* species are different from *Hydea pygmea* by 1–1.5 times coiled, dark-brown to black conidia that are not constricted at the septa and surrounded by sheath when they are immature (Abdel-Wahab et al. 2010).

Sequence data are available in GenBank only for 18S and 28S rDNA loci of *Hydea pygmea*. Abdel-Wahab et al. (2010) showed that *H. pygmea* formed a basal group to the genera *Lulworthia, Cumulospora, Lindra, Kohlmeyeriella* and *Spathulospora*.

Type species – *Hydea pygmea* (Kohlm.) K.L. Pang & E.B.G. Jones, in Abdel-Wahab et al. (2010)

Hydea mangrovei Devadatha, V.V. Sarma & E.B.G Jones, sp. nov. Fig. 11

Index Fungorum number: IF900121

Etymology – The specific epithet indicates the mangroves on which it thrives

Saprobic on decaying mangrove wood. Hyphae hyaline to light brown, septate, branched. Sexual morph: Undetermined. Asexual morph: *Conidiophores* micronematous, mononematous, resemble non-specialized short lateral vegetative hyphae or conidiophore indistinct, conidia developing directly on hyphae. *Conidia* 10–23×7–10 µm, ($\bar{x}$=15×9 µm, n=20), solitary, thick-walled, smooth, straight, two-celled, rarely three celled strongly constricted at the septa, apical cell large, guttulate, subglobose, ellipsoidal, ovoidal to obpyriform, fuscous, reddish-brown to dark brown, 9–12×8–10 µm, ($\bar{x}$=10×9 µm, n=20), basal cell smaller hyaline to pale brown 3–5×2–5 µm, ($\bar{x}$=4.2×4 µm, n=20), obconical.

Culture characteristics – Colonies on malt extract agar slow growing, reaching 10–20 mm diameter after 15 days of incubation at room temperature, grey to pale brown, reverse grey, velvety, pulvinate, circular.

Material examined – India, Tamil Nadu, Parangipettai mangroves (11.59°N 79.5°E), on decaying wood of *Avicennia marina* (*Acanthaceae*), 23 April 2018, B. Devadatha, AMH-9999, holotype, living culture, NFCCI-4386.

GenBank numbers – ITS=OP908066, LSU=OP908068, SSU=OP908067

Notes – *Hydea mangrovei* is morphologically similar to *Trichocladium alopallonellum* (=*Halosphaeriopsis alopallonellum*) in having conidiophores that are indistinct, conidia developing directly on hyphae and two-celled ellipsoidal, ovoidal to obpyriform, fuscous, reddish-brown conidial apical cell and hyaline, smaller, basal cell (Kohlmeyer & Volkmann-Kohlmeyer 1995). *Trichocladium alopallonellum* is clearly distinct from *Hydea mangrovei* in having two celled conidia and lacks guttules. However, our phylogenetic analysis, based on combined 18S and 28S rDNA, placed our taxon in *Hydea. Hydea mangrovei* nested together with *Hydea pygmea* in a strong monophyletic clade with significant support from ML 100%, MP 100% and 1.00 BYPP. *Hydea mangrovei* produces one dark cell which is completely black, guttulate and a hyaline end cell, and rarely three-celled. Whereas *H. pygmea* has two dark-coloured cells completely black, which are connected by a crook-like shape and hyaline (Abdel-Wahab et al. 2010). Based on the differences found in morphological and molecular sequence data among closely related species we introduce a novel species, *H. mangrovei*, in the genus *Hydea*.

Trichocladium alopallonellum has been widely confused in the literature as shown in Fig. 12 of its conidia and conidiophores. Likewise, Goh and Hyde (1999) in their review of the genus *Trichocladium,* illustrated the great diversity of conidial morphology of its species. A strain of *Humicola* (=*Trichocladium*) *alopallonella* isolated by S. P. Meyers from *Tilia americana* collected in Florida (CBS 207.60) grouped with *Trichocladium achraspora* (= *Halosphaeriopsis mediosetigera* in the *Halosphaeriaceae* (Calabon et al. 2023). In our analyses, *Hydea mangrovei* isolated from decaying mangrove wood is placed in the *Lulworthiales* as a sister taxon to *H. pygmea*.

Hydea pygmea (Kohlm.) K.L. Pang & E.B.G. Jones, in Abdel-Wahab, Pang, Nagahama, Abdel-Aziz & Jones, (2010) Fig. 13

Index Fungorum number: IF298091

Basionym – *Cirrenalia pygmea* Kohlm., Ber. dt. bot. Ges. 79: 35 (1966)

Saprobic on wood. Sexual morph: Undetermined. Asexual morph: *Conidiophores* micronematous. *Conidiogenous cells* integrated, monoblastic, terminal, determinate. *Conidia* solitary, acrogenous, reniform, brown to black, helicoid, contorted 1/2 or one time, 3-septate, not constricted at the septa, fist shaped or reniform, fulgent (upper three cells dark, lower cell light colored); cells increasing in diameter from base to apex, distinctly dissimilar; terminal cell subglobose to reniform, basally flattened, irregularly conical or almost wedge-shaped.

Material examined – Japan, Shiira Riv., Iriomote, *Bruguiera gymnorhiza*, on fallen leaf, July 8 1997, I. Okane, (IFO-H 12229, non-type)

Notes – *Hydea pygmea* is a mangrove wood inhabiting fungus, especially on *Rhizophora* species, growing on the bark, with slow growth in culture but sporulates readily (Abdel-Wahab et al. 2010). The fungus differs from all other cirrenalia-like species by the dark-brown to black

hooked nature of the conidia that are internally proliferate (Kohlmeyer & Kohlmeyer 1979, Abdel-Wahab et al. 2010). *Hydea pygmea* has been widely reported from the tropics, usually from mangrove habitats, including Andaman Islands, Australia, Brazil, Brunei, Cuba, India, Liberia, Malaysia, Maldives, Mexico, Philippines, Sierra Leone, Sumatra, Thailand, Trinidad (Devadatha et al. 2021), on many substrates, wood, dead roots, bark of *Avicennia alba, A. lanata, A. marina, Bruguiera cylindrica, B. gymnorhiza, Kandelia candel, K. obovata, Mangifera indica, Nypa fruticans, Rhizophora apiculata, Rh. mangle, Rh. mucronata, Rh. racemosa, Sonneratia alba, S. griffithii, Xylocarpus granatum*, and non-mangrove wood.

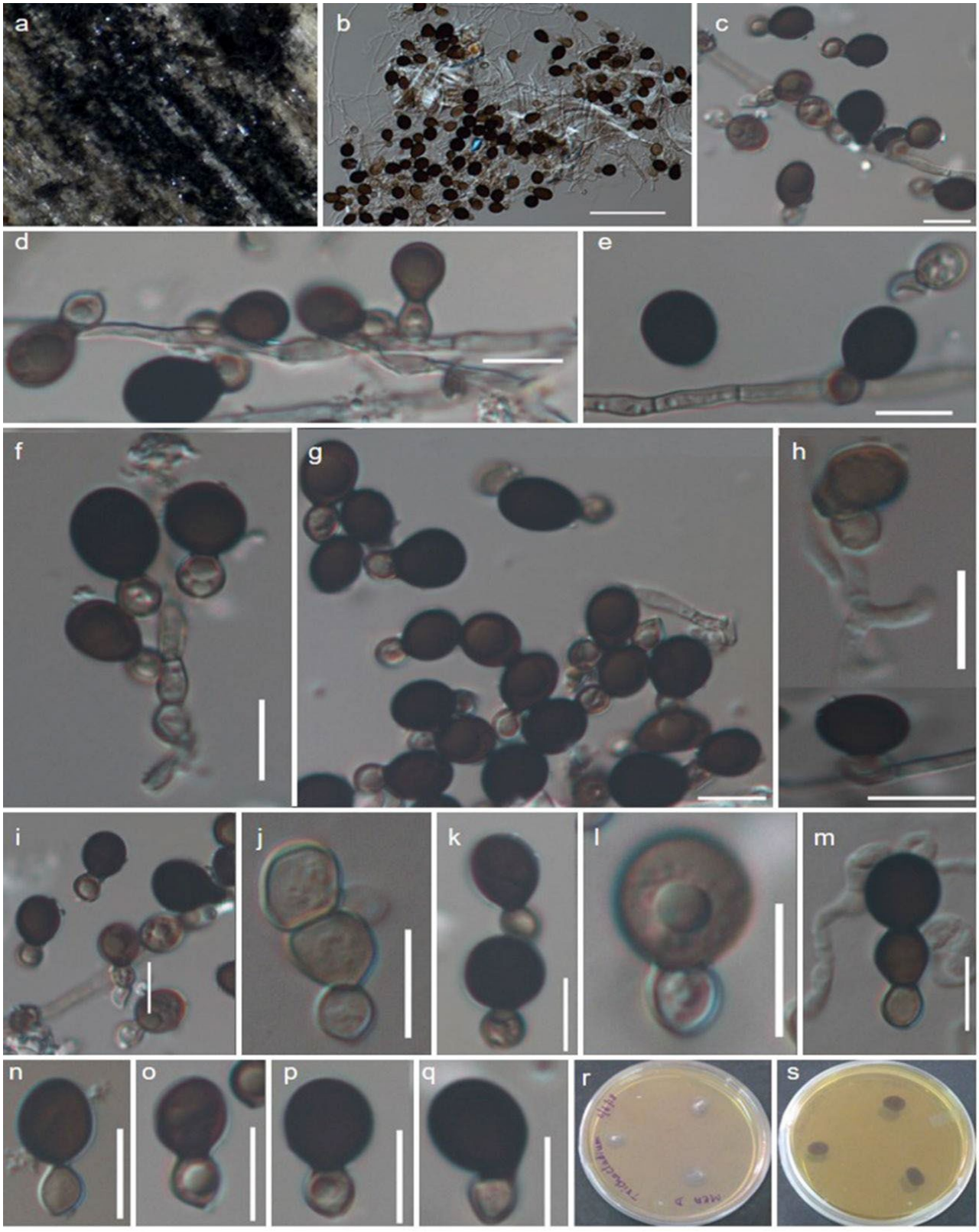

Figure 11 – *Hydea mangrovei* (AMH-9999, holotype). a Colonies on decaying wood. b–h Conidia directly developing on the hyphae. j, m Three-celled conidia. k–l, n–q Two-celled conidia. r–s Colonies on MEA after 10 days. Scale bars: b = 50 µm, c–q = 10 µm.

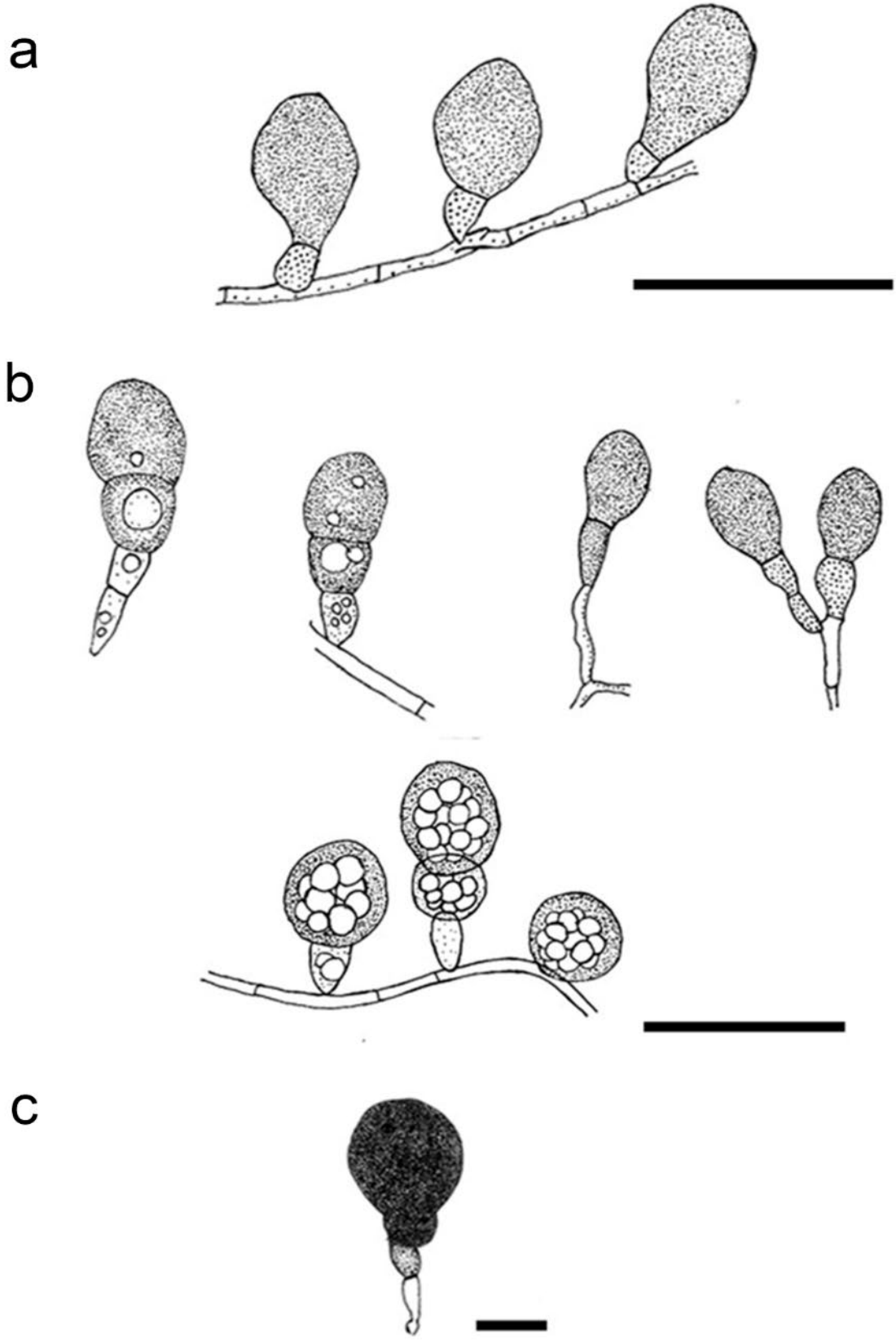

Figure 12 – *Trichocladium alopallonellum.* a Conidia and conidiophores from Meyers and Moore (1960). b Conidia and conidiophores on submerged wood *Fagus* sp., *Pinus* sp., *Tilia americana,* rotten driftwood (Kohlmeyer 1964). Conidia on dead mangrove wood from Pang et al. (2011). Scale bars: A = 35 µm, B = 15 µm C = 10 µm.

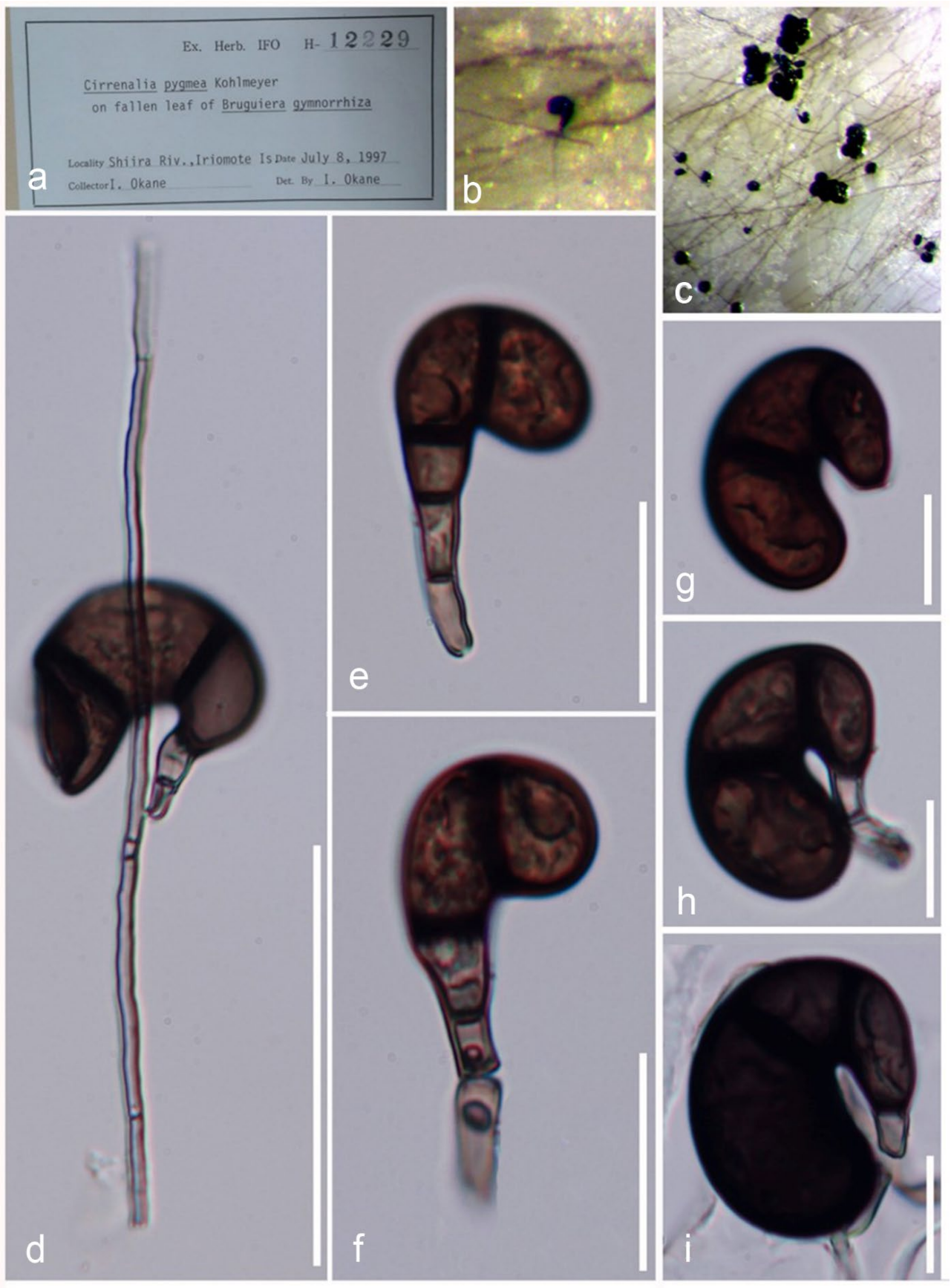

Figure 13 – *Hydea pygmea* (IFO-H 12229, non-type). a Herbarium label. b–c Appearance of conidia and conidiophores on cornmeal seawater agar. d–f Conidia attached to the *Conidiophores*. g–i Helicoid conidia. Scale bars: d–f = 20 μm, g–i =10 μm.

Koralionastes Kohlm. & Volkm.-Kohlm., Mycologia 79(5): 765 (1987)

Index Fungorum number: IF25184

Saprobic on coralline covered rocks, sponges or on algae, found in marine habitats. Sexual morph: *Ascomata* ellipsoidal, superficial, ostiolate, periphysate, papillate, black, subiculate, single. *Peridium* composed of several layers of pseudoparenchymatous cells, forming a *textura angularis,* more or less incrusted with melanin. *Paraphyses* simple, rarely branched, septate, filling immature ascomata, later surrounding the asci. *Asci* 8-spored, clavate to ellipsoidal, lacking an apical apparatus, with a short pedicel, dissolving at maturity, unitunicate, arising from an ascogenous tissue at the base of the locule. *Ascospores* overlapping, ellipsoidal to oval, with several cross septa, mostly septate near the apices, hyaline, thick-walled, lacking a sheath or appendages, germinating apically. Asexual morph: *Spermatia* enteroblastic, with basipetal succession, subglobose, wall cup shaped, hyaline, sticky.

Type species – *Koralionastes ovalis* Kohlm. & Volkm-Kohlm., Mycologia 79(5): 765 (1987)

Notes – *Koralionastes angustus, K. ellipticus* and *K. ovalis* (type species) were first included in *Koralionastes* which was introduced by Kohlmeyer and Volkmann-Kohlmeyer (1987a). Later, Kohlmeyer and Volkmann-Kohlmeyer (1990) introduced two other species, *K. giganteus* and *K. violaceus,* which are found on dead coralline covered rocks among crustose sponges (Campbell et al. 2009). Hence, the genus comprises five species and molecular data is available only for *K. ellipticus* in the GenBank. *Koralionastes* members have been recorded to have a unique association with crustaceous sponges, developing their ascomata on or within these hosts (Kohlmeyer & Volkmann-Kohlmeyer 1990, Wang 2006). *Koralionastes* is the only marine genus associated with marine sponges (Wang et al. 2008)

Kohlmeyer and Volkmann-Kohlmeyer (1987a) introduced the family *Koralionastetaceae* which was referred to the new order *Koralionastetales* by Campbell et al. (2009) based on sequence data from only two species: *Koralionastes ellipticus* (DNA obtained from herbarium material) and *Pontogeneia microdictyi* (fresh material collected Bahamas: Sweetings Cay, on thalli of *Microdictyon* sp.), neither the type species of the genus. The order has been accepted by Hyde et al. (2017) and Hongsanan et al. (2017). Hongsanan et al. (2017) placed the divergence date of *Koralionastetales* (*Koralionastes ellipticus* and *Pontogeneia microdictyi*) as 286 MYA, with a later divergence figure for the *Lulworthiales* of 266 MYA.

Koralionastes ovalis Kohlm. & Volkm-Kohlm., 1987 Fig. 14

Index Fungorum number: IF132447

Saprobic on coralline covered rocks, sponges or on algae, found in marine habitats. Sexual morph: *Ascomata* 530–550 μm subglobose to ampulliform or ovoid, ostiole central with minute papilla, periphysate, glabrous, dark brown. *Peridium* 30–45 μm composed of several polygonal cell layers, *textura angularis*, arranged in two strata; outer stratum thick, dark brown to black; inner stratum hyaline. *Paraphyses* 4–10 μm diam., dense, hyaline, septate, usually unbranched. *Asci* 140–200×60–90 μm, 8-spored, unitunicate, clavate, apically rounded with short pedicel, thin-walled. *Ascospores* 80–100×45–60 μm, overlapping, 2–3 seriate, ellipsoidal, 1–6 septa, thick-walled, walls hyaline, two layered, smooth- with small guttules. Asexual morph: Undetermined.

Material examined – Belize, back reef of South Water Cay, subtidal coral slab (0.2–0.5 m deep), November, 1986, J. J. Kohlmeyer; NY 1317811, NY 1317823, NY 1317828, NY 1317838, Micro slides of holotype.

Notes – This poorly known species is rarely collected due to its unique habitat and growth on dead coral rubble, and further collections are required to supplement our current knowledge.

Koralionastes is characterized by the thick ascomatal wall and ascospores with double walls that are ellipsoidal or fusiform, none are filamentous as those found in the in the *Lulworthiales*.

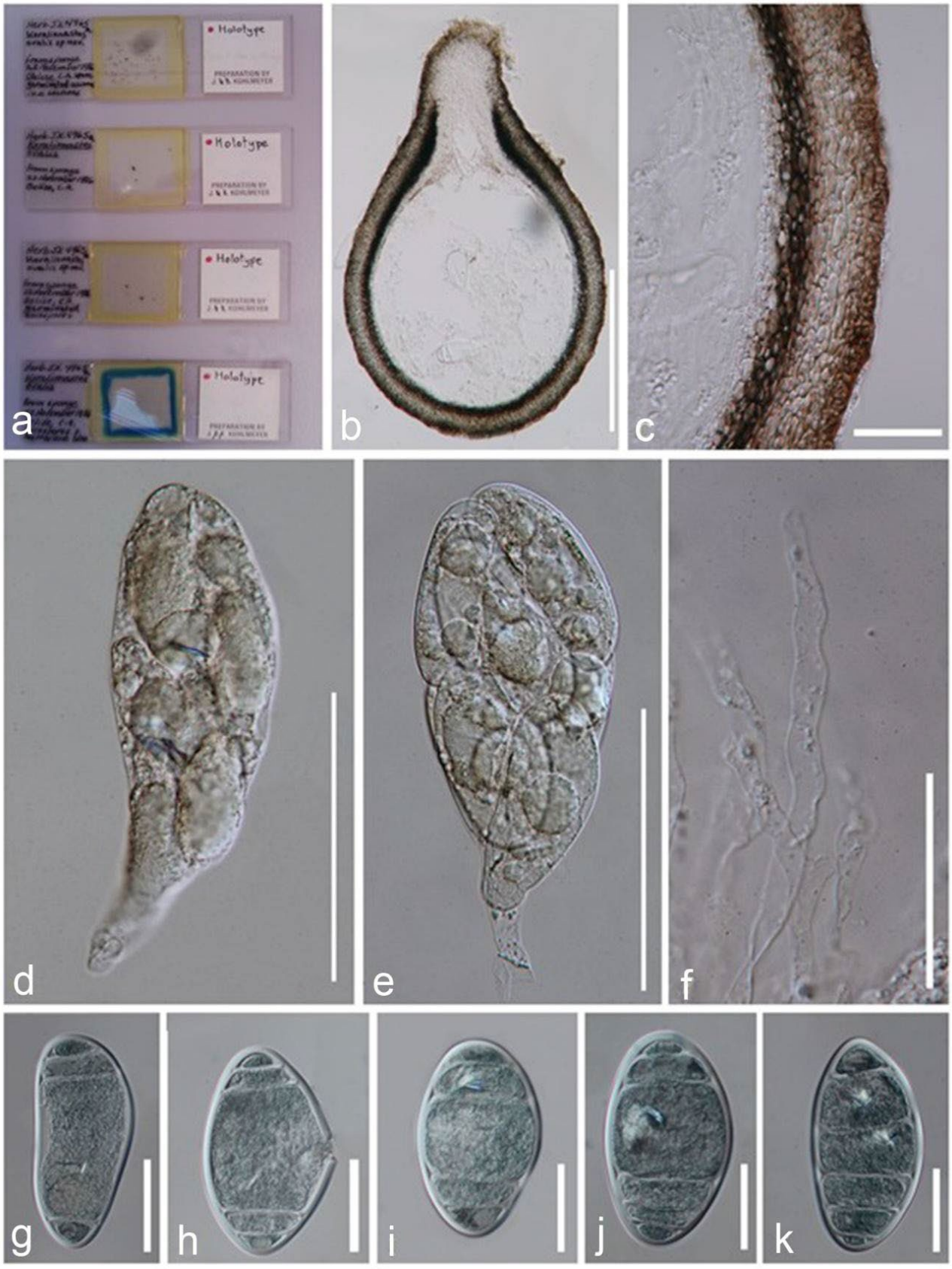

Figure 14 – *Koralionastes ovalis* (Belize, back reef of South Water Cay, subtidal coral slab (0.2–0.5 m deep), November 1986, J. Kohlmeyer; NY 1317811, NY 1317823, NY 1317828, NY

1317838, slides from holotype). a Microslides. b Section through ascoma (NY 1317811). c Section through peridium. d–e Asci (NY 1317828). f Paraphyses (NY 1317828). g–k Ascospores (NY 1317838). Scale bars: b, f = 200 μm, d–e = 100 μm, c–d, g–k = 50 μm.

Kohlmeyeriella E.B.G. Jones, R.G. Johnson & S.T. Moss, Bot. J. Linn. Soc. 87 (2): 208 (1983)

Index Fungorum number: IF25816

Saprobic on submerged wood in marine habitats. Sexual morph: *Ascomata* solitary, sub-globose to globose, immersed to superficial, ostiolate, papillate, subcarbonaceous, dark brown to black, lacking periphyses. *Pseudoparenchyma* thin-walled, deliquescing at maturity, with pit-connections. *Paraphyses* lacking. *Asci* 8-spored, fusiform to clavate, unitunicate, thin-walled, deliquescing early. *Ascospores* unicellular, fusiform, sigmoid to lunate, thick-walled, with polar appendages. *Appendages* spine or tube-like, filled with mucilage. At maturity and in water, a drop of mucilage is released which aides in the attachment of the ascospore (Jones 1994). Asexual morph: Undetermined.

Type species – *Kohlmeyeriella tubulata* (Kohlm.) E.B.G. Jones, R.G. Johnson & S.T. Moss, J. Linn. Soc., Bot. 87(2): 210 (1983)

Notes – Jones et al. (1983) introduced the genus *Kohlmeyeriella* as the ascospore appendage ontogeny of *Corollospora tubulata* differed markedly from that of *Corollospora maritima*, the type species of the genus. *Corollospora* species possess ascospores that are 1-many times septate, with polar and equatorial appendages: polar appendages spine-like or thorn-like with fragments of the exospore, while equatorial appendages are sheet-like (Jones et al. 1983). The genus comprises two species: *Kohlmeyeriella tubulata* and *K. crassa* (syn. *Lulworthia crassa*) (Campbell et al. 2005). Molecular data are available for both species.

Kohlmeyeriella tubulata (Kohlm.) E.B.G. Jones, R.G. Johnson & S.T. Moss, Bot. J. Linn. Soc. 87(2): 210 (1983)

Synonymy – *Corollospora tubulata* Kohlm., Ber. dt. bot. Ges. 81: 53 (1968)

Index Fungorum number: IF108104

Saprobic on submerged wood in marine habitats. Sexual morph: *Ascomata* 430–880 μm high, 440–913 μm diam., solitary, sub-globose to globose, immersed to superficial, ostiolate, papillate, subcarbonaceous, dark brown to black, lacking periphyses. *Neck* 55–200 μm high, 70–130 μm in diam., pointing down to the basal subiculum, with or without periphyses. *Peridium* 28–144 μm thick, three-layered; outer layer with large cells, middle layer of small, irregular flat cells and inner layer of large elongate cells. *Pseudoparenchyma* thin-walled, deliquescing at maturity, with pit-connections. *Paraphyses* lacking. *Asci* 135–193×24–32 μm, 8-spored, fusiform to clavate, unitunicate, thin-walled, deliquescing early. *Ascospores* 137–152×17.5–18.5 μm, unicellular, fusiform, sigmoid to lunate, thick-walled, with polar appendages. *Appendages* spine or tube-like, filled with mucilage. *Polar spine* 38–47×4–4.5 μm. Asexual morph: Undetermined.

Material examined – Denmark, Gronhoj and Blokhaus, driftwood collected at Lokken, 20 November, 1966, J. J. Kohlmeyer; IMS No. 66 (Iso type).

Notes – Spore appendage ontogeny of *K. tubulata* has been studied at the scanning and transmission microscope level, and the polar spine is formed from the outer region of the mesosporium, the centre comprising amorphous material which is released as a drop of mucilage and aides attachment of the spore to surfaces (Rees & Jones 1984, Jones 1994). Initially collected on intertidal wood in Denmark, also known from Canada. Many collections have been reported in Denmark by Koch (1974), Rees et al. (1979), and Koch and Jones (1984), often associated with wood in sand dunes. *Kohlmeyeriella crassa* was initially described as a *Lulworthia* species from Japan (Nakagiri 1984). Cambpbell et al. (2005) showed *Lulworthia crassa* was closely related to *K. tubulata* and transferred it to *Kohlmeyeriella.* Both species are arenicolous with ascomata developing on sand grains, and the necks growing down close to the subiculum, a common feature of many arenicolous ascomycetes (Jones & Pang 2022). *Kohlmeyeriella tubulata* and *K. crassa*

grouped to form a sister clade to *Sammeyersia grandispora* and *Matsusporium tropicale* with high support (Poli et al. 2021).

Lindra I.M. Wilson, Trans. Br. mycol. Soc. 39(4): 411 (1956)

Index Fungorum number: IF2205

Saprobic on submerged wood, test panels, foam in marine habitats. Sexual morph: *Ascomata* solitary or gregarious, semi-globose or ellipsoidal, immersed becoming superficial, ostiolate, papillate, carbonaceous or coriaceous, dark coloured. *Asci* 8-spored, cylindrical sometimes curved, unitunicate, thin-walled, multi-septate, deliquescing early. *Ascospores* filiform, multiseptated, hyaline with globose tips. Asexual morph: *Hyphomycetous* with conidiophores simple or branched, monoblastic, terminal, percurrent. *Conidia* solitary, filiform, septate, swollen at their tips, hyaline.

Type species – *Lindra inflata* I.M. Wilson, Trans. Br. mycol. Soc. 39(4): 411 (1956)

Notes – *Lindra* was introduced by Wilson (1956), from intertidal wood, driftwood and test panels with members of the genus collected exclusively from the marine environment (Wilson 1956, Nakagiri & Tubaki 1983). The genus resembles *Lulworthia*, but differs in lacking ascospores with apical chambers filled with mucilage. The genus comprises two species: *Lindra inflata*, and *L. obtusa*, the latter with an asexual morph: *Anguillospora marina.* Three other species have been transferred to a new genus (*Lindriella)* in this monograph. Molecular data only available for *L. obtusa*.

Although Wilson (1956) described the ascospores of *L. inflata* as appendaged, examination of the type material (IMI 62909) revealed that the tips are inflated but cannot be considered "appendaged". They do not contain or release mucus and can be considered homologous with the apical chambers of *Lulworthia* but with a loss of function (Yusoff et al. 1995, Campbell et al. 2005), which is also supported by the molecular data as *Lindra* is nested within the *Lulworthiales* (Fig. 1). Drawings of ascospore tips by Wilson (1956: Figs. 29–30) and a photograph in Hyde et al. (1986, Fig. 1) show a gelatinous film that attaches the ascospore to the substrate (Campbell et al. 2005). No other *Lindra* species has ascospore tips like *L. inflata.* Yusoff et al. (1995) undertook an ultrastructure study of both *Lulworthia* and *Lindra* ascospores, the latter showing no signs of an apical thickening or chamber. No cultures are available for *L. inflata* and those at the Portsmouth Culture Collection were lost due to lack of maintenance. A rarely collected species with records from England, Wales (United Kingdom), Newfoundland (Canada), Denmark, Germany, Norway, and North Carolina (USA).

Lindra inflata I.M. Wilson, Trans. Br. mycol. Soc. 39(4): 411 (1956) Fig. 15

Index Fungorum number: IF299825

Saprobic on submerged wood, test panels, in marine habitats. Sexual morph: *Ascomata* 250–390 µm high, 308–611 µm in diam., solitary or gregarious, semi-globose or ellipsoidal, immersed becoming superficial, ostiolate, papillate, carbonaceous, thick-walled 40–60 µm, dark coloured. *Asci* 231–463×22–38 µm, 8-spored, cylindrical sometimes curved, unitunicate, thin-walled, deliquescing early. *Ascospores* 210–415×4–6 µm, filiform, 30–50-septate, hyaline with globose tips 7.5–18.5 µm. Asexual morph: Undetermined.

Material examined – Type material deposited at the Fungarium, Kew Gardens: Km165868 collected on submerged wood, Aberystwyth, Wales; IMI 68138 to 68140, including two microscope slides; IMI 320096, from Shetland, collected by D. Minter on 19/06/1987, coll. no. HU4624 on a small piece of driftwood.

Notes – *Lindra inflata* differs from *L. obtusa* in the number of ascospore septa (30–50 vs. 9–16 (–21), in spore measurements (210–415 µm vs. 182–250 (–313) µm), the apical region of the ascospores (distinctly globose vs rounded), orientation of ascomata (upright vs downward to the basal subiculum) and asexual morph: (undetermined vs hyphomycetous). *Lindra obtusa* was isolated from sea foam and collection on driftwood at Langstone harbour, UK (Yusoff et al. 1995). Nakagiri and Tubaki (1983) opined that the tips of the ascospores of *L. obtusa* are rounded. Poli

et al. (2021) showed that *L. obtusa* strains formed a discrete and highly supported clade within the *Lulworthiales* with the asexual morph: *Moleospora maritima*.

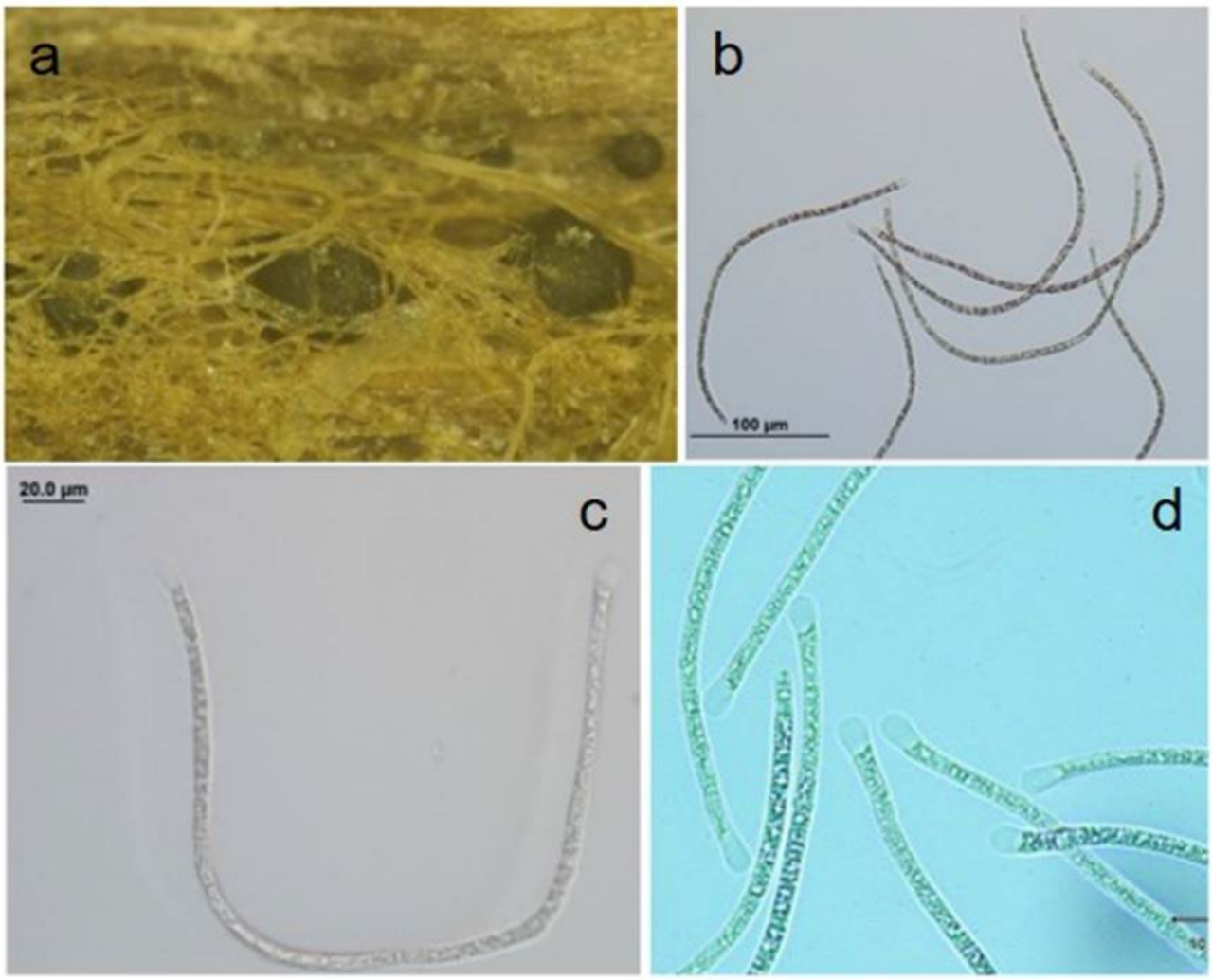

Figure 15 – *Lindra inflata* (Km165868, holotype) a Ascomata on surface of wood. b–d Septate ascospores with terminal inflated tips. Scale bars: b = 100 µm. c–d = 20 µm.

Lindriella Dayar., K.L. Pang & E.B.G. Jones, **gen. nov.**

Index Fungorum number: IF9000099

Etymology – The generic name *Lindra* and *ella* refers to the genus *Lindra* and small

Perthophytic and *saprobic* on leaves of the seagrass *Thalassia*, marine algae, driftwood, sea foam. Sexual morph: *Ascomata* globose, immersed, ostiolate, papillate, coriaceous, dark brown to black. *Asci* 8-spored, cylindrical or subclavate, unitunicate, thin-walled, no apical apparatus, early deliquescing. *Ascospores* multi-septate, hyaline, tips only slightly inflated. Asexual morph: Undetermined.

Notes – Currently three *Lindriella*-like species are listed in Index Fungorum (January 2022), however there is confusion as to whether they are sufficiently distinct. Kohlmeyer and Volkmann-Kohlmeyer (1991) regarded *Lindra thalassiae* var. *crassa* as a synonym of *L. crassa*. Campbell et al. (2005) proposed that *Lindra marinera* be reduced as a synonym of *L. thalassiae*, but this was not formally undertaken. *Lindra hawaiiensis* differs from the other two species in possessing shorter ascospores, with fewer septa and catenophyses. Therefore, currently we accept *Lindriella thalassiae*, *L. hawaiiensis* and *L. crassa* in the genus until further collections are sequenced. In the phylogenetic tree of Campbell et al. (2005), three *Lulworthia* isolates grouped in the same clade as the *Lindriella* taxa, indicating there may be other species awaiting characterization.

The only morphological difference between *Lulworthia* and *Lindra/Lindriella* taxa is that the former has apical chambers full of mucilage which is discharged as drop when spores are in seawater (Jones 1994, Yusoff et al.1995), with Campbell et al. (2005) suggesting that the "loss of the apical chambers has not occurred once but twice in the Lulworthiales."

Lindriella crassa (Kohlm.) Dayar., K.L. Pang & E.B.G. Jones, comb. nov.

Basionym – *Lindra crassa* (Kohlm.) Kohlm. & Volkm-Kohlm., Bot. Mar. 34(1): 23 (1991)

Holotype – JK 4321a

Molecular data available – SSU, LSU rDNA genes

Lindriella hawaiiensis (Kohlm. & Volkm-Kohlm.) Dayar., K.L. Pang & E.B.G. Jones, comb. nov.

Basionym – *Lindra hawaiiensis* Kohlm. & Volkm-Kohlm., Can. J. Bot. 65(3): 574 (1987)

Holotype – JK 4485a

Lindriella thalassiae (Orpurt, Meyers, Boral & Simms) Dayar., K.L. Pang & E B G Jones, comb. nov. Fig. 16

Index Fungorum number IF900341

Basionym – *Lindra thalassiae* Orpurt, Meyers, Boral & Simms, Bull. mar. Sci. Gulf Caribb. 14: 406 (1964)

Synonymy – *Lindra marinera* Meyers, Mycologia 61: 488 (1969)

Holotype – JK 4321; isotype JK 4321b

Molecular data available – 18S, 28S, ITS rDNA, TEF1α, RPB1, RPB2, mitochondrial 16S rDNA

Perthophytic and *saprobic* on leaves of the seagrass *Thalassia,* and marine algae. Sexual morph: *Ascomata* 115–200 µm, 127–200 µm in diam., globose, subglobose, immersed, ostiolate, papillate, coriaceous, dark brown to black. *Asci* 8-spored, cylindrical, sub-clavate, unitunicate, thin-walled, deliquescing early. *Ascospores* 230–390×3–6 µm, filiform, tapering towards the tips (after Kohlmeyer & Kohlmeyer 1979). Asexual morph: Undetermined.

Notes – *Lindriella* species differ morphologically as outlined in Table 3. Sequence data only available for five strains of *L. thalassiae* which forms a sister clade to the asexual morph: *Cumulospora marina* with high statistical support and distantly placed from *Lindra obtusa* (Poli et al. 2021). Collections are known from Belize, Fiji, Mexico, and Thailand in the tropics on a variety of substrates including shells of Foraminifera, empty bryozoan skeletons, sea foam, calcareous materials (Kohlmeyer 1984). *Lindriella hawaiiensis* differs from the other *Lindriella* species in possessing catenophyses (Kohlmeyer & Volkmann-Kohlmeyer 1987b).

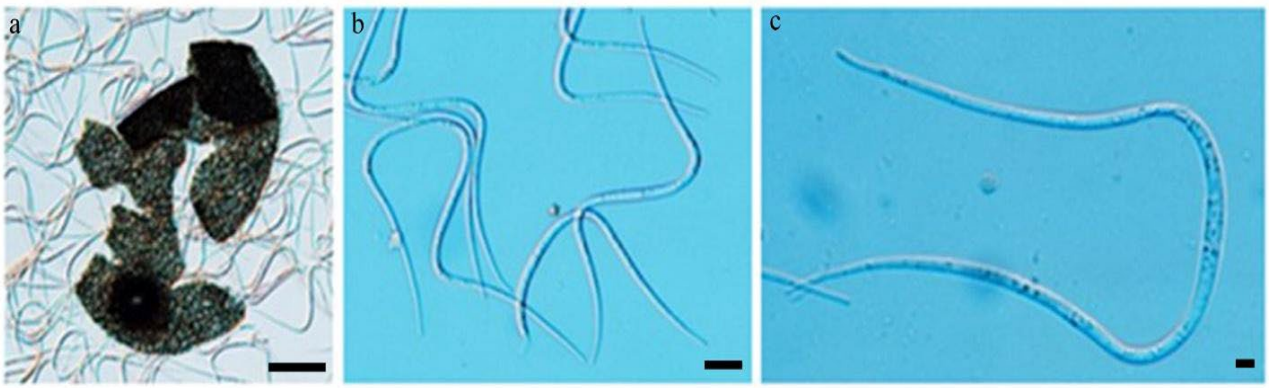

Figure 16 – *Lindriella thalassiae.* a Crushed ascoma. b–c Ascospores. Scale bars: a = 250 µm, b = 50 µm, c = 5 µm.

Table 3 Morphological features of ascospores of *Lindriella* species.

	L. crassa	***L. hawaiiensis***	***L. thalassiae***
Size (µm)	320–520×8–10	(101–) 110–179 (–188)×3.4–5.3	(220–) 230–390×3–6
Number of septa	15–23	8–17	4–26
Apices	Tapering	Slightly inflated	Tapering, slightly inflated
Habitat	Intertidal wooden stick	Leaves of *Thalassia testudinum*	Vesicles of *Sargassum* sp.
Distribution	Belize, Virgin Islands, Hawaii, Belize, Fiji, Mexico, Puerto Rico, Thailand, Virgin Islands	Hawaii	Belize, Fiji, Mexico, Thailand

Lulwoana Kohlm., Volkm-Kohlm., J. Campbell, Spatafora & Gräfenhan, Mycol. Res. 109 (5): 562 (2005)

Index Fungorum number: IF28935

Saprobic on wood Sexual morph: *Ascomata* superficial or partly immersed in wood, globose to subglobose, ostiolate, coriaceous, dark brown or black. *Papilla* or neck cylindrical, straight or irregular. *Peridium* two layered; outer layer composed of small, polygonal or irregular dark cells; inner layer composed of flat or rhomboid hyaline cells. *Hamathecium* absent; immature ascomata filled with a pseudoparenchyma of polygonal, thin-walled and hyaline cells. *Asci* 8-spored, fusiform, curved, thin-walled, unitunicate, deliquescing early. *Ascospores* filiform, hyaline, 1-septate, with a conical chamber at each end, releasing mucus from the tip. Asexual morph: *Hyphomycetous*, conidiogenous cells short, light to dark brown, septate, simple, conidia coiled, solitary, septate, constricted at the septa, fuscous to black.

Type species – *Lulwoana uniseptata* (Nakagiri) Kohlm., Volkm-Kohlm., J. Campb., Spatafora & Gräfenhan, Mycol. Res. 109(5): 562 (2005).

Notes – *Lulwoana* was introduced by Campbell et al. (2005) for a *Lulworthia uniseptata* strain which did not group with the Type species of *Lulworthia* (*L. fucicola*). *Lulwoana uniseptata* was collected on wood at Shimoda, Japan, with *Zalerion maritima* as its asexual morph (Nakagiri 1984). This was later confirmed by Campbell et al. (2005) and Jones et al. (2008). Phylogenetically supported by 18S, 28S and ITS rDNA datasets.

Lulwoana uniseptata (Nakagiri) Kohlm., Volkm-Kohlm., J. Campb., Spatafora & Gräfenhan, Mycol. Res. 109(5): 562 (2005) Fig. 17

Basionym – *Lulworthia uniseptata* Nakagiri, Trans. Mycol. Soc. Japan 25(4): 382 (1984)

Synonyms – *Helicoma maritimum* Linder, Farlowia 1(3): 405 (1944)

Helicoma salinum Linder, Farlowia 1(3): 406 (1944

Zalerion eistla R.T. Moore & Meyers, Can. J. Microbiol. 8: 413 (1962)

Zalerion maritima (Linder) Anastasiou, Can. J. Bot. 41: 1136 (1963)

Zalerion nepura R.T. Moore & Meyers, Can. J. Microbiol. 8: 413 (1962)

Zalerion raptor R.T. Moore & Meyers, Can. J. Microbiol. 8: 415 (1962)

Zalerion xylestrix R.T. Moore & Meyers, Can. J. Microbiol. 8: 414 (1962)

Zalerion pseudomaritima M. Gonçalves, A. Abreu & A. Alves, Mycologia: 10.1080/00275514.2021.1875710, 11 (2021)

Index Fungorum number: IF369395

Saprobic on wood. Sexual morph: *Ascomata* 430–520 µm, superficial or partly immersed in wood, globose to subglobose, ostiolate, coriaceous, dark brown or black. *Papilla* or neck cylindrical, straight or irregular. *Peridium* 30–50 µm, two layered; outer layer composed of small, polygonal or irregular dark cells; inner layer composed of flat or rhomboid hyaline cells. *Hamathecium* absent; immature ascomata filled with a pseudoparenchyma of polygonal, thin-

walled and hyaline cells. *Asci* 98–150×35–70 µm, 8-spored, fusiform, curved, thin-walled, unitunicate, deliquescing early. *Ascospores* 94–148×2.5–5.0 µm, filiform, hyaline, 1-septate, with a conical chamber at each end (3.5–12.5 µm), releasing mucus from the tip. Asexual morph: *Hyphomycetous*, conidiophores 12–22×2.5–7.5 µm, conidiogenous cells short, light to dark brown, septate, simple, conidia 14–35 µm, coiled, solitary, septate, constricted at the septa, fuscous to black.

Material examined – Japan, Shizuoka Pref., Izu Pen., Shimoda, on submerged wood, 27 Aug. 1982, A. Nakagiri (TKB-F-5050, holotype).

Notes – Nakagiri (1984) introduced the species *Lulworthia uniseptata* with the anamorph *Zalerion maritima* (Anastasiou 1963), thus accepting the generic name *Lulworthia* over *Zalerion.* Campbell et al. (2005) as the result of a phylogenetic study of the genus *Lulworthia* transferred *Lulworthia uniseptata* to *Lulwoana* based on sequence data as it did not group with the type species. Anastasiou (1963) had previously transferred *Helicoma maritimum* to *Zalerion* as *Z. maritima*, he also synonymized all marine *Zalerion* species (*Helicoma salinum, Z. eistla, Z. nepura, Z. raptor and Z. xylestrix*) under *Z. maritima.* The four *Zalerion* species had been introduced based on quantitative physiological characters rather than on their morphology (Moore & Meyers 1962). This argument was accepted by Kohlmeyer and Kohlmeyer (1964, 1979). In subsequent studies, *Z. xylestrix* grouped with *Z. maritima* (Poli et al. 2021). In www.marinefungi.com the name *Lulwoana uniseptata* has been given priority over its anamorph, thus following the practice for other marine fungi (Réblová et al. 2016). However, Gonçalves et al. (2021) introduced *Zalerion pseudomaritima,* and synonymised *Lulwoana uniseptata* under *Zalerion maritima* and stated "As the holotype contains only the asexual morph, a specimen containing the sexual morph is designated as the epitype". While the genus *Zalerion* has been shown to be polyphyletic and *L. uniseptata*, *Z. maritima* and *Z. pseudomaritima* formed a well-supported monophyletic group in this study (Fig. 1), we suggest the name *Lulwoana* to be used to avoid confusion and the synonymy of *Z. pseudomaritima* with *L. uniseptata*. Other *Zalerion* species have been referred to *Microthyriaceae*, *Mytilinidiaceae*, and *Tricladiaceae* (Index Fungorum).

The anamorph is the most commonly stage recorded on a wide variety of woody substrates with a worldwide distribution in temperate waters of the Atlantic and Pacific Oceans, Baltic Sea, and the Mediterranean. The sexual morph has been reported from Japan and South Wales (UK).

Lulwoidea Kohlm., Volkm-Kohlm., J. Campbell, Spatafora & Gräfenhan, Mycol. Res. 109 (5): 564 (2005)

Index Fungorum number: IF28936

Saprobic on wood Sexual morph: *Ascomata* superficial, mostly on grains of sand, subglobose to ellipsoidal, subiculate, carbonaceous, black. *Papilla* conical, near the basal subiculum. *Peridium* two-layered; outer layer composed of large cells with large lumina; inner layer composed of flat cells with narrow lumina. *Hamathecium* absent; immature ascomata filled with pseudoparenchyma of polygonal, thin-walled and hyaline cells. *Asci* 8-spored, clavate, pedunculate, thin-walled, unitunicate, early deliquescing. *Ascospores* filiform, hyaline, multiseptate, with a conical chamber at each end, releasing mucus from the tip. Asexual morph: Undetermined.

Notes – Campbell et al. (2005) introduced the genus *Lulwoidea* to accommodate a *Lulworthia* species that did not group with type species *Lulworthia fucicola*. Two strains of *Lulwoidea lignoarenaria* formed a highly supported clade basal to a clade comprising the genera *Sammeyersia, Kohlmeyeriella, Spathulospora* and *Lindra* (Campbell et al. 2005). However, in a study by Poli et al. (2021) it grouped with *Lulworthia atlantica.*

Type species – *Lulwoidea lignoarenaria* (Jørg. Koch & E.B.G. Jones) Kohlm., Volkm-Kohlm., J. Campb., Spatafora & Gräfenhan, Mycol. Res. 109(5): 564 (2005)

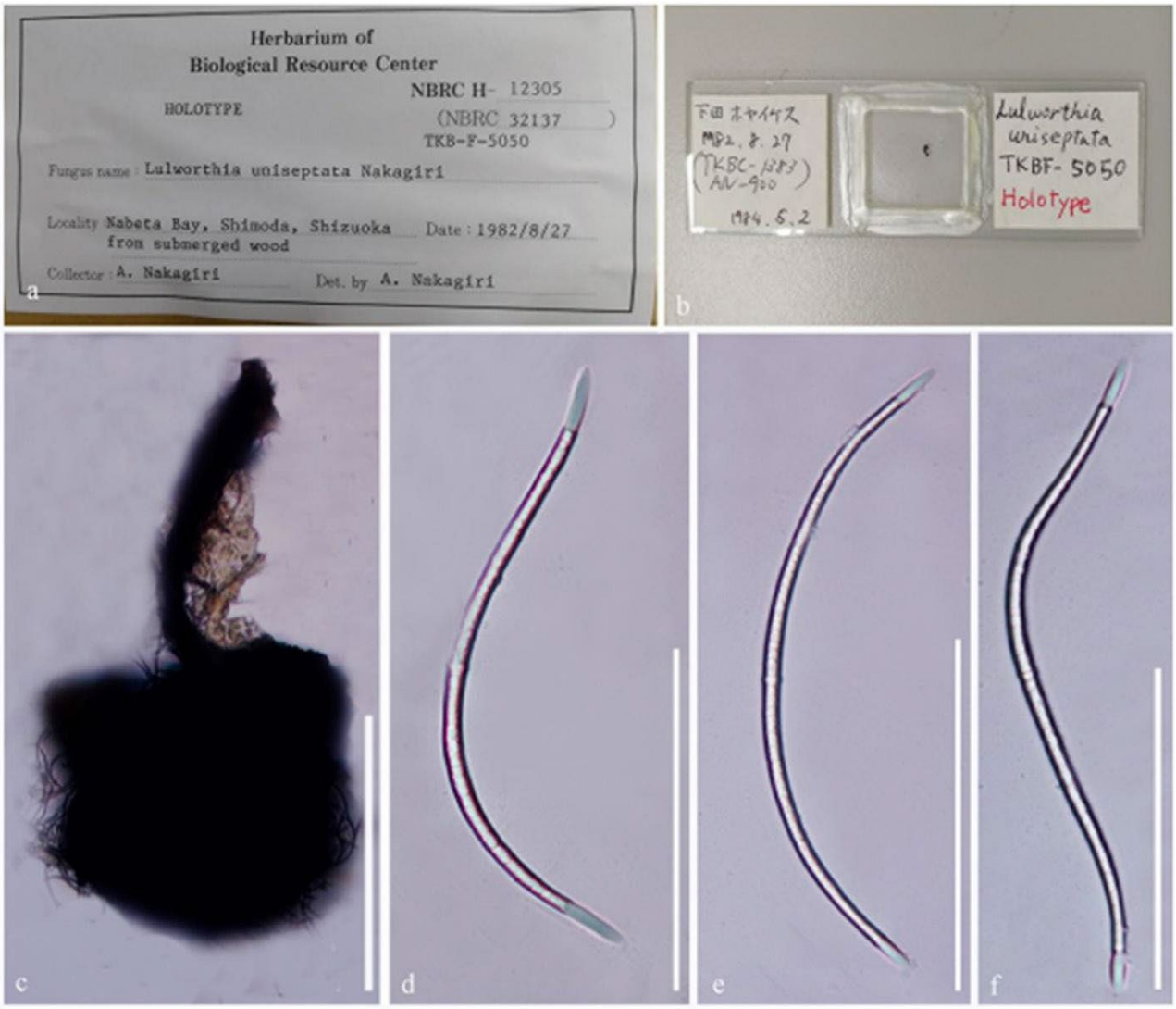

Figure 17 – *Lulwoana uniseptata* (TKB-F-5050, holotype). a Herbarium material. b Microslide of the holotype. c An ascoma. d–f Ascospores. Scale bars: c = 100 µm, d–f = 50 µm.

Lulwoidea lignoarenaria (Jørg. Koch & E.B.G. Jones) Kohlm., Volkm-Kohlm., J. Campb., Spatafora & Gräfenhan, Mycol. Res. 109(5): 564 (2005)

Index Fungorum number: IF369336

Basionym – *Lulworthia lignoarenaria* Jørg. Koch & E.B.G. Jones, Mycotaxon 20(2): 389 (1984)

Material examined – Denmark, wood associated with sand, Gronhoj, Jutland. Herb. J. Koch, 398, slides 1–5, April, 1981.

Saprobic on wood. Sexual morph: *Ascomata* 350–405 µm high, superficial, mostly on sand grains, subglobose to ellipsoidal, subiculate, carbonaceous, black. *Papilla* 75–135 µm long, at base 45µm in diam., conical, directed downwards towards the subiculum. *Peridium* two-layered; outer layer composed of large dark cells with large lumina, 28 µm high, 16 µm broad; inner layer composed of flat cells with narrow lumina. *Hamathecium* absent; immature ascomata filled with pseudoparenchyma of polygonal, thin-walled, hyaline cells. *Asci* 450–505×28 µm, 8-spored, clavate, pedunculate, thin-walled, unitunicate, early deliquescing. *Ascospores* 409–436 (–472) ×6.0–6.5 (–8.0) µm, filiform, hyaline, multiseptate, with a conical chamber at each end, 32–35.5 (–40) µm long, releasing mucus from the tip. Asexual morph: Undetermined.

Notes – *Lulwoidea lignoarenaria* shares many characteristics with the genus *Lulworthia* with long filiform ascospores and an apical chamber filled with mucous, but differs in possessing septate

ascospores. *Lulwoidea lignoarenaria* is a poorly known marine ascomycete originally found growing on wood associated with sand and generally found growing on sand with the ascomatal neck directed towards the basal subiculum. A characteristic feature of the genus is the very large dark peridial cells and septate ascospores, and in these respects differs from *Lulworthia.* Another species with these features is *Lulworthia lindroidea* but no sequence data is available for this species, therefore it cannot be assigned to *Lulwoidea. Lulworthia lindroidea* differs from *Lulwoidea* in having shorter ascospores (170–240 µm) with fewer septa (9–12), coriaceous ascomata partly immersed in wood (Kohlmeyer 1980).

Lulwoidea lignoarenaria is known from many collections in Jutland, Denmark and a similar species referred to as a *Lindra* sp. from Hakkaido, Kyushu and Nansei Islands, Japan (Tokura 1982, Tubaki & Nakagiri 1982, Tokura & Nakagawa 1983). Koch (1974), Rees et al. (1979), Koch & Jones (1984) and Farrant et al. (1985) have all collected *L. lignoarenaria* at the sand dunes in Gronhoj and Sletterande, Denmark and classified it as frequent with a frequency of occurrence of 17.3% (46 total number of taxa). *Lulwoidea lignoarenaria* is an arenicolous species that is well adapted to sand-inhabiting conditions: the presence of a subiculum for attachment to sand grains, thick carbonaceous ascomata wall, and a downward directed neck close to the subiculum which prevents its abrasion.

Matsusporium E.B.G. Jones & K.L. Pang, in Abdel-Wahab, K.L. Pang, Nagahama, Abdel-Aziz & Jones, Mycol. Progr. 9: 550 (2010)

Index Fungorum number: IF543120

Saprobic on submerged marine substrates. Sexual morph: *Ascomata* immersed, oval, ellipsoidal or subglobose, coriaceous, brown to dark brown, ostiolate and papillate. *Peridium* thick, one-layered, forming *textura angularis*. *Necks* cylindrical, brown to dark brown. *Paraphyses* absent. *Asci* 8-spored, fusiform, unitunicate, thin-walled, early deliquescing. *Ascospores* filamentous, curved, hyaline, tapering at each end into an elongate, conical process or apical chamber, filled with mucus that is released through an apical pore as long bifurcating filaments or ascospores end with irregular ellipsoidal or subglobose structure and apical chambers. Asexual morph: *Hyphae* septate, superficial or immersed, light brown. *Conidiophores* obsolete or present, when present micronematous, cylindrical, light-brown, cylindrical, septate, acrogenous or lateral. *Conidia* acrogenous or lateral, solitary, helicoid, up to 12 septate, immature conidia are surrounded by sheath, dark-brown to black, not constricted at the septa, cells increasing in diameter and pigmentation from the base to the apex.

Notes – Initially it was a monotypic marine asexual genus in the *Lulworthiales* (Abdel-Wahab et al. 2010), and formed a sister clade to *Sammeyersia grandispora*. The type species is *M. tropicale,* initially described as *Cirrenalia tropicalis,* but it was transferred to *Matsusporium* because it was distantly placed from the type species *Cirrenalia macrocephala* that is affiliated with *Halosphaeriaceae*. The genus *Matsusporium* is different from other helicoids genera by having 12-septate conidia that usually have a long stalk (Abdel-Wahab et al. 2010).

In this study, a new species (*Matsusporium japonica*) is introduced with a sexual morph, further establishing its link with the *Lulworthiales*.

Type species – *Matsusporium tropicale* (Kohlm.) E.B.G. Jones & K.L. Pang

Matsusporium japonica Abdel-Wahab & E.B.G. Jones, sp. nov. Fig. 18

Index Fungorum number: IF900345

Etymology – Named after the country name “Japan”, where this fungus was collected.

Holotype – SUMCC H-08001 (Sohag University Microbial Culture Collection).

Saprobic on submerged decaying mangrove wood in the intertidal zone. Sexual morph: *Ascomata* 270–400 µm high, 150–240 µm wide, immersed, horizontal with neck bending upward, oval, ellipsoidal or subglobose, coriaceous, brown to dark brown, ostiolate and papillate. *Peridium* 22–32 µm thick, one-layered, forming *textura angularis*, 4–9 layers of polygonal brown to dark-brown melanized cells. *Necks* lateral bending upward, 185–906 µm long, 36–84 µm wide,

cylindrical, brown to dark brown. *Paraphyses* absent. *Asci* 220–260×15–20 µm, 8-spored, fusiform, unitunicate, thin-walled, early deliquescing. *Ascospores* 270–320×4–6 µm (294×5 µm, n=50) filamentous, curved, hyaline, tapering at each end into an elongate, conical process or apical chamber (4–6×2–2.5 µm), filled with mucus that is released through an apical pore as long bifurcating filaments or ascospores end with irregular ellipsoidal or subglobose structure (14–48×4–7 µm) and apical chambers. Asexual morph: *Hyphae* 3–5 µm in diameter, septate, superficial or immersed, brown to dark-brown, thick-walled. *Conidiophores* 22–55 µm long, 5–7 µm in diameter, cylindrical, 0-4-septate, simple, acrogenous or laterally on hyphae, often remaining connected with detached conidia, sometimes obsolete, straight or curved, brown to dark brown. *Conidiogenous cells* monoblastic, integrated, terminal, determinate. *Conidia* 52–170 µm long, 30–103 µm in diam. (89×64 µm, n=30), acrogenous, solitary, regularly or irregularly helicoid, semi- to 2 times contorted, 4-9-septate, not or slightly constricted at the septa, reddish-brown to black, cells increasing in size and pigmentation from base to apex; terminal cell 24–36 µm high, 25–39 µm in diameter, subglobose, ellipsoidal or barrel-shaped, basally flattened; central cells subglobose, obtusely horizontal conical, barrel- or discoid-shaped; basal cells 18–33 µm high, 6–20 µm in diam., obtusely conical, clavate or cylindrical. Producing long chains of chlamydospores that are 230–420 µm long, 5-7 µm in diameter, brown to dark-brown in color.

Type material – Japan, Okinawa, Higashi-son, Gesashi mangroves, on decaying mangrove wood collected from the intertidal zone, 17 July 2008, coll. M.A. Abdel-Wahab (holotype, SUMCC H-08001).

Notes – *Matsusporium japonica* (52–170×30–103 µm) has larger conidial dimensions than *M. tropicale* (20–38.5 µm). Conidia in *M. japonica* have fewer transverse septa (4–9) than *M. tropicale*. Terminal cells of conidia in *M. japonica* are larger (24–36×25–39 µm) than those of *M. tropicale* (9–15 × 10–20 µm) (Kohlmeyer 1968, Abdel-Wahab et al. 2010).

Matsusporium tropicale (Kohlm.) E.B.G. Jones & K.L. Pang, in Abdel-Wahab, K.L. Pang, Nagahama, Abdel-Aziz & Jones, Mycol. Progr. 9: 550 (2010) Figs. 19–20

Basionym – *Cirrenalia tropicalis* Kohlm. 1968

Index Fungorum number: IF543121

Saprobic on mangrove wood. Sexual morph: Undetermined. Asexual morph: *Hyphae* 2.5–5 µm in diameter, septate, superficial or immersed, light brown. *Conidiophores* 25–42 µm long, 2.5–5 µm in diameter, cylindrical, 0-4-septate, simple acrogenous or laterally on hyphae, often remaining connected with detached conidia, sometimes obsolete, straight or curved, light brown. *Conidiogenous cells* monoblastic, integrated, terminal, determinate. *Conidia* acrogenous, solitary, regularly or irregularly helicoid, mostly 1 to 1 ½ times contorted, rarely semicontorted, six- to twelve-septate, not or slightly constricted at the septa, umber to reddish-brown; cells increasing in diameter from base to apex, distinctly dissimilar; spirals 20–38.5 µm in diameter; terminal cell 9–15 µm high, 10–20 µm in diameter, subglobose to ellipsoidal, basally flattened; basal cells 5.5–10 µm high, 3–5 µm in diameter, cylindrical; central cells subglobose, obtusely conical or doliiform.

Material examined – Japan, Iriomote Island, Okinawa, submerged wood of *Rhizophora stylosa,* NBRC32499; Thailand, on mangrove wood, IT061; Thailand, on mangrove wood, IT061. Atlantic Ocean, Liberia, pilings of iron-ore pier infested by teredinids and gribble, 25 Feb. 1965, J. K. Nos NY, Kohlmeyer 1888a holotype and NY, Kohlmeyer 1892 paratype

Notes – *Matsusporium tropicale* is a widely distributed asexual marine fungus in tropical and subtropical mangroves, growing on the bark of mangrove trees. The fungus differs from other asexual taxa in *Lulworthiales* by the repeated coiled nature of the conidia that are dark brown in colour and surrounded by a sheath when young (Abdel-Wahab et al. 2010).

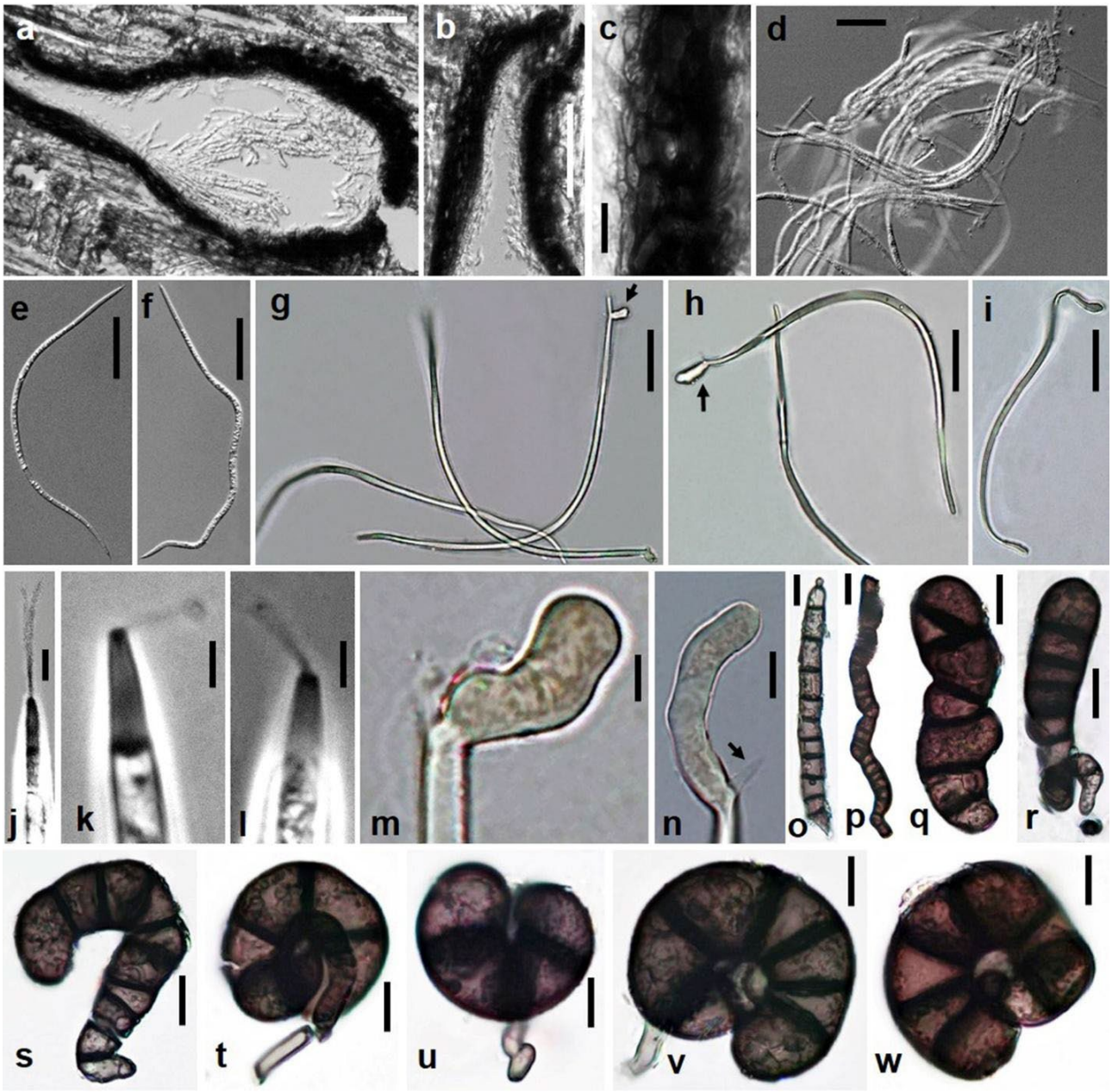

Figure 18 – *Matsusporium japonica* (SUMCC H-08001, holotype). a Vertical section of the ascoma. b Neck. c Magnified part of the peridium. d Deliquesced asci. e–i Variously shaped ascospores, sometimes with apical structures arrowed (g–h). j–l Apical chambers. m–n Apical structures to the ascospores with apical chambers in a side position arrowed (n). o–p. Chlamydospores. q–w Variously shaped conidia. Scale bars: a–b = 10 µm, c = 15 µm, d–i = 50 µm, j = 5 µm, k–n = 10 µm, o–p = 10 µm, q–w = 30 µm.

Moleospora Abdel-Wahab, Abdel-Aziz & Nagah., in Abdel-Wahab, Pang, Nagahama, Abdel-Aziz & E.B.G. Jones, Mycol. Progr. 9: 547 (2010)

Index Fungorum number: IF543116

Saprobic on submerged marine substrates. Sexual morph: Undetermined. Asexual morph: *Hyphae* septate, branched, yellow-brown, superficial and immersed. *Conidiophores* present or obsolete, macronematous, septate, hyaline to light-brown, cylindrical to clavate. *Conidiogenesis* is holoblastic. *Conidia* helicoid when young and quickly become a mass of cells, dark brown to black, lateral, single, determinate. *Conidial cells* are generally similar in shape, colour and size that are globose, subglobose, rounded or with truncate base, brown to dark brown.

Notes – This is a monotypic marine asexual genus in the *Lulworthiales* (Abdel-Wahab et al. 2010) isolated from *Phragmites australis* collected in Egypt. Morphologically it is similar to *Halenospora varia* and *Cumulospora marina*, but differs in conidial dimensions and shape and size of the conidial cells and phylogenetically distant from these genera (Abdel-Wahab et al. 2010).

Type species – *Moleospora maritima* Abdel-Wahab, Abdel-Aziz & Nagah.

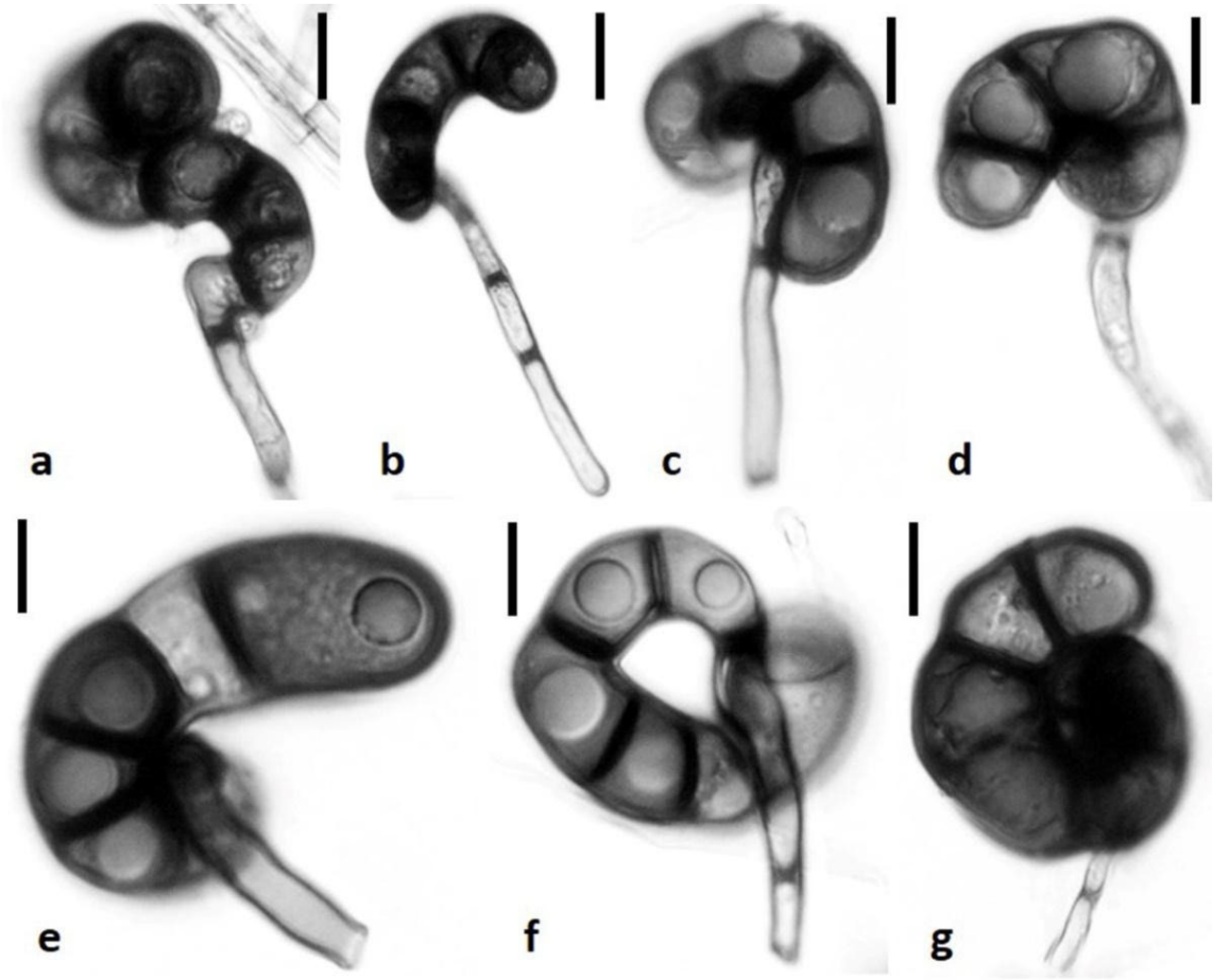

Figure 19 – *Matsusporium tropicale*. a–g Variously shaped mature conidia. Scale bars: a–g = 10 μm.

Moleospora maritima Abdel-Wahab, Abdel-Aziz & Nagah., in Abdel-Wahab, K.L. Pang, Nagahama, Abdel-Aziz & E.B.G. Jones, Mycol. Progr. 9(4): 548 (2010) Fig. 21

Index Fungorum number: IF543117

Saprobic on submerged marine substrates. Sexual morph: Undetermined. Asexual morph: *Hyphae* 2.5–4 μm in diameter, septate, branched, yellow-brown, superficial and immersed. *Conidiophores* present or obsolete, when present are 25–60 μm long, 6–10 μm in diameter, macronematous, 0-5-septate, hyaline to light brown, cylindrical to clavate. *Conidiogenesis* holoblastic. *Conidia* helicoid when young and quickly becomes mass of cells 40–225×36–175 μm, dark brown to black, lateral, single, determinate. *Conidial cells* 10–14×12–14 μm, generally similar in shape, color and size that are globose, subglobose, rounded or with truncate base, brown to dark brown.

Material examined – Egypt, Port Said, Mediterranean Sea coast, on decayed drift stems of *Phragmites australis,* June 2006, M.A. Abdel-Wahab and F. A. Abdel-Aziz, IMI 397965, holotype.

Notes – Several marine fungi, namely *Halenospora varia*, *Cumulospora marina* and *C. varia,* have conidia which are a mass of cells when mature and helicoid when young. However, *Moleospora maritima* differs from the previously mentioned fungi in having larger solid black conidia (like immature ascomata when mature, or sclerocarps) with a large number of conidial cells that are small in size. *Moleospora maritima* is similar to *Halenospora varia* in having complex and massive conidia that contain hundreds of small cells, with *M. maritima* having larger conidia (40–225×36–175 µm) than those of *H. varia* (15–65.2×13.5–55.8 µm). Phylogenetic analyses of the ITS sequence placed *H. varia* in *Leotiaceae* (Bills et al. 1999), while *M. maritima* is a member of the *Lulworthiaceae*.

Figure 20 – *Matsusporium tropicale* (NY, Kohlmeyer 1888a holotype and NY, Kohlmeyer 1892 paratype). a Herbarium material. b Appearance of conidia and conidiophores on wood surface. c–e Conidiophores. f–h Helicoid conidia. Scale bars: c = 50 µm, d–e = 20 µm, f–h = 10 µm.

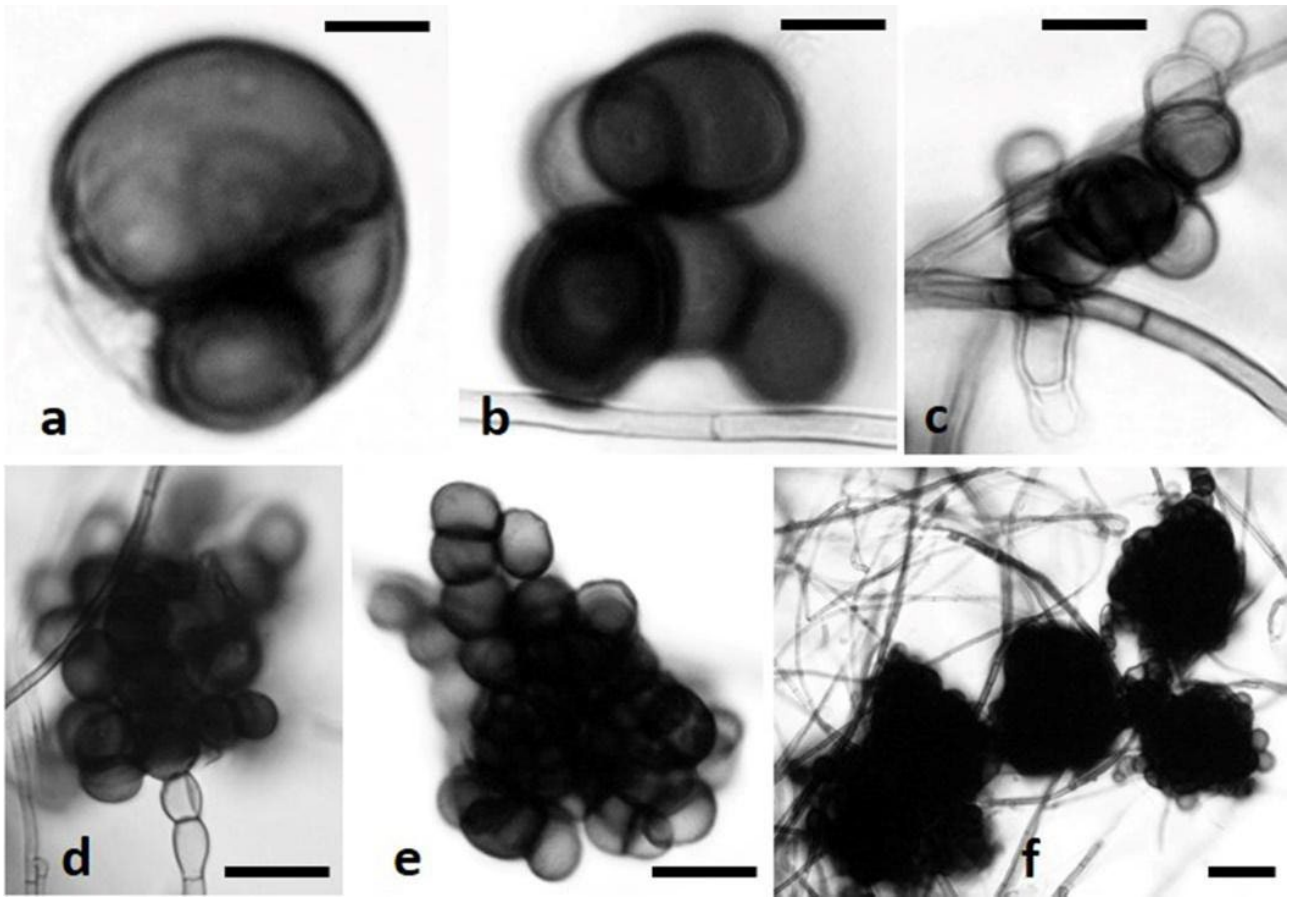

Figure 21 – *Moleospora maritima.* a–f Variously shaped conidia at different stages of maturity. Scale bars: a–f = 10 µm

Moromyces Abdel-Wahab, K.L. Pang, Nagah., Abdel-Aziz & E.B.G. Jones, in Abdel-Wahab, Pang, Nagahama, Abdel-Aziz & E.B.G. Jones, Mycol. Progr. 9: 555 (2010)

Index Fungorum number: IF543127

Saprobic on submerged marine substrates. Sexual morph: Undetermined. Asexual morph: *Hyphae* septate, branched, superficial or immersed, pale-brown. *Conidiophores* absent. *Conidiogenous cells* holoblastic, integrated, terminal, determinate. *Conidia* dark-grey to fuscous, solitary, scattered or gregarious, muriform. *Conidia* initially spiral, but cell divisions in several planes, leads to a tangled knot of cells.

Notes – This is a marine monotypic asexual genus in the order *Lulworthiales* forming a sister clade to *Lulwoana.* The genus was introduced for the species *Cumulospora varia*, as it was distantly placed from the type species, *Cumulospora marina* (Abdel-Wahab et al. 2010).

Type species – *Moromyces varius* (Chatmala & Somrith.) Abdel-Wahab, K.L. Pang, Nagah., Abdel-Aziz & E.B.G. Jones

Moromyces mangrovis Dayar., K.D. Hyde & E B G Jones, sp. nov. Fig. 22

Index Fungorum number: IF900101

Etymology – In reference to its mangrove habitat.

Holotype – MFLU 18-0522

Saprobic on submerged wood of *Bruguiera cylindrica*. Sexual morph: Undetermined. Asexual morph: *Hyphae* septate, branched, superficial, black. *Conidiophores* not observed. *Conidiogenous cells* holoblastic, integrated, terminal, determinate. *Conidia* 55–100×30–80 µm brown, solitary, scattered or gregarious, muriform.

Culture characteristics – Colonies on seawater PDA reaching 10 cm diam. after 2 weeks at 25°C, dense, circular, slightly raised, surface smooth with entire edge, fluffy, colony from above: blackish gray; from below grey.

Material examined – Thailand, Ranong Province, Ranong, on decaying submerged wood of *Bruguiera cylindrica* (*Rhizophoraceae*), 12 June 2016, M.C. Dayarathne, MCD 032 (MFLU 18-0522, holotype), ex type living culture MFLUCC 17-0392.

GenBank numbers – SSU=OP884603, LSU=OP884599

Notes – Conidia of *M. mangrovis* (55–100×30–80 µm) are larger than those of *M. varius* (24–87×21–50 µm) (Pang et al. 2011). Base pair differences of 28S rDNA region of *M. mangrovis* (MFLU 18-0522) and *Moromyces varia* (EU848578) were 13 out of 868 (1.5 %). *Moromyces mangrovis* formed a sister lineage to *M. varia* with high statistical support (100% MP, 97% ML, 1.00 pp) (Fig. 1). Therefore, based on both morpho-molecular analyses we here introduce *M. mangrovis* to *Moromyces*.

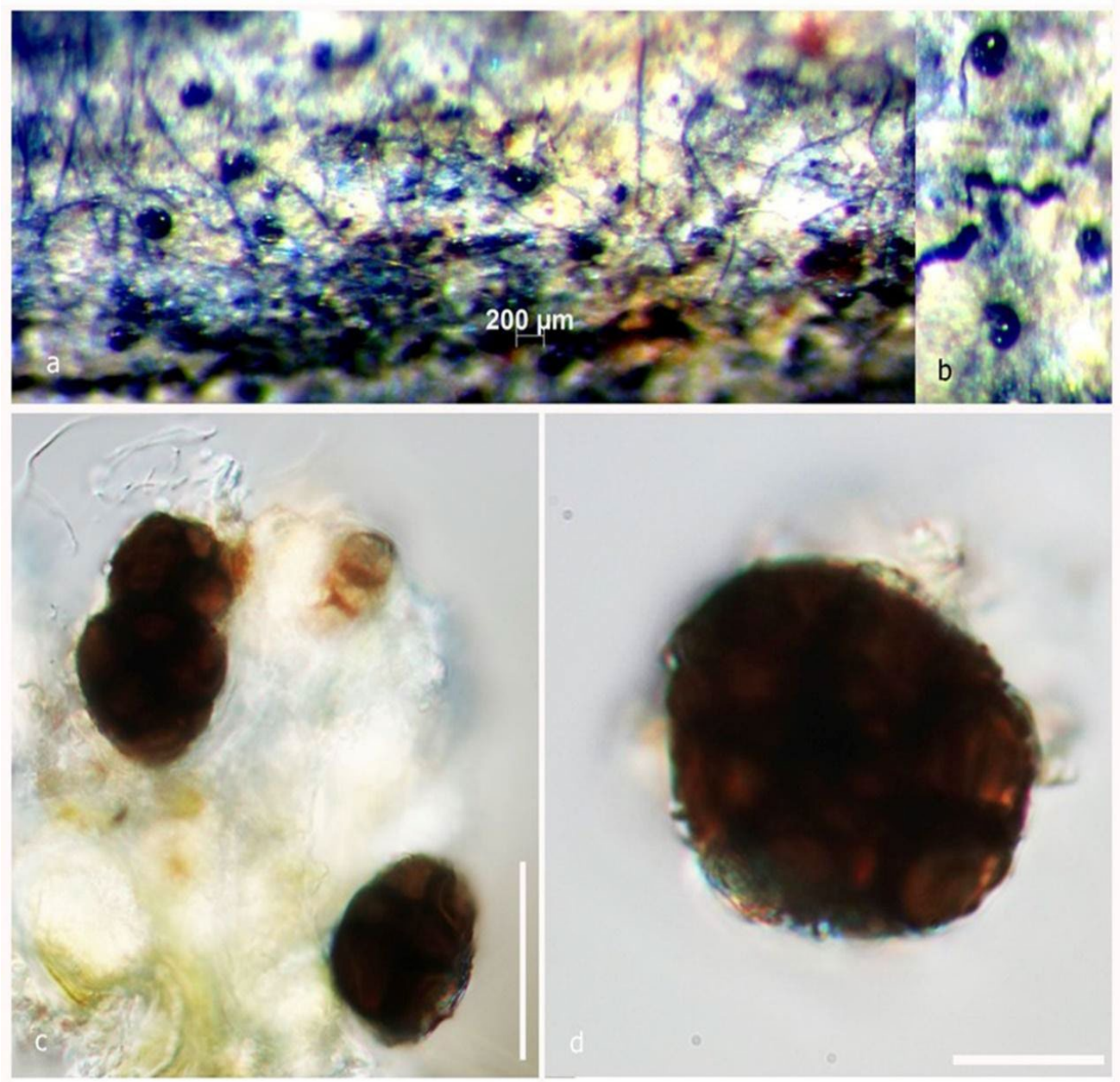

Figure 22 – *Moromyces mangrovis* (MFLU 18-0522, holotype). a–b Colonies on submerged wood. c–d Conidia. e–f Cultures on potato dextrose agar (e–top view, f–bottom view). Scale bars: a = 200 µm, c–d = 50 µm.

Moromyces varius (Chatmala & Somrith.) Abdel-Wahab, K.L. Pang, Nagah., Abdel-Aziz & E.B.G. Jones, in Abdel-Wahab, Pang, Nagahama, Abdel-Aziz & E.B.G. Jones, Mycol. Progr. 9: 555 (2010) Figs. 23–24

Basionym – *Cumulospora varia* Chatmala & Somrith., in Chatmala, Sakayaroj, Somrithipol & Phongpaichit, Fungal Divers. 17: 3 (2004)

Index Fungorum number: IF543128

Saprobic on submerged marine substrates. Sexual morph: Undetermined. Asexual morph: *Hyphae* septate, branched, superficial or immersed, pale brown. *Conidiophores* absent. *Conidiogenous cells* holoblastic, integrated, terminal, determinate. *Conidia* 24–87×21–51 µm, dark grey to fuscous, solitary, scattered or gregarious, muriform. *Conidia* initially spiral, but cell division in several planes, leads to a tangled knot of cells that may number 40 or more and up to 20 µm diameter or more of each individual cell.

Material examined – Thailand, Gulf of Thailand, Mu Ko Chang National Park, Trat province, on decaying driftwood, Feb. 2001, I. Chatmala, IT152 (BBH); Thailand, Gulf of Thailand, Mu Ko Chang National Park, Trat province, unidentified driftwood, Feb. 2001, re-inoculated on decayed wood by I. Chatmala, holotype BBH 34419.

Notes – *Moromyces varius* is different from *Cumulospora marina* by having a muriform, irregularly helicoid conidia, while the latter fungus has rosette-like conidia, globose conidial cells that form pseudo-chains and can be separated from each other when pressed under cover glass. *Cumulospora marina* has conidia that are differentiated into small basal cells which form a filament and larger rounded apical cells, while conidia in *M. varius* form a knot of cells that are similar in shape and size. *Moromyces varius* formed a sister group to *Lulwoana uniseptata* and its anamorph *Zalerion maritima* (Jones et al. 2008), but the clade that contains the three taxa had received weak bootstrap support. Morphologically the conidia are initially coiled but cell division in many planes leads to a tangled knot of cells, thus differing it from *Z. maritima* whose conidia are distinctly coiled. We could not observe hyphae and conidiogenous cells in the holotype from Thailand.

Orbimyces Linder, Farlowia 1(3): 404 (1944)

Index Fungorum number: IF9170

Saprobic on wood panels, intertidal and wood, driftwood, sandy soil. Sexual morph: Undetermined. Asexual morph: *Conidiophores* lacking, *conidia* developing on short conidiogenous cells, large, dark, sub-globose with a crown of radiating, septate appendages at the distal end.

Type species – *Orbimyces spectabilis* Linder, Farlowia 1: 404 (1944)

Notes – The genus was introduced by Barghoorn and Linder (1944) on wood collected in Massachusetts, USA, with its unique, large, dark conidia with radiating arms and known only from the marine environment. Phylogenetic data available: one isolate in the USA, one from material collected in Denmark (Jones et al. 2008).

Orbimyces spectabilis Linder, Farlowia 1: 404 (1944)

Index Fungorum number: IF288988

Material examined – Collections made in Denmark and living cultures.

Saprobic on wood panels, intertidal and wood, driftwood, sandy soil. Sexual morph: Undetermined. Asexual morph: *Conidiophores* lacking, conidia developing singly on short, truncate, conidiogenous cells on the mycelium. *Conidia* 24–41.5×18–37 µm, large, shining black cell wall, sub-globose to ovoid, a large black basal cell and a crown of 4–5 radiating arms, one polar and 4 latterly placed, arms 15–50×4–6.5 µm, 1–4 septate, pale brown, fading towards the tip. Germination of the conidia from the tips of the arms, and never from the basal cell.

Notes – Collections of *Orbimyces spectabilis* have been reported from Canada, Denmark, Germany, Sweden, UK, Ivory Coast, however it is an infrequent species, and known only from the marine environment. Koch and Jones (unpublished data) collected *O. spectabilis* growing on sandy soil on a cliff side in Denmark. Rarely isolated.

Sequence data – A 18S rDNA sequence is available in the GenBank (Jones et al. 2008). Jones et al. (2008) showed that the anamorph *O. spectabilis* grouped basal to the *Lulwoidea* clade (*Lulwoidea lignoarenaria*, but with weak support in the *Lulworthiaceae*, *Lulworthiales*). Based on morphological and molecular data *Lulworthia lignoarenaria*, was referred to the new genus *Lulwoidea* by Campbell et al. (2005).

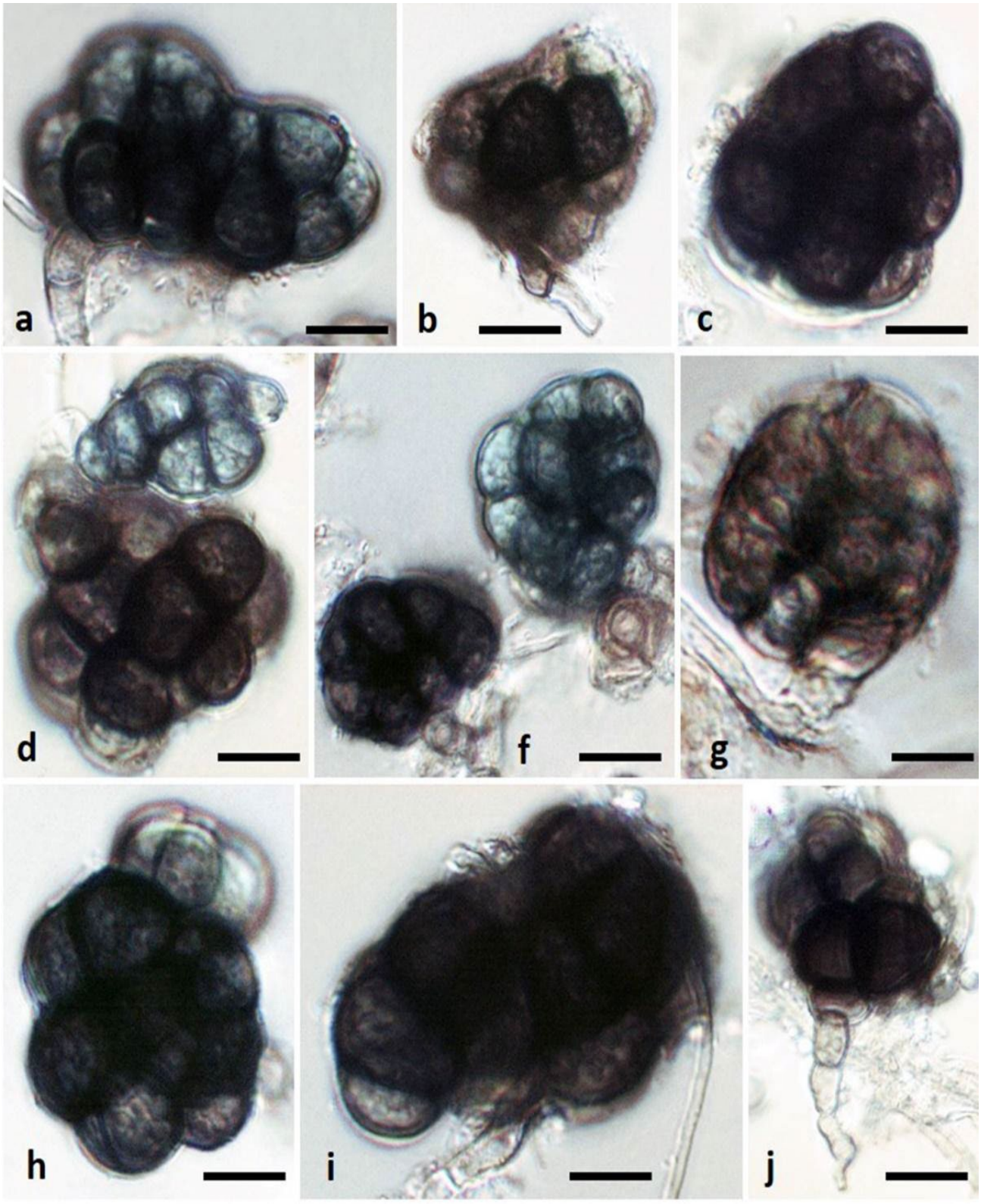

Figure 23 – *Moromyces varius.* a–j Variously shaped conidia at different stages of maturity. Scale bars: a–j = 10 µm.

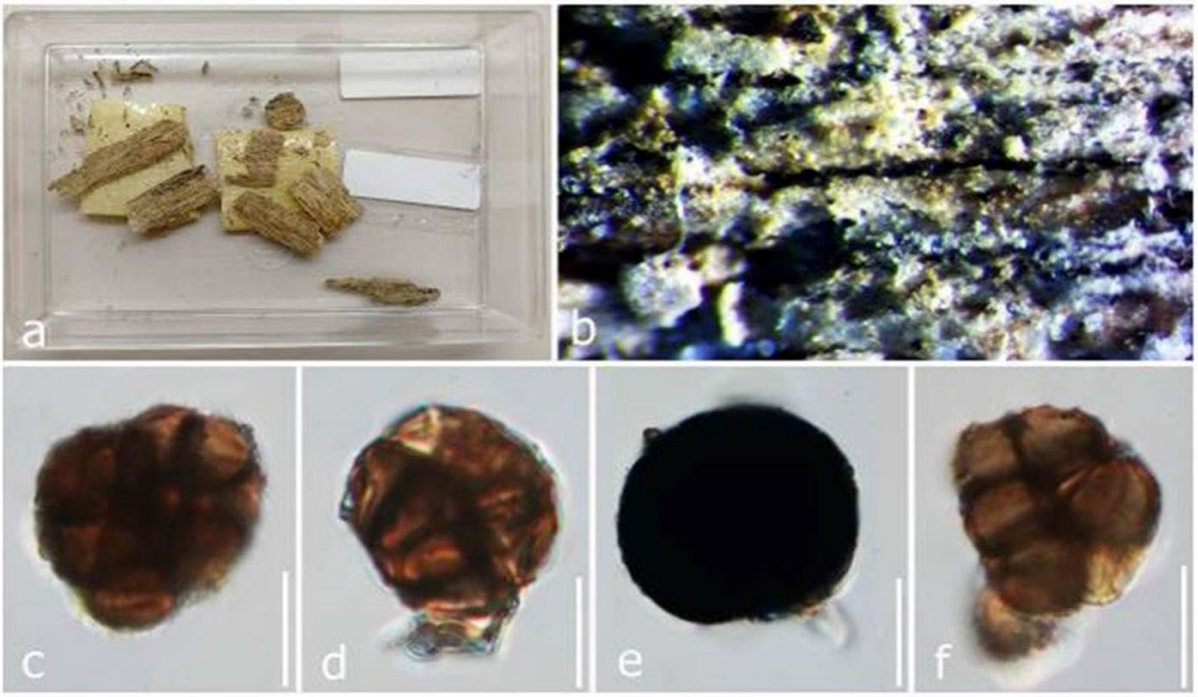

Figure 24 – *Moromyces varius* (BBH 34419, holotype). a Herbarium material. b Conidia on host surface. c–f Conidia at different stages of development. Scale bars: c–f = 10 μm.

Paralulworthia A. Poli, E. Bovio, L. Ranieri, G.C. Varese & V. Prigione, Frontiers in Microbiology 11 (no. 933): 6 (2020) **emend. Rämä, Hagestad, K.L. Pang, E. Azevedo, M.F. Caeiro & E.B.G. Jones**

Index Fungorum number: IF833285

Saprobic on wood and *Posidonia oceanica* rhizomes. Sexual morph: *Ascomata* globose–subglobose to ellipsoidal, superficial, partly immersed, brown, blackish, coriaceous. *Peridium* dark brown, 2-layered. *Necks* are cylindrical. No paraphyses or catenophyses. *Asci* 8-spored, cylindrical with pointed ends, unitunicate, thin-walled and early deliquescing, without an apical apparatus. *Ascospores* hyaline, filiform, curved, coiled, tapering towards both ends, no septa, with oil droplets and with apical, cone-shaped end chambers. Asexual morph: *Chlamydospores* numerous, solitary and multicellular, from 1–3 septate, globose to subglobose, light to dark brown.

Type species – *Paralulworthia gigaspora* A. Poli, E. Bovio, L. Ranieri, G.C. Varese & V. Prigione, Frontiers in Microbiology 11(no. 933): 9 (2020)

Notes – Poli et al. (2020) introduced *Paralulworthia* from material collected on the rhizomes of the sea grass *Posidonia oceanica,* in the Mediterranean Sea, Elba Island, Tuscany, Italy. *Paralulworthia gigaspora* differs from other genera in the *Lulworthiales* by its 1–3 septate brown ascospores. A second sexual morph (*Paralulworthia posidoniae)* was also isolated from *P. oceanica* and has ascospores similar to *P. gigaspora*. The ascomata and spore morphology of *P. gigaspora* and *P. posidoniae* are atypical for *Lulworthiales* species and the conspecificity of the sporulating and non-sporulating stage was not confirmed using a sequencing approach. Poli et al. (2020) obtained the sporulating material by growing cultures on plates for four weeks, then adding the wood and incubating for a further four weeks. Finally, the wood was placed in seawater and after a further 4 weeks ascomata were formed (E.B.G. Jones communication with the authors of Poli et al. 2020). This workflow can be prone to contamination. There are no voucher specimens of the teleomorph stages available for study, DNA extraction or sequence analysis. Thus, we cannot exclude the possibility of the sporulating forms representing contaminants and other species than were originally isolated and cultured in their vegetative form on plates.

Due to the ambiguity in the morphology of the sexual morphs of these two species, clarification of the holotype is required. The holotype was designated as “Europe, Italy, Tuscany,

Mediterranean Sea, Elba Island (LI), Ghiaie ISL, 3–5 m depth, 42◦490 04″N,10◦190 2000E March 2010, R. Mussat-Sartor and N. Nurra, on the sea grass *Posidonia oceanica* rhizomes, MUT 435 holotype, living culture permanently preserved in metabolically inactively state by deep-freezing at MUT. MUT 672 and MUT 5413=paratypes", with no mention of the sexual stage illustrated in their manuscript. We therefore regard the chlamydospore structures as the basis of the type material, which was not illustrated (Poli et al. 2020). Subsequent *Paralulworthia* species did not include the sexual morphs ascribed to *P. gigaspora* and *P. posidoniae* (Poli et al. 2020).

A review of the species descriptions of *P. gigaspora* and *P. posidoniae* reveals that *P. gigaspora* has in general larger ascomata, asci and spores (Poli et al. 2020) that may be explained by variation related to different stages of ascoma and spore production. Moreover, these two species, as well as the other three *Paralulworthia* species introduced in Poli et al. (2020, 2021), have the same ecology being isolated from *Posidonia* rhizomes in the same locality with same collection month and year, except *P. elbensis* which was collected on the same island of Elba, but from a different location. Our multi-gene phylogenetic analyses (Fig. 3) show that *P. gigaspora* and the other *Paralulworthia* species formed a well-supported clade with extremely short branches and polytomy representing small variations in a population structure of a single species, rather than distinctive species. The collection of a new taxon from Norway with characters identical to the genus *Lulworthia* further casts doubt as to the description provided by Poli et al. (2020). Consequently, we have emended the generic protologue for *Paralulworthia*.

Fig. 3 is based on phylogenetic inferences on a combined dataset of nrITS, nrSSU, nrLSU, RPB1, RPB2, TEF1α and TUB2 where many clades are non-supported within *Paralulworthia*. Poli et al. (2020, 2021) list six *Paralulworthia* species isolated from *Posidonia oceanica* (*P. gigaspora, P. posidoniae, P. candida, P. elbensis, P. mediterranea*), submerged wood (*P. halima*) and oil-contaminated seawater (*P. gigaspora*) and supported by molecular data. Based on the ecology and the phylogeny of the described *Paralulworthia* species, we suggest to keep the type species, *P. gigaspora*, until further materials are available to resolve their phylogenetic relationships and morphological ambiguity. We also introduce *P. lignicola* from collections made in Norway. Accepted species in *Paralulworthia* are listed here.

Paralulworthia gigaspora A. Poli, E. Bovio, L. Ranieri, G.C. Varese & V. Prigione, Frontiers in Microbiology 11(no. 933): 9 (2020)

Synonyms – *Paralulworthia mediterranea* A. Poli, E. Bovio, G.C. Varese & V. Prigione, in Poli, Prigione, Bovio, Perugini & Varese, Journal of Fungi 7(11, no. 940): 8 (2021)

Paralulworthia posidoniae A. Poli, E. Bovio, L. Ranieri, G.C. Varese & V. Prigione, Frontiers in Microbiology 11(no. 933): 9 (2020)

Paralulworthia halima (Anastasiou) M. Gonçalves, A. Abreu & A. Alves, Mycologia: 10.1080/00275514.2021.1875710, 12 (2021)

Index Fungorum number: IF833288

Paralulworthia lignicola Rämä & Hagestad, sp. nov. Fig. 25

Index Fungorum number: IF900120

Etymology – The species epithet refers to the isolation source and only known substrate of the species.

Saprobic on wood. Sexual morph: *Ascomata* gregarious or solitary, superficial or partly immersed, brown to blackish, coriaceous, easily rupturing, globose or subglobose, covered with mycelium and chlamydospores, with an elongated neck, 245–789×223–700 µm (excluding neck dimensions). *Peridium* 2-layered, outer layer consisting of pigmented (brown) hyphae, 2.3–4.3 in diameter, forming *textura intricata* and thick-walled chlamydospores produced at hyphal tips, inner layer *textura angularis* with melanized cells that are 5.1–12.7–28.5×3.4–6.2–16.2 µm in size. No paraphyses or catenophyses. *Necks* are cylindrical, concolorous with rest of the ascomata, sometimes partly paler, shorter than ascomata, 264–323 µm in length, 93–129 µm in width in the apical region and 127–212 µm in the basal part. Inner part of ascoma is filled with mature and

deliquescing asci, released spores and mucus. *Asci* 8-spored, cylindrical with pointed ends, unitunicate, thin-walled and early deliquescing, without an apical apparatus, 200–221×13.4–15.8 µm. *Ascospores* 165–222–278×3.2–3.6–4.1 µm, hyaline, filiform, coiled, tapering towards both ends, aseptate, with oil droplets and with apical, cone-shaped end chambers, 6.2–7–8.6 µm in length, filled with mucus, exuded when mounted in water. *Chlamydospores* 1–2(–4)-celled, subglobose to cylindrical with frequent irregularities in shape, brown, constricted at septa, 7.3–9.6 (median)–21.2×5.0–6.5–10.9 µm, solitary or in aggregates, infrequently arranged in distinct threads. Asexual morph: Undetermined.

Colony morphology – Colonies after 28 d incubation at 18°C, on CMA prepared with Instant Ocean Sea Salts (Aquarium Systems, Sarrebourg, France) reaching 63 mm in diam., flat, circular with filiform margin, whitish grey – translucent. On low nutrient MEA (with 4g malt extract per liter) prepared with sea salts reaching 85 mm in diam., flat with some tufts of elevated hyphae near margins of a fully-grown Petri dish, circular with filiform margin, greyish green.

Holotype – Norway, North Atlantic Ocean, Nordland County, Bodø, Skjerstadfjorden, Vågan (station M10TMU0025), 67.2925492 N 14.8607174 E, isolated from a piece of deciduous tree (diameter 5 cm, length 20 cm, decay class 2 at scale from 1 to 5) with holes from marine boring invertebrates, in the intertidal zone, Coll. Hans Christian Eilertsen 14.10.2010, TRä107aIA.

Material examined – The type material consists of a dried culture with fruiting structures, microscope slides and is preserved in the collections of the Arctic University Museum of Norway (TROM-F26842).

Notes – The description of the sexual morph of the species is based on one fruiting culture on low-nutrition malt extract agar that was prepared in filtered seawater (4 g malt extract per 1 litre water). Not all ascomata were fully developed and only few were used for the diagnosis. The species is characterized by abundant chlamydospore production and spores containing plenty of oil. Phylogenetically based on nuclear rDNA sequences representing the 18S and 28S genes and the ITS area (including 5.8S gene) and protein coding genes (TEF1α, RPB1, RPB2 and MCM7) the species is a sister taxon to the type species of *Paralulworthia*, *P. gigaspora*, and *P. elbensis*.

Paramoleospora M. Li & L. Cai, In: Li et al. Microbiome 11:272 (2023).

Index Fungorum number: IF571528

Etymology – Referring to the close phylogenetic relationship with the genus *Moleospora.*

Saprobic in marine sediments**.** Sexual morph: Undetermined. Asexual morph: *Conidiophores* present or obsolete, when present mononematous, micronematous, septate, hyaline to light brown, cylindrical to clavate. *Conidiogenous cells* holoblastic, born on conidiophores or directly on mycelia, hyaline to brown. *Conidia* terminal or intercalary, subglobose, ellipsoidal to ovoid, thick- and smooth-walled, brown to dark brown, aseptate, guttulate.

Type species – *Paramoleospora guttulata* M. Li & L. Cai

Notes – *Paramoleospora* is herein introduced to accommodate the asexual morph of *P. guttulata.* It forms a distinct clade sister to *Moleospora*, but differs from the latter by the conidial shape (subglobose, ellipsoidal to ovoid vs. helicoid).

Paramoleospora guttulata M. Li & L. Cai, In: Li et al. Microbiome 11:272 (2023).

Index Fungorum number: IF352449.

Etymology – Referring to the guttulate conidia of this species.

Saprobic in marine sediments. Hyphomycetous. Sexual morph: Undetermined. Asexual morph: *Hyphae* hyaline, septate, smooth, branched, 2.0–3.0 µm wide. *Conidiophores* present or obsolete, when present mononematous, micronematous, 2–6-septate, hyaline to light brown, cylindrical, 32–92×1.5–2.0 µm. *Conidiogenous cells* holoblastic, born on conidiophores or mycelia, hyaline to brown, 2.0–5.0 µm width at base. *Conidia* terminal or intercalary, sometimes forming directly from mycelium, without the formation of conidiogenous cells, subglobose, ellipsoidal to ovoid, thick- and smooth-walled, brown to dark brown, aseptate, 12–2×7.5–14 µm (av.=16.6±1.94×10.2±1.23 µm, n=50), guttulate.

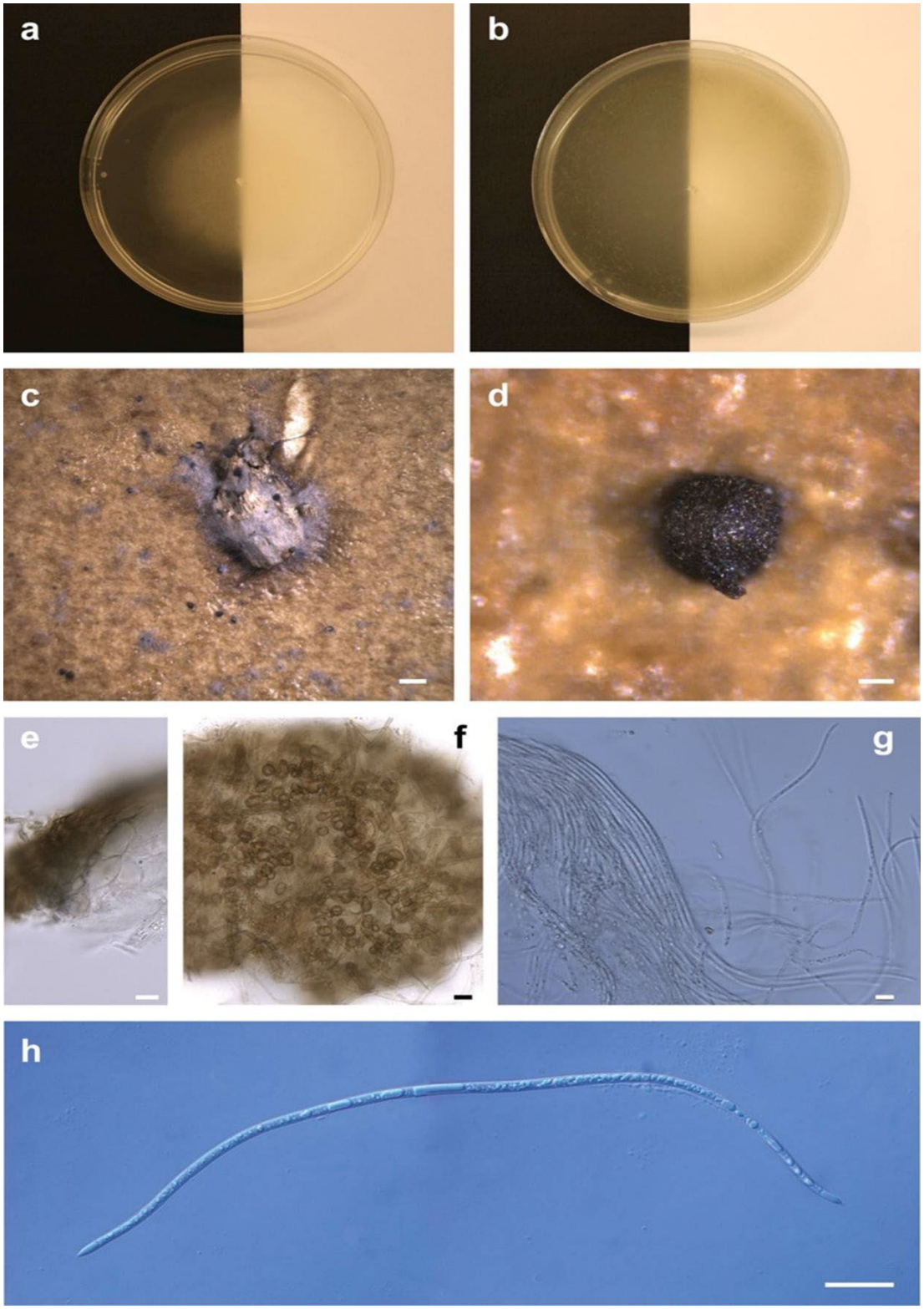

Figure 25 – *Paralulworthia lignicola* (TROM-F26842, holotype). a A pure culture plate with the fungus on low-nutrition malt extract agar prepared with artificial seawater, cultured for 28 days at 18 °C, from above. b A pure culture plate with the fungus on low-nutrition cornmeal agar prepared with artificial seawater, cultured for 28 days at 18°C. c The dried holotype specimen of the fungus with ascomata and mycelium on a wooden cube and surrounding culture medium. d An ascoma of the fungus. e A micrograph showing inner cell wall structure with melanized cells. f Chlamydospores and hyphae of the outer cell wall of an ascoma. g Deliquescing asci and spores,

in differential interference contrast (DIC) microscope. h A single ascospore, in DIC. Scale bars: c = 1000 µm, d = 200 µm, e–g = 10 µm, h = 20 µm.

Culture characteristics – colonies after 3 weeks at 25°C, on PDA reaching 48–53 mm diam., flat, felty to pulverulent, margin irregular, whitish grey, sea green to black, aerial mycelium moderately abundant. Reverse black near the center, sea green with whitish grey edge.

Material examined – China, Guangdong Province, National Mangrove Nature Reserve of Zhanjiang, isolated from sediment, November 2019, M. Li and J. E. Huang, HMAS352449 (holotype designated here, dried culture), ex-type living culture CGMCC3.22494=LC15932; ibid., CGMCC 3.22495=LC15933.

Notes –Morphologically *P. guttulata* differs from the phylogenetically closely related species *Moleospora maritima* in producing micronematous conidiophores, whereas species in *M. maritima* produces macronematous conidiophores. Furthermore, conidia in *P. guttulata* are terminal or intercalary, solitary and guttulate, while in *M. maritima* conidia are lateral, eguttulate, and helicoid when young and quickly become mass. Additionally, the conidia of *P. guttulata* are longer than *M. maritima* (12–21×7.5–14µm vs. 10–14×12–14 µm) (Abdel-Wahab et al. 2010). *Paramoleospora guttulata* bears a resemblance to *Halosphaeriopsis alopallonella* which has conidia 14–24 µm×7–11 µm, solitary, thick-walled, smooth, straight, 2–4-septate, strongly constricted at the septa, apical cell large subglobose, ellipsoidal, ovoidal to obpyriform, fuscous, reddish-brown to dark brown, basal cell smaller, obconical, light brown (Calabon et al. 2023). Phylogenetically *H. alopallonella* groups in the Halosphaeriaceae with strong support (Calabon et al. 2023).

Pontogeneia Kohlm., Bot. Jb. 96(1-4): 201 (1975)

Index Fungorum number: IF4335

Parasitic on marine algae (Phaeophyta**).** Sexual morph: *Ascomata* solitary to gregarious, subglobose or ovoid, superficial or semi-immersed ostiolate, papillate or epapillate, coriaceous, black. *Paraphyse*s distinct, thick, septate, or indistinct. *Asci* 8-spored, clavate or fusiform, unitunicate, thin-walled, early deliquescing, attached in the lower part of the locule. *Ascospores* filiform, rarely ellipsoidal, hyaline, often covered, phragmosporous. Asexual morph: Undetermined.

Type species – *Pontogeneia padinae* Kohlm., Bot. Jb. 96(1-4): 201 (1975)

Notes – Kohlmeyer (1975) introduced *Pontogeneia* which comprises five perithecial ascomycetes parasitizing marine algae, belonging to the Chlorophyta or Phaeophyta (Kohlmeyer & Kohlmeyer 1979, Kohlmeyer & Demoulin 1981). Later, three more species have been added (Kohlmeyer & Kohlmeyer 1979, Kohlmeyer & Demoulin 1981, Campbell et al. 2009). Campbell et al. (2009) assigned *Koralionastes* and *Pontogeneia* to a new order *Koralionastetales* based on phylogenetic analyses of combined SSU and LSU rDNA sequence data and morphological comparisons. Maharachchikumbura et al. (2015) placed this under Sordariomycetes, genera *incertae sedis,* while Jones et al. (2015) accepted the placement of both *Koralionastes* and *Pontogeneia* under *Koralionastetaceae.* Sequence data available in the GenBank is only for one species. *Pontogeneia* species are known as algal inhabiting fungi and few collections have been reported and further collections are required for sequencing.

Pontogeneia padinae Kohlm., Bot. Jb. 96(1-4): 201 (1975) Fig. 26

Index Fungorum number: IF320920

Parasitic on living plants near the base among rhizoids of the holdfast. Sexual morph: *Ascomata* sub solitary, scattered, immersed to semi immersed in host filaments, uniloculate, globose to sub globose, glabrous, ostiole central with minute papilla. *Peridium* 32–52 µm thick, composed of several layers of thick, dark brown to black, cells. *Paraphyses* septate, constricted and branched. *Asci* 140–200×25–46 µm, 8-spored, fusiform to clavate, stipitate, unitunicate, thin-walled, early deliquescing. *Ascospores* 99–167 (–172) ×10–12 µm, elongate, fusiform, hyaline,

slightly curved with rounded ends, septate, not constricted at the septa. Asexual morph: Undetermined.

Material examined – Intertidal zone at the Marine Laboratory of the University of Arizona, on living plants near the base among rhizoids of the holdfast, 22 Jun 1974, J. J. Kohlmeyer, NY 985934, holotype.

Notes – This species is known only from the brown alga *Padina durvillaei* from the Mexico, Pacific coast. Further collections are required to determine its ecological role in the marine environment and how the host becomes colonized.

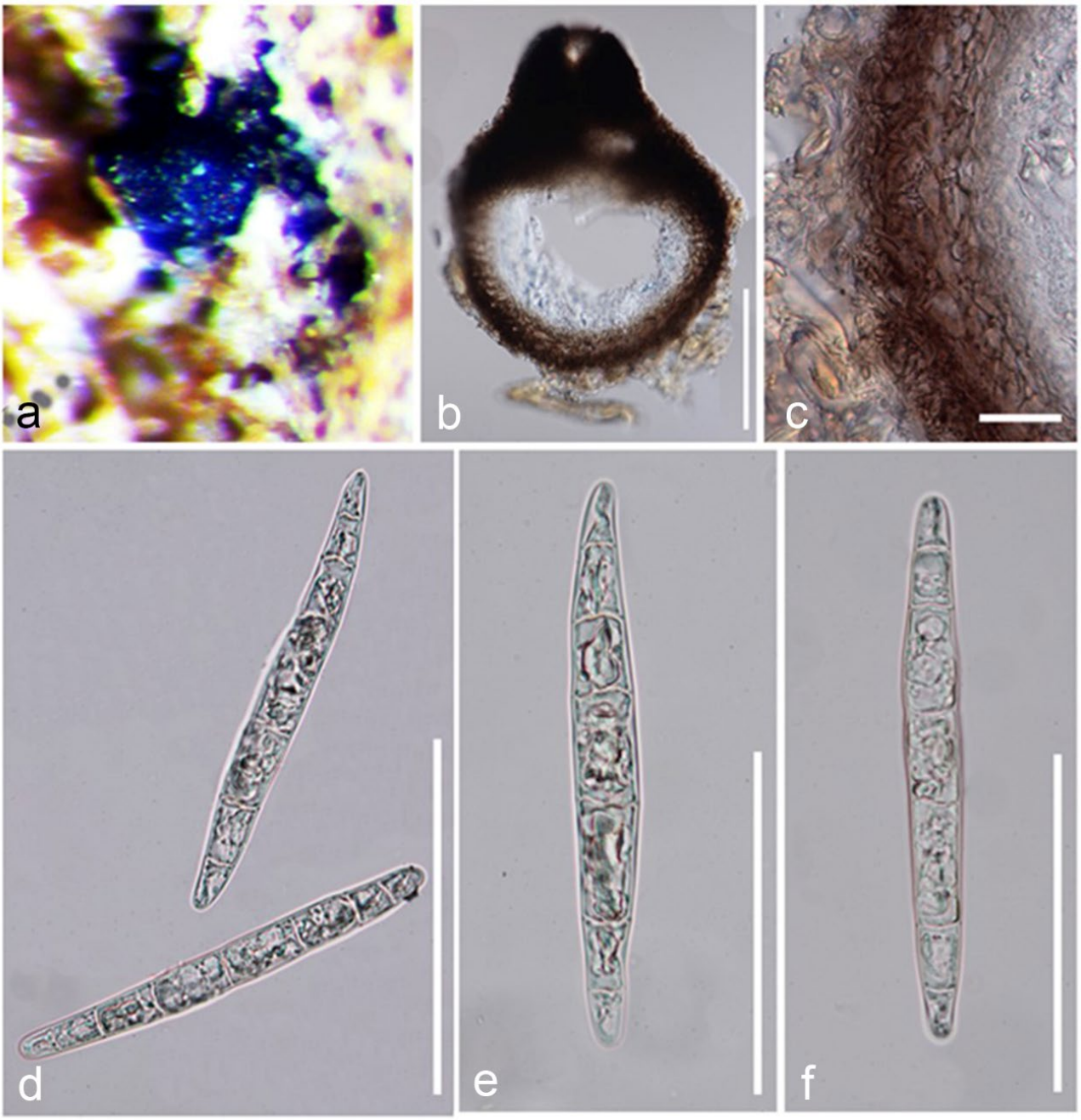

Figure 26 – *Pontogeneia padinae* (NY 985934 holotype) a Herbarium material. b Section through an ascoma. c Peridium. d–f Ascospores. Scale bars: b = 100 µm, c = 20 µm, d–f = 10 µm.

Rambellisea Pasqual. & Braconcini, J. Fungi 10 (2, no. 127): 8 (2024)

Index Fungorum number: IF850303

Type species – *Rambellisea gigliensis* Pasqual. & Braconcini, J. Fungi 10 (2, no. 127): 8 (2024)

Epizooic on the tunicate *Halocynthia paillosa* (red sea squirt). Sexual morph: Undetermined. Asexual morph: *Hyphae* septate, sub-hyaline sometimes lightly pigmented, assuming a toruloid aspect mainly in submerged mycelium, with dark concretions like small droplets on hyphae in old cultures. *Chlamydospores* subhyaline to light brown, globose to sub-globose, monocellular, sometimes one septate, and pyriform.

Notes – *Rambellisea* was established by Braconcini et al. (2024) with *Rambellisea gigliensis* as the type species, based on the multi-locus phylogenetic analysis of nuclear ITS, 28S, and 18S rDNA sequence data. *Rambellisea gigliensis* was isolated from sporulating material on the tunica of ascidians or sea squirts, *Halocynthia papillosa*, and characterised by enlarged hyphae and chlamydospore production. No sexual or asexual structures were reported. *Rambellisea* forms a sister clade with *Paralulworthia* while a second species, *R. halocynthiae*, was also isolated from tunica of *H. papillosa* collected at Giglio Island (Grosseto), Punta Gabbianara, Mediterranean Sea, Tuscany, Italy.

Rambellisea gigliensis Pasqual. & Braconcini, J. Fungi 10 (2, no. 127): 8 (2024)

Index Fungorum number: IF850306

Epizooic on the tunicate *Halocynthia papillosa* (red sea squirt). Sexual morph: Undetermined. Asexual morph: *Hyphae* 3.0–4.6 µm wide, septate, sub-hyaline sometimes lightly pigmented, assuming a toruloid aspect mainly in submerged mycelium. In old cultures, dark concretions like small droplets were observed on hyphae. *Chlamydospores* 10.5–20.0 µm, subhyaline to light brown, globose, sub-globose, monocellular, sometimes one septate, and pyriform.

Culture characteristics – Colonies on PDASW, reaching 8 mm diameter after 28 days at 25◦C, dome-like, surface flocculose, smoke-grey to brown; aerial mycelium, whitish to light brown; margins regular, reverse brown. Soluble pigment is yellowish to orange, lacking exudates.

Material examined – Italy, Tuscany, Mediterranean Sea, Giglio Island (Grosseto), Punta Gabbianara, 42◦21′50″ N, 10◦55′24″ E, 25 m depth. Isolated from the tunic of *Halocynthia papillosa*, March 2022, Martina Braconcini. Holotype MUT 6843 (strain HPa3), living culture permanently preserved in a metabolically inactive state at MUT.

Notes – *Rambellisea gigliensis*, like many *Paralulworthia* species, lacks any of the morphological features associated with members of the Ascomycota, let alone the *Lulworthiales*. Phylogenetically, *Rambellisea* was well separated from the sister clade consisting of *Paralulworthia* and *Haloguignardia irritans* (Fig. 1). No sexual and asexual morphologies were produced from both species but *R. gigliensis* produced chlamydospores. Attempts were made to induce sporulation on bark (*Quercus cerris*), wood (*Pinus pinaster*), and tunica of *H. papillosa* (Braconcini et al. 2024), but were negative. Details of the location of where the type material is deposited is lacking as well as deposition of the living cultures and molecular data.

Rostrupiella Jørg. Koch, K.L. Pang & E.B.G. Jones, Bot. Mar. 50(5-6): 295 (2007)

Index Fungorum number: IF29175

Saprobic on wood. Sexual morph: *Ascomata* gregarious, deeply embedded, subhyaline. ellipsoidal-cylindrical, ostiolate, coriaceous, papillate. *Peridium* two-layered, outer layer of flat melanized cells, inner layer thin-walled, hyaline flattened pseudoparenchyma cells. *Paraphyses*/catenophyses lacking. *Asci* 8-spored, cylindrical, short pedunculate, unitunicate, thin-walled, deliquescing early, lacking apical apparatus. *Ascospores* filiform, hyaline, aseptate, curved or twisted with an apical conoid end chamber filled with mucilage. Asexual morph: Undetermined.

Type species – *Rostrupiella danica* Jørg. Koch, K.L. Pang & E.B.G. Jones, Bot. Mar. 50(5/6): 295 (2007)

Notes – *Rostrupiella* was introduced by Koch et al. (2007) from wood collected at Vedbaek harbour, Denmark with typical filiform ascospores with end chambers of *Lulworthia* species.

However, a phylogenetic analysis of 28S rDNA showed it did not group with the type species *Lulworthia fucicola* (Campbell et al. 2005).

Rostrupiella danica Jørg. Koch, K.L. Pang & E.B.G. Jones, Bot. Mar. 50(5/6): 295 (2007) Fig. 27

Index Fungorum number: IF528978

Saprobic on wood. Sexual morph: *Ascomata* 702–1092 µm long, 358–468 µm high, 360–430 µm wide, gregarious, deeply embedded, subhyaline, ellipsoidal-cylindrical, ostiolate with long cylindrical neck, coriaceous, papillate. *Peridium* two-layered 12–20 µm; outer layer of 3–5 cells thick, flat and melanized, inner layer of 3–5 cells thick, thin-walled, hyaline, flattened pseudoparenchyma cells. *Necks* 750–1170 µm long, 30–50 µm wide, brownish. *Paraphyses*/*catenophyses* lacking. *Asci* 270–360×12–13 µm, 8-spored, cylindrical, short pedunculate, unitunicate, thin-walled, deliquescing early, lacking apical apparatus. *Ascospores* 259–286 (–331) ×4 µm, filiform, hyaline, aseptate, curved or twisted with an apical conoid end chamber filled with mucilage. Asexual morph: Undetermined.

Material examined – Denmark, JK 539, holotype, on hardwood (*Fagus sylvatica*) from wood trapped between stones 28/05/1985 Vedbaek harbour, herb. CP.

Notes – *Rostrupiella danica* is distinguished from other taxa in the Lulworthiales by deeply immersed ascomata, with long protruding necks, black bladder cells in the vessels of the host tissue, and the presence of a bell-like structure at the juncture of the neck and ascomata centrum. Phylogenetically, *R. danica* did not group with the type species *L. fucicola* but formed an unsupported clade with *Lulwoana* strains (Koch et al. 2007). Many collections have been made along the Danish seashore on both hard and coniferous wood (Koch et al. 2007). Current collections from temperate waters: Denmark and San Juan Island, USA. A further species is introduced for collections made in Norway.

Rostrupiella longispora Rämä & Hagestad, sp. nov. Figs. 28–29

Index Fungorum number: IF900118

Etymology – The species epithet refers to the long ascospores of the species.

Holotype – Arctic University Museum of Norway (TROM- F26837).

Saprobic on wood. Sexual morph: *Ascomata* gregarious, deeply embedded in the substrate, dark (black) with thin melanized walls or walls missing, ellipsoid, occasionally irregular within cavities of the wood, up to 1600 µm long, 900 µm wide and 1700 µm high (without neck), with the long axis parallel to wood fiber orientation, with an ostiolate neck. *Peridium* 2-layered, 13–35 µm thick, outer layer of 3-4 cells, approximately 20 µm thick and consisting of melanized, prismatic-slightly flattened cells, usually only prominent in the upper part of ascomata (near the neck); inner layer 3–5 cells, 10–13 µm thick and consisting of pseudoparenchymatic hyaline–yellowish cells. "False" wall 10–15 µm thick comprising of compressed and partly decomposed cells. Centrum consisting of an ascogonial layer that is 60 µm thick, asci at different stages of development and released spores, and lacking paraphyses or catenophyses. *Necks* up to 1400 µm in length and 70–120 µm in diam., in the apical and basal part, wall thickening into adjoining wood vessels, cylindrical-flattened, blackish, ostiole channel between melanized cells 45–95 µm diam., arising from the central upper part of the ascomata. The base of the neck protrudes into the upper part of the ascoma center with a bell-like structure formed of prismatic melanized cells that become less melanized towards the base of the bell. The cells increase in size towards the bell base, where the cells are 8–14 µm long and 5–12 µm wide. Similar, bladder-like cells can be found in wood vessels and old fruit body cavities where they form giant cells up to 103 µm in length and filling the whole cavity of the wood vessel (diam. of fungal cells 27–38 µm). *Asci* 8-spored, cylindrical with rounded, pointed ends, thin-walled and early deliquescing, without an apical apparatus, 450–470 (median)–500 µm x 15–17.5–18.5 µm (n=10). *Ascospores* 390–476–540 µm long, 3.3–4.6 µm wide (n=21), hyaline, filiform, curved or moderately twisted, tapering towards both ends, aseptate, with apical long cone-shaped end-chambers, 13–14.8–16 (21) µm in length, filled with mucus that is released. Ascospore tips swell before germination. Asexual morph: Undetermined.

Type material – Norway, Svalbard, TRa3137A, several pieces of wood and 9 microscope slides from the original collection is a piece of wood collected at 73 meters depth in Hinlopen Straight in the Northern parts of the Spitsbergen archipelago (station M11HEL0162, 79°34'65"N 18°51'88"E), collected by the crew of MabCent bioprospecting cruise 2011 using a triangle scrape on Oct 7, 2011. The species is only known to date from its type collection site. No cultures are deposited as ascospores did not germinate.

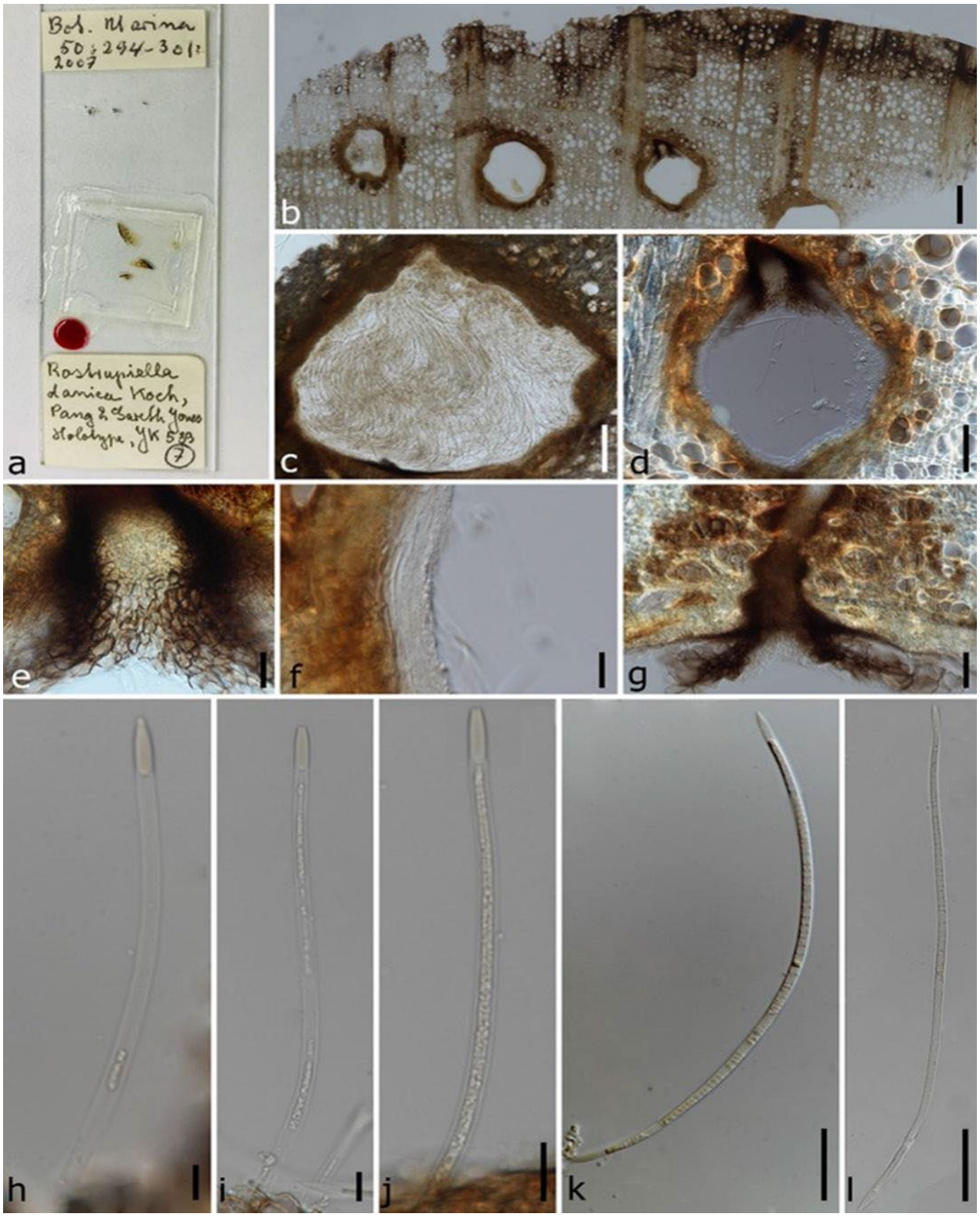

Figure 27 – *Rostrupiella danica* (CP1027825). a Herbarium microslide. b Section through ascoma. c Outer layer of cells and spore layer with ascus wall nearly dissolved. d Longitudinal section

through the neck. e Ostiole. f Peridium. g Section of neck and neck wall thickening into adjoining vessels. h–l Ascus and spores with apical end chamber. Scale bars: b = 150 µm, c = 1 µm, d–g = 5 µm, h–j = 10 µm, k–l = 30 µm.

Notes – The species is similar to *Rostrupiella danica* with bladder cells in the host wood vessels, and also in old fruiting body cavities. Bladder cells can also be found in the bell-like structure of the ascoma. However, *R. longispora* has significantly longer and broader asci and longer spores with larger end-chambers containing mucilage. Analysis of the rRNA genes also shows that the species is distinct from the type species of the genus, *R. danica*, but clearly placed in the same genus.

Rostrupiella longispora is found on wood on the sea-bottom in the High Arctic. The substrate has abundant old fruiting bodies, and the fungus-infected wood is dark (black grey) in colour. Phylogeny based on nuclear rRNA sequences of 18S, 28S genes and ITS regions (including 5.8S gene) and the species groups in *Rostrupiella* forming a sister taxon to the type of the genus, *R. danica.* The phylogeny supports the morphological observations of *R. longispora* being a distinct species.

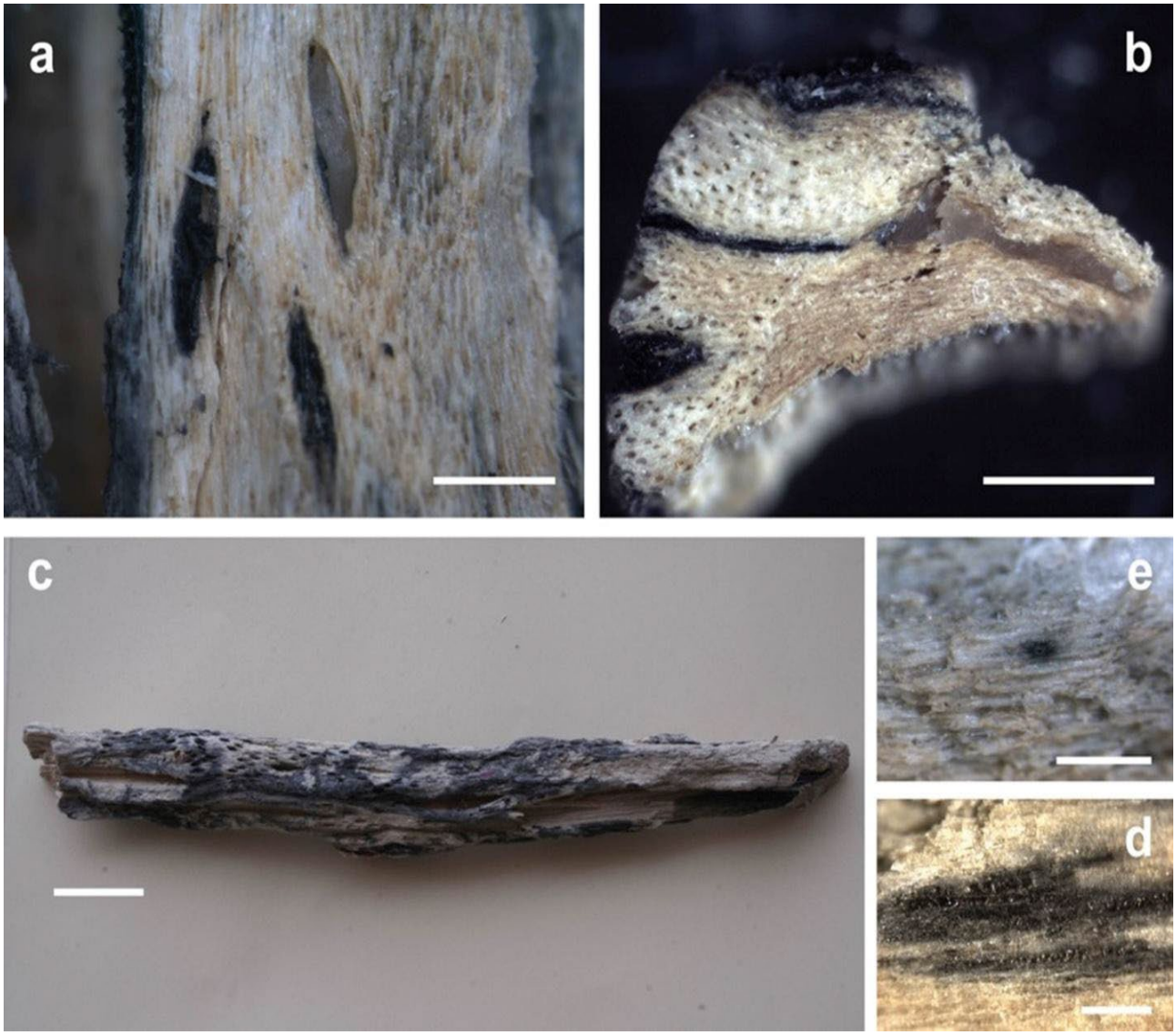

Figure 28 – *Rostrupiella longispora*. a Horizontal section of wood revealing ascomata. b Vertical section of wood showing an irregular fruiting body in the wood cavity. c The holotype specimen showing cavities in the wood that have been formed by ascomata. d Bladder cells in a horizontal section of the wood. e Apical part of an ostiole neck protruding from the wood. Scale bars: a–d = 1 cm, e = 500 µm.

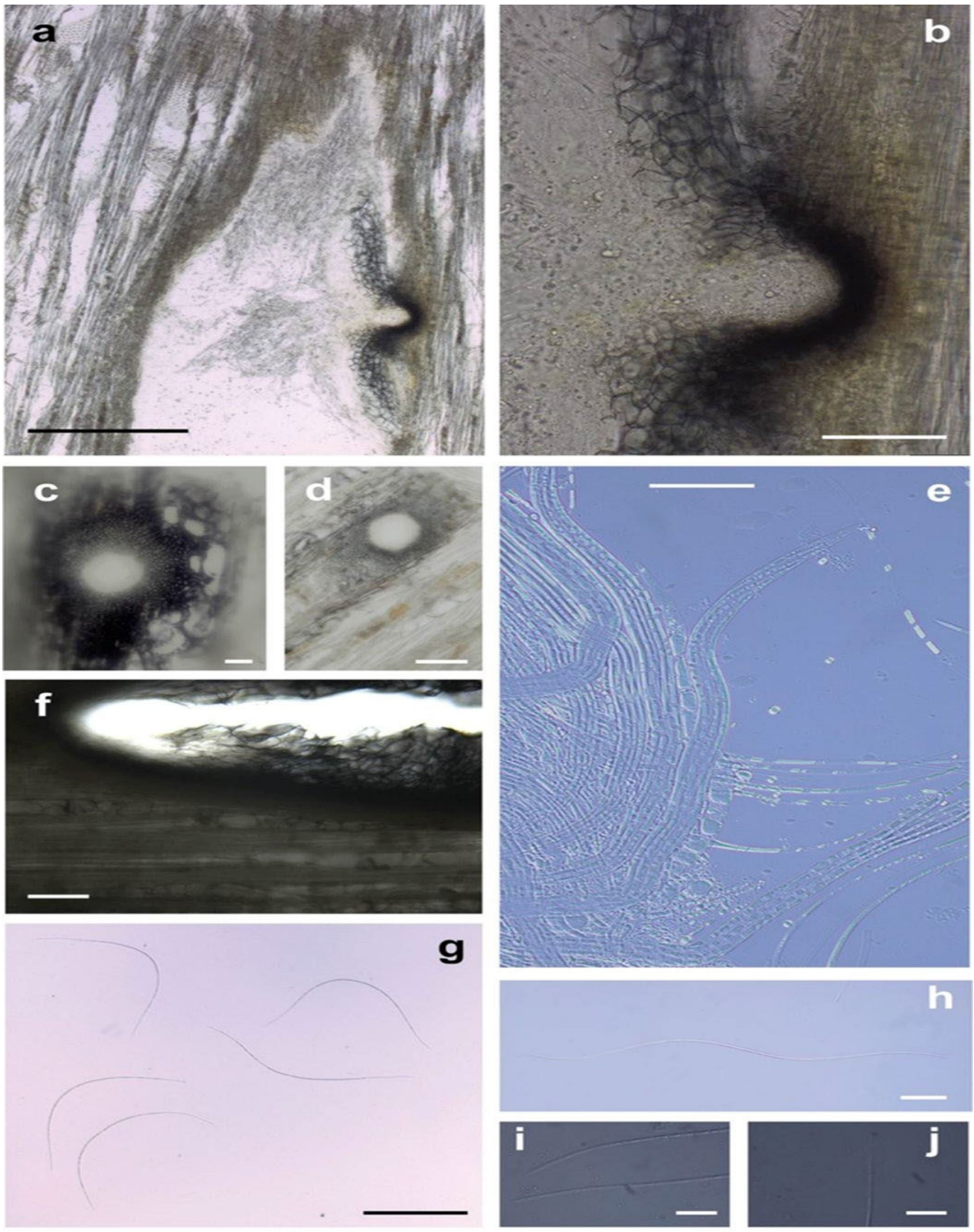

Figure 29 – *Rostrupiella longispora* (TROM- F26837, holotype). a Horizontal section of an ascoma showing the melanized cells of the bell-like structure, ascoma wall and ascogonial layer. b Details of the bell-like structure at the basal part of an ostiole neck. c Apical part of an ostiole neck showing thickening of the neck wall to adjoining tree cells (on the left). d Basal part of an ostiole neck. e Intact and deliquescing asci containing spores, in differential interference contrast (DIC). f Bladder cells filling wood vessels and an old ascoma cavity. g Spores in bright field.

h One spore, in DIC. i–j Details of spores showing end chambers, in DIC. Scale bars: a = 250 μm, b, d–e, h = 50 μm, c, i–j = 20 μm, f = 100 μm, g = 200 μm.

Sammeyersia S.Y. Guo, E.B.G. Jones & K.L. Pang, in Abdel-Wahab et al., Bot. Mar. (2017)

Index Fungorum number: IF820458

Saprobic on mangrove wood, submerged *Casuarina* sp. fruits, test panels. Sexual morph: *Ascomata* globose or subglobose to pyriform, immersed or superficial, ostiolate, with a long neck, brown to black, solitary or gregarious. *Necks* cylindrical, straight or curved, sometimes two on one ascoma. *Peridium* two-layered, composed of an outer layer of cells of *textura angularis* and an inner layer of elongated cells with large lumina; inner layer thickened at the base of the neck, composed of cells with thickened and highly melanized wall. *Paraphyses* absent. *Asci* 8-spored, elongate-fusiform or cylindrical, unitunicate, thin-walled, early deliquescing. *Ascospores* filamentous, curved, hyaline, tapering at each end into an elongate, conical process or apical chamber, acute or rounded, filled with mucus that is released through an apical pore. Asexual morph: Undetermined.

Notes – *Sammeyersia* was introduced by Guo et al. (in Abdel-Wahab et al. 2017) to accommodate *Sammeyersia grandispora* (=*Lulworthia grandispora*). This genus is characterized based on the melanized region at the base of the neck of the ascomata and long ascospores. Initially monophyletic, but the phylogenetic analysis of the various *Sammeyersia* strains (Fig. 1) indicates the genus is polyphyletic. A literature search confirms this with measurement's falling into three groups (Table 4).

Type species – *Sammeyersia grandispora* (Meyers) S.Y. Guo, E.B.G. Jones & K.L. Pang

Table 4 Morphological features of *Sammeyersia* species.

Collection	Ascomata (μm)	Asci (μm)	Ascospores (μm)	Reference
Group 1				
S. grandispora (Type species)	785–1400	N/A	500–756×3–5	Meyers (1957)
S. grandispora	180–306	N/A	500–756×3–5	Kohlmeyer & Kohlmeyer (1979), on wood and mangrove wood
S. grandispora			345–756	Campbell (2005)
S. grandispora	100–406×135–400	312–450	275–756×2–5	This study, on mangrove wood
Group 2				
S. thailandica MCD033	120–400×130–350	300–460	320–470×2-4	This study, on mangrove wood
Group 3				
S. yanbuensis LN01	250–480×100–200	400–510	380–500	This study, on mangrove wood
S. yanbuensis SUMCC H-11020	200–320	240–290×18–21	(180–)240–370×2.5–4	This study, on mangrove wood

Sammeyersia grandispora (Meyers) S.Y. Guo, E.B.G. Jones & K.L. Pang, in Abdel-Wahab et al., Bot. Mar. (2017) Fig. 30

Basionym – *Lulworthia grandispora* Meyers 1957

Index Fungorum number: IF820461

Saprobic on wood. Sexual morph: *Ascomata* 100–405.7×135–400.4 μm, globose or subglobose, immersed, dark brown to black, with a long neck. *Necks* 75–1400×15–42.3 μm,

cylindrical, straight or curved, sometimes two on one ascoma. *Peridium* 14–47.5 µm, two-layered, composed of an outer layer of cells of *textura angularis* and inner layer of elongate cells with large lumina; inner layer thickened at the base of the neck, composed of cells with thickened and highly melanized wall, 11.3–16.9 µm thick. *Paraphyses* absent. *Asci* 312–450 µm, 8-spored, elongate-fusiform or cylindrical, unitunicate, thin-walled, early deliquescing. *Ascospores* 275.3–756×2–5 µm, filamentous, curved, tapering at each end into elongate, conical process or apical chamber, processes 3.1–9.2 µm long, acute or rounded, filled with mucus released through an apical pore. Asexual morph: Undetermined.

Material examined – Miaoli County, Zhunan (GPS: 24°40′01.5″N 120°50′38.0″E) on decayed mangrove wood, 30 May 2008 Ka-Lai Pang, living culture NTOU3843; 10 September 2009, Ka-Lai Pang, living culture NTOU3847, Tainan city, Sicao (GPS: 23°01′39.0″N 120°08′15.5″E) on decayed mangrove wood; 26 March 2010, Ka-Lai Pang, living culture NTOU3849, Hualien county, Nanbin park (GPS: 23°58′01.5″N 121°36′41.4″E) on driftwood; 23 April 2011, Ka-Lai Pang, living culture NTOU3841.

Notes – *Sammeyersia grandispora* is commonly found on mangrove wood in tropical and subtropical areas around the world. Generally, its identification has been based on the long length of the ascospores and therefore some species may have been missed. This species was initially described by Meyers (1957) as *Lulworthia grandispora* with an ascospore length in the range of 565–756 µm. Campbell (2005) updated the ascospores length to 345–756 µm while establishing a neotype for *L. fucicola*. Long ascospores of *L. grandispora* was the only distinguishing feature from *L. fucicola* (type species) but isolates of *L. grandispora* always formed a monophyletic group. Guo et al. (in Abdel-Wahab et al. 2017) examined four specimens derived from mangrove wood and driftwood, and paraffin sections revealed several layers of thickened melanized cells at the base of the neck of the ascomata, a character does not present in *L. fucicola* and other *Lulworthia* species. A new genus*, Sammeyersia*, was consequently created to accommodate *L. grandispora* based on both morphological and phylogenetic results.

Sammeyersia grandispora has been widely collected in tropical locations on various prop roots and submerged wood of different mangrove trees, on submerged *Casuarina* sp. fruits and test panels exposed in the sea.

Collecting sites include – Bahamas (Various islands), Bermuda, Brazil, Guatemala, Liberia, Malaysia, Peru, Thailand, Senegal, and the USA (Florida) (Kohlmeyer & Kohlmeyer 1979, Abdel-Wahab et al. 2017). Devadatha et al. (2021) reported this species from 39 countries, 26 different host species, and present in the Atlantic, Indian and Pacific Oceans, making it one of the most documented marine fungus.

Sammeyersia grandispora is undoubtedly a species complex, with a wide range of ascospore measurement, and as the phylogenetic data indicates in Fig. 1. Currently, many isolates of *S. grandispora* do not have voucher material or morphological data to support the introduction of new species. Here we introduce two species: *Sammeyersia thailandica* and *Sammeyersia yanbuensis.* Further studies are therefore required for new collections and supported by both morphological and sequence data.

Sammeyersia thailandica (MCD 033) Dayar., K.D. Hyde & E B G Jones, sp. nov. Fig. 31

Index Fungorum number: IF900100

Etymology – Named after country of origin

Holotype – MFLU 18-0523

Saprobic on submerged mangrove wood. Sexual morph: *Ascomata* 120–400×130–350 µm, globose or subglobose to pyriform, immersed or superficial, ostiolate, with a long neck, brown to black, solitary or gregarious. *Necks* up to 600–900 long, cylindrical, straight or curved, sometimes two on one ascoma. *Peridium* 22–35 µm wide, two-layered, composed of an outer layer of *textura angularis* and an inner layer of elongated cells with large lumina; inner layer thickened at the base of the neck, composed of cells with thickened and highly melanized wall. *Paraphyses* absent. *Asci* 300–460 µm ($\bar{x}$=400, n=10), long 8-spored, elongate-fusiform or cylindrical, unitunicate, thin-

walled, early deliquescing. *Ascospores* 320–47×2.1–4 µm ($\bar{x}$=365×3.5 µm, n=10), long filamentous, curved, hyaline, tapering at each end into an elongate, conical process or apical chamber, acute or rounded, filled with mucus that is released through an apical pore. Asexual morph: Undetermined.

Material examined – Thailand, Ranong Province, Amphoe Maung, Mu 4 Tombol Ngao, Ranong Mangrove Research Center (GPS: 9°43' to 9°57'N; 98°29' to 98°39'E) on decaying wood of *Rhizophora* sp. (Rhizophoraceae), 7 December 2016, M.C. Dayarathne, MCD 033 (MFLU 18-0523); living culture MFLUCC 17-0393.

Notes – Phylogenetically, *S. thailandica* formed a long branch from a clade of *S. grandispora* isolates with good support (Fig. 1). Ascospores of *S. thailandica* are shorter than those of the type species *S. grandispora* (320–470×2-4 and 275–756×2–5, respectively, Table 4). These differences confirm *S. thailandica* as a new species in the genus.

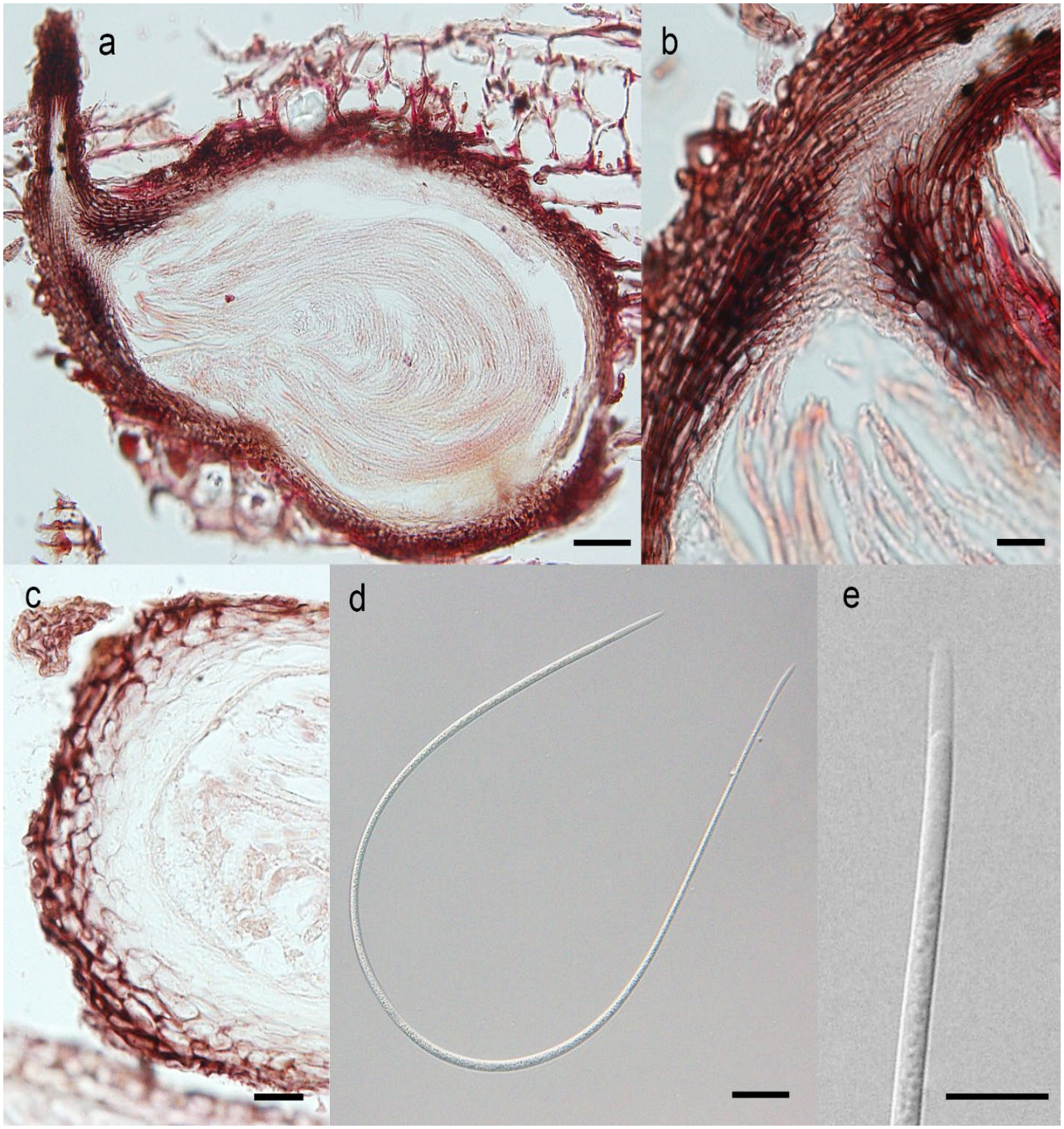

Figure 30 – *Sammeyersia grandispora*. a Section of ascoma in wood. b Thickened cells with melanization at base of the neck. c Two-layered peridium. d Filamentous ascospore. e End chamber of ascospore with mucus releasing. Scale bars: a, d = 30 µm, b–c, e = 10 µm.

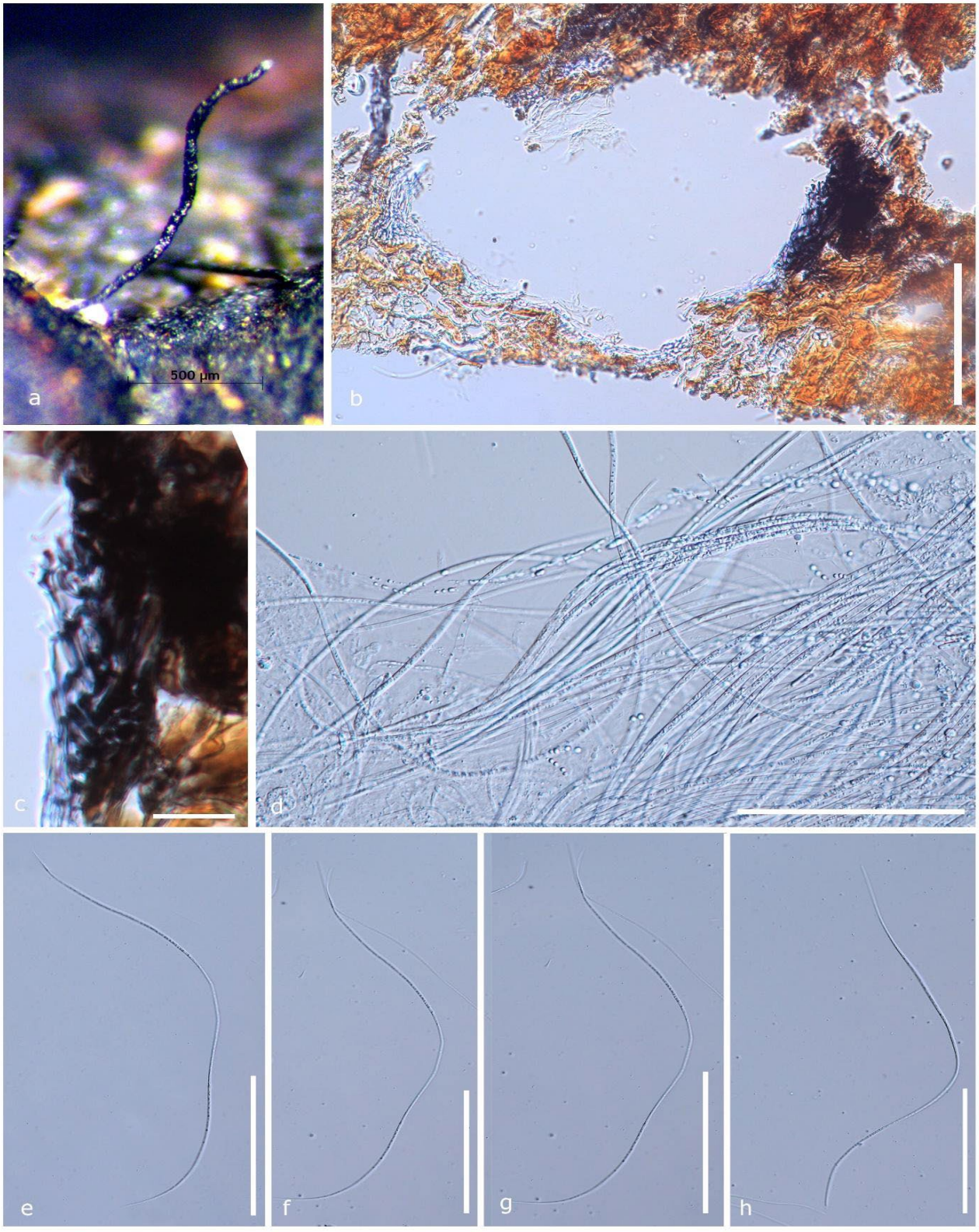

Figure 31 – *Sammeyersia thailandica* (MFLU 18-0523, holotype). a An ascoma on surface of the wood. b Vertical section of the ascoma. c Magnified part of the peridium. d Asci and ascospores. e-h Ascospores. Scale bars: a = 200 µm, b, d–h = 200 µm, c = 20 µm.

Sammeyersia yanbuensis Abdel-Wahab & E.B.G. Jones, sp. nov. Fig. 32

Index Fungorum number: IF900346

Etymology – Named after Yanbu city, where this fungus was collected.

Holotype – SUMCC H-11020 (Sohag University Microbial Culture Collection).

Saprobic on submerged decaying mangrove wood in the intertidal zone. Sexual morph: *Ascomata* 200–320 µm in diameter, superficial, subcarbonaceous, dark brown to black in colour, surrounded by thick, septate hyphae with the rough and ornamented surface, 3–5 µm thick. *Peridium* 35–60 µm thick, two-layered, outer layer 25–32 µm thick, dark brown to black, consists of 5–8 layers of polygonal, melanized, thick-walled cells, inner layer 15–25 µm, hyaline to light-brown, consists of 6–7 layers of polygonal, flattened, thick-walled cells with narrow lumen. *Paraphyses* absent. *Asci* 240–290×18–21 µm, 8-spored, fusiform, unitunicate, thin-walled, early deliquescing. *Ascospores* (180–) 240–370×2.5–4 µm (= 302.1×3 µm, n=50), filamentous, curved, hyaline, tapering at each end into an elongate, conical process or apical chamber (7–11×2–2.5 µm), filled with mucus that is released through an apical pore as globular mass of gelatinous material. Asexual morph: Undetermined.

Type material – Saudi Arabia, Yanbu city, the Red Sea coast, Yanbu mangroves 23° 55′ 57″ N 38° 17′ 31″ E, on decaying intertidal wood of *Avicennia marina*, 17 November 2011, coll. M.A. Abdel-Wahab (holotype, SUMCC H-11020).

GenBank number – LSU=OP646429.

Notes – The morphology of *Sammeyersia yanbuensis* is distinct from the type species *S. grandispora*: ascospores in *S. yanbuensis* are shorter than those of *S. grandispora* (180–370×2.5–4 µm vs. 565–756×2.9–4.3 µm for *S. yanbuensis* and *S. grandispora,* respectively). Apical chambers to the ascospores in *S. yanbuensis* are longer than those *in S. grandispora* (7–11 µm vs. 3.6–4.3 µm for *S. yanbuensis* and *S. grandispora,* respectively). However, ascomata in both species are surrounded by thick-walled, dark septate hyphae (Meyers 1957).

Spathulospora A.R. Caval. & T.W. Johnson, Mycologia 57(6): 927 (1965)

Index Fungorum number: IF5071

Parasitic on red alga *Ballia callitricha*. Sexual morph: *Ascomata* globose to subglobose, immersed or superficial, carbonaceous or sub carbonaceous, dark brown to black, covered with long, dark, septate, curved or curled hairs. *Peridium* composed of several cell layers, brown to dark brown. *Asci* thin-walled, unitunicate, early deliquescing. *Ascospores* one-celled, hyaline, with appendages or gelatinous sheaths. Asexual morph: Undetermined.

Type species – *Spathulospora phycophila* A.R. Caval. & T.W. Johnson, Mycologia 57(6): 927 (1965)

Note – *Spathulospora* was introduced by Cavaliere and Johnson (1965) with *S. phycophila* as the type species. Currently four additional species are accepted in the genus: *S. adelpha, S. antarctica, S. calva* and *S. lanata* and assigned to the new family and order Spathulosporaceae, Spathulosporales, *Incertae sedis*, Sordariomycetes (Kohlmeyer 1973). All have been found as parasitic on the red algae *Ballia callitricha* or *B. scoparia*, in the Pacific Ocean (Kohlmeyer & Kohlmeyer 1979). They are characterised by producing stalked or sessile antheridia with spermatia on a crust or stromata, and ascogonia with trichogynes, ascomata superficial, ostiolated, with a thick, hairy or glaborous subiculum, asci thin-walled, unitunicate, early deliquescing, with hyaline ascospores and an apical one-celled appendage (end chamber) (Kohlmeyer & Kohlmeyer 1979). The unusual antheridia and trichogynes of *Spathulospora* gave rise to comparison with red algae and was proposed in the theory that the Ascomycota and Rhodophyta had "branched off from a common ancestor", the so-called Floridean theory (Sachs 1874, Kohlmeyer 1973, Demoulin 1974).

Inderbitzin et al. (2004) provided the only sequence data available for *Spathulospora* when they obtained partial SSU and LSU DNA sequences from dried herbarium specimens of *S. adelpha* and *S. antarctica.* This indicated that both *Spathulospora* species grouped within the Lulworthiales (Sordariomycetes, Ascomycota) with support in all analyses. The *Spathulospora* species formed a sister clade to *Lindra thalassiae* (currently *Lindriella thalassiae*) with high statistical support

(Inderbitzin et al. 2004). In the current study, *S. adelpha* and *S. antarctica* formed a sister clade to *Lulworthia* species.

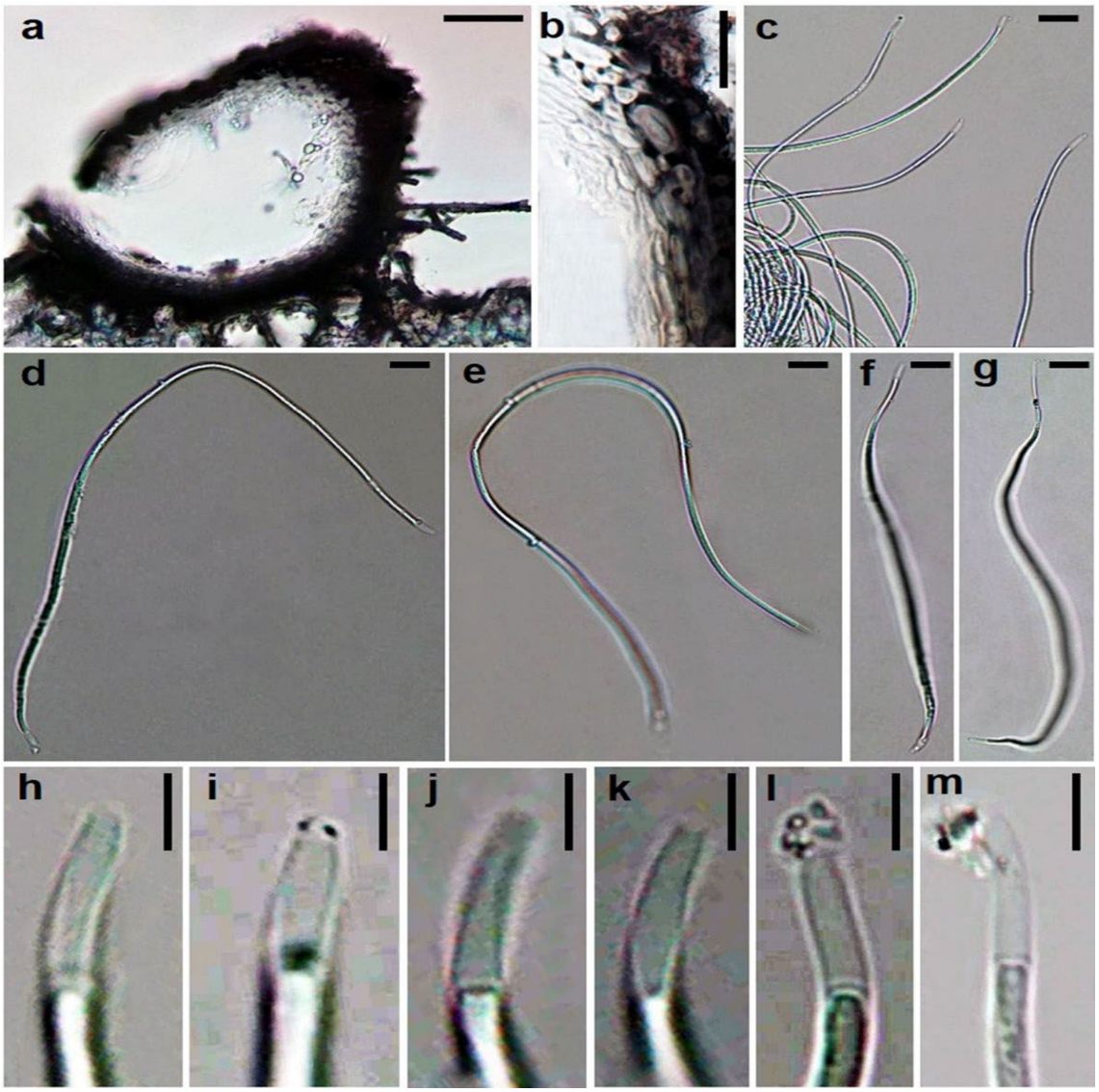

Figure 32 – *Sammeyersia yanbuensis* (SUMCC H-11020, holotype). a Vertical section of the ascoma. b Magnified part of the peridium. c–g Variously shaped ascospores. h–m Apical chambers. Scale bars: a = 50 µm, b = 20 µm, c–g = 20 µm, h–m = 5 µm.

Spathulospora shares few features with the *Lulworthiales*: parasitic versus saprophytes, ascomata hairy vs no hairs, ascospores broad vs. filiform, however both possess end chambers containing mucus. This is evident in the illustrations in Kohlmeyer and Kohlmeyer (1979), while in Fig. 8 of Inderbitzin et al. (2004), shows mucilage oozing from the ascospore of *S. antarctica*. Similar observations have been made for ascospores of *Lulworthia* spp. by Jones (1994), implicating a role in spore attachment.

Based on the data in Inderbitzin et al. (2004) and Fig. 33, there is strong evidence for the inclusion of *Spathulospora* within the *Lulworthiales*, and the redundancy of the taxa *Spathulosporaceae*, *Spathulosporales*. Clearly, further collections of *Ballia* species are required to enable better sequences than those currently available. Herbarium material of *Ballia* species indicated that they are frequently infected by *Spathulospora* (Haythorn & Jones, unpublished data, based on collections in various herbaria).

Spathulospora phycophila A.R. Caval. & T.W. Johnson, Mycologia 57(6): 927 (1965) Fig. 33

Index Fungorum number: IF339366

Parasitic on red algae. Sexual morph: *Ascomata* (110-)157-320 µm in diam., subglobose, superficial solitary, ostiolate, fuscous, leathery, subiculate, woolly. *Peridium* 12-40 µm thick, two-layered; cells of the outer layer irregularly pyramidal or subglobose, brown, giving rise to the hairs; cells of the inner layer flattened, hyaline. *Antheridia* lageniform, 20-22 µm long; venters ellipsoidal, 9.5-14×2.5-9 µm, necks obconical or cylindrical, 4-9.5×2.2-3.3 µm, forming spermatia; spermatia hyaline, non-septate, filiform, 8.5×0.5 µm. *Trichogynes* 27×8.5-9 µm, simple, cylindrical, hyaline. *Papillae* short or lacking. *Paraphyses* lacking. *Asci* 80-125×30-40 µm, eight-spored, cylindrical to clavate, thin-walled, early deliquescing. *Ascospores* 80-110×10-13 µm (including appendages), fusiform, straight or curved, apically spathulate, one-celled, appendage-like covering around the tips. Asexual morph: Undetermined.

Material examined – Australia - Warrnambool, Victoria, on *Ballia callitricha,* 1959 Apr. BPI 580727, type. Australia - Warrnambool, Victoria, on *Ballia callitricha,* NY 01350180, NY 01350182 NY 01350186, NY 01350185, NY 01350187, NY 01350178, NY 01350183, micro slides of holotype.

Notes – No sequence data is available for this species, and further collections are required to confirm its position in the *Lulworthiales*.

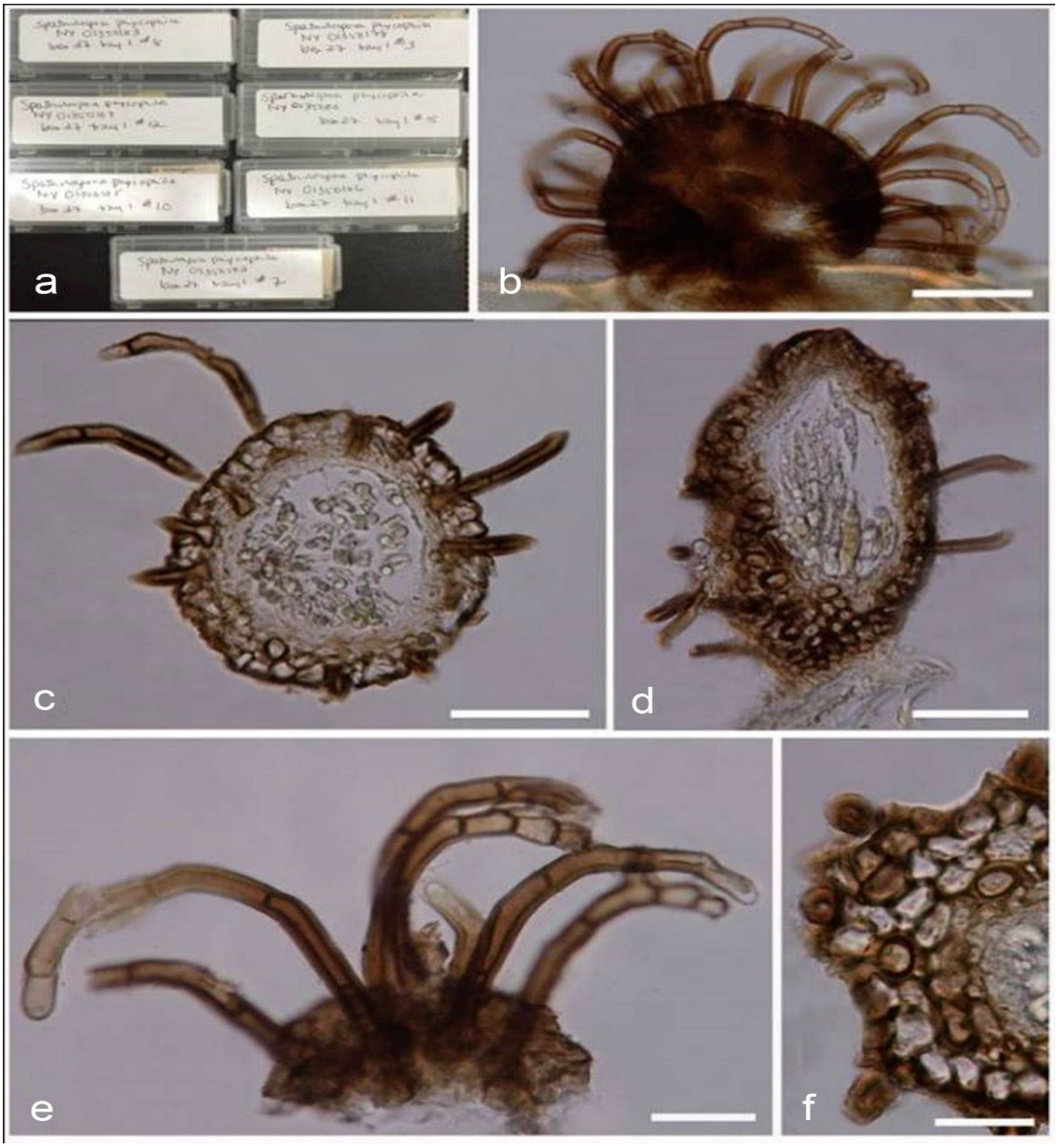

Figure 33 – *Spathulospora phycophila* (microslides of holotype). a Herbarium material. b Ascoma on host surface. c–d Section through ascoma. e Hairs. f. Peridium. Scale bars: b = 50 μm, c–f = 100 μm.

Discussion

Using morphology and phylogenetic analyses of various rDNA regions and protein genes, one new genus *Lindriella* and eight new species (*Hydea mangrovei*, *Lulworthia norwegica*, *Matsusporium japonica*, *Moromyces mangrovis*, *Paralulworthia lignicola*, *Rostrupiella longispora*, *Sammeyersia yanbuensis*, *S. thailandica*) are described in the order *Lulworthiales*. The genus *Spathulospora* is also considered to be a member of the *Lulworthiales* while *Koralionastes* and *Pontogeneia* are referred to *Koralionastetales* until more species/sequences are available to resolve their phylogenetic relationship with the *Lulworthiales*. Currently, the subclass includes 23 genera and 69 species (Table 5).

The number of genera in the order *Lulworthiales* has increased from two (*Lindra* and *Lulworthia*) (Kohlmeyer et al. 2000) to 21 (this study), mainly based on the results of phylogenetic studies. Genera of this order express dissimilar ascospore shape morphology, from taxa with oval, ellipsoidal, cylindrical, fusiform ascospores (*Haloguignardia*, *Kohlmeyeriella*, *Spathulospora*), to those with filamentous ascospores (*Lindra*, *Lindriella*, *Lulwoana*, *Lulwoidea*, *Lulworthia*, *Paralulworthia*, *Rostrupiella*, *Sammeyersia*). Also, a number of asexual morphs are affiliated with genera of this order: *Cumulospora*, *Halazoon*, *Hydea*, *Matsusporium*, *Moleospora*, *Moromyces* and *Orbimyces*. In this monograph we follow Nakagiri (1984) in accepting the name *Lulwoana* over the asexual morph: *Zalerion*.

The systematics of the order *Lulworthiales* has been problematic due to several reasons. Many genera have rarely been collected and are difficult to culture and these hinder a phylogenetic study to determine their placement in the order, such as, *Haloguignardia* and *Spathulospora*. However, genomic DNA can be extracted directly from centrum material of these unculturable taxa and used for PCR (Pang et al. 2003). Studies of saprobic fungal species, which form fruiting bodies on macroalgae, have been few in recent years, although culture-based and metabarcoding studies have revealed a diverse lineage of fungi associated with macroalgae (Cha et al. 2021). The most taxonomically problematic taxa are those that produce filamentous ascospores. *Lindra* and *Lindriella* can be differentiated from the other taxa in lacking apical chambers at both ends of the ascospores. *Lulwoana* and *Lulwoidea* both produce septate ascospores (Campbell et al. 2005). *Rostrupiella* and *Sammeyersia* differ from the rest with *Rostrupiella danica* and *R. longispora* forming black bladder cells in the vessels of the host tissue, and a bell-like structure at the juncture of the neck and ascomata centrum (Koch et al. 2007), while the inner layer of the peridium of *Sammeyersia grandispora* is thickened at the base of the neck, and is made of cells with thickened and highly melanized walls (Abdel-Wahab et al. 2017). Sadly, the morphology of ascomata of the taxa in the *Lulworthiales* has been overlooked and was only used as a secondary character to delineate the taxa.

The validity of the genus *Paralulworthia* is doubtful. Morphology of the type species *P. gigaspora* presented in Poli et al. (2020) and sequences of *P. gigaspora* may represent two unrelated fungi because: (1) the method used in inducing the production of fruiting bodies of this fungus was prone to contamination, (2) key characteristics including asci and ascospore morphology were not presented clearly and the ascomata and ascospores resemble those of the *Dothideomycetes*, and (3) the new species *P. lignicola* described in this paper was phylogenetically related to other *Paralulworthia* spp. (Figs. 1–2) and produces filamentous ascospores with apical chambers filled with mucilage.

Lulworthia fucicola, *L. atlantica*, *L. fundyensis*, *L. floridana*, *L. norwegica*, and *L. opaca* formed a monophyletic group based on phylogenetic analysis of 18S and 28S rDNA (Fig. 1). No sexual morphology *of L. fundyensis* is known (Taylor et al. in Crous et al. 2022) and thus no evolutionary significant morphological character(s) can be inferred from this species. Seven *Lulworthia* species (*L. bulgariae, L. calcicola, L. curalii, L. halima, L. kniepii, L. lindroidea*,

L. longirostris) lack molecular data and need to be recollected, isolated and sequenced before resolution of their phylogenetic status.

To solve the current taxonomic problems of *Lulworthia* and allied taxa, the morphology of every collection of *Lulworthia* species should be carefully studied and photographed. The fungi should be isolated, cultured and sequenced. Both morphology and phylogenetic analyses will lead to a robust taxonomy of the genera in this complex.

Ecologically, species of the order *Lulworthiales* occur widely on different substrates, are worldwide in distribution and play an important role in the recycling of complex organic material and likely impact their algal hosts. They are often early colonizers of wood in the marine environment and are the source of a wide range of enzymes (Bucher et al. 2004, Velmurugan & Lee 2012) and antimicrobials (Jenssen et al. 2021); an unidentified lulworthia-like species produced lulworthinone (a dimeric biarylic naphthoα-pyrone substituted with a sulfate group) and showed antibacterial activity against reference strains of *Staphylococcus aureus* and *Streptococcus agalactiae*, as well as several clinical MRSA isolates. They are unique in that all taxa are marine, and phylogenetically form a diverse group in a subclass (*Lulworthiomycetidae*) in the *Sordariomycetes*.

Table 5 Species list of the *Lulworthiomycetidae*.

List of genera and species in the *Lulworthiomycetidae*
Cumulospora I. Schmidt
Cumulospora mangrovei Karamchand & K.R. Sridhar
Cumulospora marina I. Schmidt
Halazoon Abdel-Aziz, Abdel-Wahab & Nagah.
Halazoon fuscus (I. Schmidt) Abdel-Wahab, K.L. Pang, Nagah., Abdel-Aziz & E.B.G. Jones
Halazoon melhae Abdel-Aziz, Abdel-Wahab & Nagah.
Halazoon purpurea (I.M. Wilson) Dayar., K.L. Pang, E. Azevedo, M.F. Caeiro, Hagestad, Rämä & E B G Jones, comb. nov.
Haloguignardia Cribb & J.W. Cribb
Haloguignardia cystoseirae Kohlm. & Demoulin
Haloguignardia decidua Cribb & J.W. Cribb
Haloguignardia irritans (Setch. & Estee) Cribb & J.W. Cribb
Haloguignardia oceanica (Ferd. & Winge) Kohlm.
Haloguignardia tumefaciens (Cribb & Herbert) Cribb & J.W. Cribb
Halophilomyces X. Wang, L. Pecoraro & H.B. Liu
Halophilomyces hongkongensis X. Wang, L. Pecoraro & H.B. Liu
Hydea K.L. Pang & E.B.G. Jones
Hydea mangrovei Devadatha, V.V. Sarma & E.B.G Jones, sp. nov.
Hydea pygmea (Kohlm.) K.L. Pang & E.B.G. Jones
Kohlmeyeriella E.B.G. Jones, R.G. Johnson & S.T. Moss
Kohlmeyeriella crassa (Nakagiri) Kohlm., Volkm-Kohlm., J. Campb., Spatafora & Gräfenhan
Kohlmeyeriella tubulata (Kohlm.) E.B.G. Jones, R.G. Johnson & S.T. Moss
Koralionastes Kohlm. & Volkm-Kohlm.
Koralionastes angustus Kohlm. & Volkm-Kohlm.
Koralionastes ellipticus Kohlm. & Volkm-Kohlm.
Koralionastes giganteus Kohlm. & Volkm-Kohlm.
Koralionastes ovalis Kohlm. & Volkm-Kohlm.
Koralionastes violaceus Kohlm. & Volkm-Kohlm.

Table 5 Continued

List of genera and species in the *Lulworthiomycetidae*
Lindra I.M. Wilson
Lindra inflata I.M. Wilson
Lindra obtusa Nakagiri & Tubaki
Lulwoana Kohlm., Volkm-Kohlm., J. Campbell, Spatafora & Gräfenhan
Lulwoana uniseptata (Nakagiri) Kohlm., Volkm-Kohlm., J. Campb., Spatafora & Gräfenhan
Lulwoidea Kohlm., Volkm-Kohlm., J. Campbell, Spatafora & Gräfenhan
Lulwoidea lignoarenaria (Jørg. Koch & E.B.G. Jones) Kohlm., Volkm-Kohlm., J. Campb., Spatafora & Gräfenhan
Lulworthia G.K. Sutherl.
Lulworthia atlantica E. Azevedo, Caeiro & Barata
Lulworthia bulgariae Parg-Leduc
Lulworthia calcicola Kohlm. & Volkm-Kohlm.
Lulworthia curalii (Kohlm.) Kohlm. & Volkm-Kohlm.
Lulworthia floridana Meyers
Lulworthia fucicola G.K. Sutherl.
Lulworthia fundyensis V.A. Taylor, S.J. Adams, Robicheau & A.K. Walker
Lulworthia halima (Diehl & Mounce) Cribb & J.W. Cribb
Lulworthia kniepii (Ade & Bauch) Petr.
Lulworthia lindroidea Kohlm.
Lulworthia longirostris (Linder) Cribb & J.W. Cribb
Lulworthia medusa (Ellis & Everh.) Cribb & J.W. Cribb
Lulworthia norwegica Rämä & Hagestad, sp. nov.
Matsusporium E.B.G. Jones & K.L. Pang
Matsusporium tropicale (Kohlm.) E.B.G. Jones & K.L. Pang
Matsusporium japonica Abdel-Wahab & E.B.G. Jones, sp. nov.
Moleospora Abdel-Wahab, Abdel-Aziz & Nagah.
Moleospora maritima Abdel-Wahab, Abdel-Aziz & Nagah.
Moromyces Abdel-Wahab, K.L. Pang, Nagah., Abdel-Aziz & E.B.G. Jones
Moromyces mangrovis Dayar., K.D. Hyde & E B G Jones, sp. nov.
Moromyces varius (Chatmala & Somrith.) Abdel-Wahab, K.L. Pang, Nagah., Abdel-Aziz & E.B.G. Jones
Orbimyces Linder
Orbimyces spectabilis Linder
Paralulworthia A. Poli, E. Bovio, L. Ranieri, G.C. Varese & V. Prigione
Paralulworthia gigaspora A. Poli, E. Bovio, L. Ranieri, G.C. Varese & V. Prigione
Paralulworthia lignicola Rämä & Hagestad, sp. nov.
Paramoleospora M. Li & L. Cai
Paramoleospora guttulata M. Li & L. Cai
Pontogeneia Kohlm.
Pontogeneia calospora (Pat.) Kohlm.
Pontogeneia codiicola (Dowson) Kohlm. & E. Kohlm.
Pontogeneia cubensis (Har. & Pat.) Kohlm.
Pontogeneia enormis (Pat. & Har.) Kohlm.

Table 5 Continued

List of genera and species in the *Lulworthiomycetidae*
Pontogeneia erikae Kohlm.
Pontogeneia microdictyi Kohlm. & Volkm.-Kohlm.
Pontogeneia padinae Kohlm.
Pontogeneia valoniopsidis (Cribb & J.W. Cribb) Kohlm.
Rambellisea Pasqualetti & Braconcini
Rambellisea gigliensis Pasqualetti & Braconcini
Rambellisea halocynthiae Pasqualetti & Braconcini
Rostrupiella Jørg. Koch, K.L. Pang & E.B.G. Jones
Rostrupiella danica Jørg. Koch, K.L. Pang & E.B.G. Jones
Rostrupiella longispora Rämä & Hagestad, sp. nov.
Sammeyersia S.Y. Guo, E.B.G. Jones & K.L. Pang
Sammeyersia grandispora (Meyers) S.Y. Guo, E.B.G. Jones & K.L. Pang
Sammeyersia thailandica Day., K.D. Hyde & E B G Jones, sp. nov.
Sammeyersia yanbuensis Abdel-Wahab & E.B.G. Jones, sp. nov.
Spathulospora A.R. Caval. & T.W. Johnson, Mycologia 57: 927 (1965)
Spathulospora adelpha Kohlm., Mycologia 65: 615 (1973)
Spathulospora antarctica Kohlm., Mycologia 65: 619 (1973)
Spathulospora calva Kohlm., Mycologia 65: 622 (1973)
Spathulospora lanata Kohlm., Mycologia 65: 625 (1973)
Spathulospora phycophila A.R. Caval. & T.W. Johnson, Mycologia 57: 927 (1965)

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REFERENCES

Abdel-Wahab MA, Dayarathne MC, Suetrong S, Guo SY et al. 2017 – New saprobic marine fungi and a new combination. Botanica Marina 60, 469–488.

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.

Abdullah SK, Abdulkadder MA, Goos RD. 1989 – *Basramyces marinus* nom. nov. (hyphomycete) from southern marshes of Iraq. International Journal of Mycology and Lichenology 4, 181–186.

Alongi G, Catra M, Cormaci M. 1999 – First record of *Haloguignardia cystoseira* (Ascomycota) parasitic on *Cystoseira elegans* (Fucophyceae) from the Mediterranean Sea. Botanica Marina 44, 33–35.

Anastasiou CJ. 1963 – The genus *Zalerion* Moore & Meyers. Canadian Journal of Botany 41, 1135–1139.

Anderson JL, Chen W, Shearer CA. 2001 – Phylogeny of *Halosarpheia* based on 18S rDNA. Mycologia 93, 897–906.

Apt KE. 1988 – Morphology and development of hyperplasia on *Cystoseira osmundacea* (Phaeophyta) associated with *Haloguignardia irritans* (Ascomycotina). American Journal of Botany 75, 979–984.

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.

Barata M. 2002 – Fungi on the halophytes *Spartina maritima* in salt marshes. In: Hyde KD (Eds), Fungi in marine environments. Fungal Diversity Press, Hong Kong, pp 179–193.

Barata M. 2006 – Marine fungi from Mira River in salt marsh in Portugal. Revista Iberoamericana de Micología 23, 179–184.

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.

Barghoorn ES, Linder DH. 1944 – Marine fungi: their taxonomy and biology. Farlowia 1, 395–467.

Bills GF, Platas G, Peláez F, Masurekar P. 1999 – Reclassification of a pneumocandin-producing anamorph, *Glarea lozoyensis* gen. *et* sp. nov., previously identified as *Zalerion arboricola*. Mycological Research 103, 179–192.

Bouckaert R, Vaughan TG, Barido-Sottani J, Duchêne S et al. 2019 – BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. PLoS computational biology, 15, e1006650.

Bucher VVC, Hyde KD, Pointing SB, Reddy CA. 2004 – Production of wood decay enzymes, loss of mass, and lignin solubilization in wood by diverse tropical freshwater fungi. Fungal Diversity 15, 1–14.

Byrne PJ, Jones EBG. 1974 – Lignicolous marine fungi. Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven Suppl. 5, 301–320.
Cai L, Tsui CK, Zhang KQ, Hyde KD. 2002 – Aquatic fungi from Lake Fuxian, Yunnan, China. Fungal Diversity 9, 57–70.
Calabon MS, Jones EBG, Pang KL, Abdel-Wahab MA et al. 2023 – Updates on the classification and numbers of marine fungi. Botanica Marina 66, 213–238.
Calabon MS, Jones EBG, Promputtha I, Hyde KD. 2021 – Fungal biodiversity in salt marsh ecosystems. Journal of Fungi 7, 648.
Calado MDL, Carvalho L, Barata M, Pang KL. 2019 – Potential roles of marine fungi in the decomposition process of standing stems and leaves of *Spartina maritima*. Mycologia 111, 371–383.
Calado MDL, Carvalho L, Pang K-L, Barata M. 2015 – Diversity and ecological characterization of sporulating higher filamentous marine fungi associated with *Spartina maritima* (Curtis) Fernald in two Portuguese salt marshes. Microbial Ecology 70, 612–633.
Campbell J. 2005 – Neotypification of *Lulworthia fucicola*. Mycologia 97, 549–551.
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, 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.
Cavaliere AR, Johnson TW Jr. 1965 – A new marine Ascomycete from Australia. Mycologia 57, 927–932.
Cavaliere AR, Johnson TW Jr. 1966 – Marine ascomycetes: ascocarp morphology and its application to taxonomy. 3. A revision of the genus *Lulworthia* Sutherland. Nova Hedwigia 10, 425–437.
Cha HJ, Chiang MWL, Guo SY, Lin SM et al. 2021 – Culturable fungal community of *Pterocladiella capillacea* at Keelung, Taiwan: effects of surface sterilization method and isolation medium. Journal of Fungi 7, 651.
Chatmala I, Sakayaroj J, Somrithipol S, Phongpaichit S. 2004 – Marine hyphomycetes of Thailand and *Cumulospora varia* sp. nov. Fungal Diversity 17, 1–9.
Chen J, Tang Y, Lee S, Chen S et al. 2024 – *Halophilomyces hongkongensis*, a novel species and genus in the Lulworthiaceae with antibacterial potential, colonizing the roots and rhizomes of the seagrass *Halophila ovalis*. Journal of Fungi 10, 474.
Cribb AB, Cribb JW. 1955 – Marine fungi from Queensland-I. University of Queensland Papers, Department of Botany 3, 77–81.
Cribb AB, Cribb JW. 1956 – Marine Fungi from Queensland-II. University of Queensland Papers, Department of Botany 3, 97–105.
Crous PW, Boers J, Holdom D. 2022 – Fungal Planet description sheets: 1383–1435. Persoonia 48, 261–371.
Dayarathne MC. 2016 – Taxonomic utility of old names in current fungal classification and nomenclature: Conflicts, confusion and clarifications. Mycosphere 7, 1622–1648.
Dayarathne MC, Maharachchikumbura SS, Jones EBG, Dong W et al. 2019 – Phylogenetic revision of Savoryellaceae and evidence for its ranking as a subclass. Frontiers in Microbiology 10, 840.
Demoulin V. 1974 – The origin of Ascomycetes and Basidiomycetes the case for a red algal ancestry. Botanical Review 42, 13–14.
Devadatha B, Jones EBG, Pang KL, Abdel-Wahab MA et al. 2021 – Occurrence and geographical distribution of mangrove fungi. Fungal Diversity 106, 137–227.
Edgar RC. 2004 – MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32, 1792–1797.
Eriksson OE. 2006 – Outline of Ascomycota. Myconet 12, 1–82.

Farrant C, Hyde KD, Jones EBG. 1985 – Further studies on lignicolous marine fungi from Danish sand dunes. Transactions of the British Mycological Society 85, 164–167.
Figueira D, Barata M. 2007 – Marine fungi from two sandy beaches in Portugal. Mycologia 99, 20–23.
Gargas A, Taylor JW. 1992 – Polymerase chain reaction (PCR) primers for amplifying and sequencing 18S rDNA from lichenized fungi. Mycologia 84, 589–592.
Goh TK, Hyde KD. 1999 – A synopsis of *Trichocladium* species, based on the literature. Fungal Diversity 2, 101–118.
Gonçalves MFM, Abreu AC, Hilário S, Alves A. 2021 – Diversity of marine fungi associated with wood baits in the estuary Ria de Aveiro, with descriptions of *Paralulworthia halima*, comb. nov., *Remispora submersa*, sp. nov., and *Zalerion pseudomaritima*, sp. nov. Mycologia 113, 664–683.
Grigoriev IV, Nikitin R, Haridas S, Kuo A et al. 2014 – MycoCosm portal: gearing up for 1000 fungal genomes. Nucleic Acid Research 42, D699–D704.
Hagestad, OC, Andersen JH, Altermark B, Hansen E et al. 2020 – Cultivable marine fungi from the Arctic Archipelago of Svalbard and their antibacterial activity. Mycology 11, 230–242.
Harvey JBJ. 2004 – Phylogenetic studies of the marine brown algae *Cystoseira* and *Halidrys* including coevolution with the associated fungal endophyte *Haloguignardia irritans*. Dissertation, University of California.
Hoang DT, Chernomor O, von Haeseler A, Minh BQ et al. 2018 – UFBoot2: improving the ultrafast bootstrap approximation. Molecular Biology & Evolution 35, 518–522.
Hongsanan S, Maharachchikumbura SSN, Hyde KD, Samarakoon MC et al 2017 – An updated phylogeny of Sordariomycetes based on phylogenetic and molecular clock evidence. Fungal Diversity 84, 25–41.
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.
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, Jones EBG, Moss ST. 1986 – How do fungal spores attach to surfaces? In: Barry S, Houghton DR, Llewellyn GC, O'Rear CE (eds) Biodeterioration 6. CAB Inter Mycol Inst, The Biodeterioration Society, London, pp 584–589.
Hyde KD, Maharachchikumbura SSN, Hongsanan S, Samarakoon MC et al. 2017 – The ranking of fungi: a tribute to David Hawksworth on his 70th birthday. Fungal Diversity 84, 1–23.
Hyde KD, Norphanphoun C, Maharachchikumbura SSN, Bhat DJ et al. 2020 – Refined families of Sordariomycetes. Mycosphere 11, 305–1059.
Inderbitzin P, Lim SR, Volkmann-Kohlmeyer B, Kohlmeyer J et al. 2004 – The phylogenetic position of *Spathulospora* based on DNA sequences from dried herbarium material. Mycol Res 108, 737–748.
James TY, Kauff F, Schoch CL, Matheny PB et al. 2006 – Reconstructing the early evolution of Fungi using a six-gene phylogeny. Nature 443, 818–822.
Jenssen M, Rainsford P, Juskewitz E, Andersen JH 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, 730740.
Johnson TW Jr. 1958 – Marine fungi. IV. *Lulworthia* and *Ceriosporopsis*. Mycologia 50, 151–163.
Johnson TW, Sparrow FK. 1961 – Fungi in oceans and estuaries. Cramer, Weinheim, Germany.
Jones EBG. 1962 – Some wood-inhabiting marine Pyrenomycetes. Transactions of the British Mycological Society 45, 587–588.
Jones EBG. 1963a – Marine fungi: II. Ascomycetes and deuteromycetes from submerged wood and drift *Spartina*. Transactions of the British Mycological Society 46, 135–144.

Jones EBG. 1963b – 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. Mycol Res 98, 961–981.
Jones EBG, Johnson RG, Moss ST. 1983 – Taxonomic studies of the Halosphaeriaceae: *Corollospora* Werdermann. Botanical Journal of the Linnean Society 87, 193–212.
Jones EBG, Klaysuban A, Pang KL. 2008 – Ribosomal DNA phylogeny of marine anamorphic fungi: *Cumulospora varia*, *Dendryphiella* species and *Orbimyces spectabilis.* Raffles Bulletin of Zoology 19, 11–18.
Jones EBG, Pang KL. 2022 – Observation of Danish marine fungi: in memoriam of Dr. Jørgen Koch. Botanica Marina 65, 13–21.
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, 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, Sakayaroj J, Bahkali AH et al. 2015 – Classification of marine Ascomycota, Basidiomycota, Blastocladiomycota and Chytridiomycota. Fungal Diversity 73, 1–72.
Kalyaanamoorthy S, Minh B, Wong T, von Haeseler A et al. 2017 – ModelFinder: fast model selection for accurate phylogenetic estimates. Nature Methods 14, 587–589.
Katoh K, Standley DM. 2013 – MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology & Evolution 30, 772–780.
Koch J. 1974 – Marine fungi on driftwood from the West coast of Jutland, Denmark. Friesia 10, 209–250.
Koch J, Jones EBG. 1984 – *Lulworthia lignoarenaria*, a new marine pyrenomycete from coastal sands. Mycotaxon 20, 389–395.
Koch J, Pang KL, Jones EBG. 2007 – *Rostrupiella danica* gen. et sp. nov., a *Lulworthia*-like marine lignicolous species from Denmark and the USA. Botanica Marina 50, 1–8.
Kohlmeyer J. 1968 – Marine fungi from the tropics. Mycologia 60, 252–270.
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, 614–647.
Kohlmeyer J. 1974 – Higher fungi as parasites and symbionts of algae. Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven Suppl 5, 339–356.
Kohlmeyer J. 1975 – Revision of algicolous *Zignoella* spp. and description of *Pontogeneia* gen. nov. (Ascomycetes). Botanische Jahrbücher fur Systematik 96, 200–211.
Kohlmeyer J. 1980 – Tropical and subtropical filamentous fungi of the Western Atlantic Ocean. Botanica Marina 23, 529–544.
Kohlmeyer J. 1984 – Tropical marine fungi. Marine Ecology 5, 329–378.
Kohlmeyer J, Demoulin V. 1981 – Parastic and symbiotic fungi on marine algae. Botanica Marina 24, 9–18.
Kohlmeyer J, Kohlmeyer E. 1964 – Synoptic plates of higher marine fungi. An identification guide for the marine environment. J Cramer, Lehre.
Kohlmeyer J, Kohlmeyer E. 1979 – Marine mycology: the higher fungi. Academic Press, New York.
Kohlmeyer J, Spatafora JW, Volkmann-Kohlmeyer B. 2000 – Lulworthiales, a new order of marine Ascomycota. Mycologia 92, 453–458.
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 Aldabra, the Galapagos, and other tropical islands. Canadian Journal of Botany 65, 571–582.
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, 1554–1559.
Kohlmeyer J, Volkmann-Kohlmeyer B. 1991 – Illustrated key to the filamentous higher marine fungi. Botanica Marina 34, 1–61.
Kohlmeyer J, Volkmann-Kohlmeyer B. 1993 – Two new genera of Ascomycotina from saltmarsh *Juncus*. Systema Ascomycetum 11, 95–106.
Kohlmeyer J, Volkmann-Kohlmeyer B. 1995 – Fungi on *Juncus roemerianus*. I. *Trichocladium medullare* sp. nov. Mycotaxon 53, 349–353.
Kohlmeyer J, Volkmann-Kohlmeyer B. 2003 – Marine ascomycetes from algae and animal hosts. Botanica Marina 46, 285–306.
Li M, Raza M, Song S, Hou L et al. 2023 – Application of culturomics in fungal isolation from mangrove sediments. Microbiome 11, 272.
Liu YJ, Whelen S, Hall BD. 1999 – Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. Molecular Biology & Evolution 16, 1799–1808.
Lloyd LS, Wilson IM. 1962 – Development of the perithecium in *Lulworthia medusa* (Ell. et Ev.) Cribb *et* Cribb, a saprophyte on *Spartina townsendii*. Transactions of the British Mycological Society 45, 359–372.
Maharachchikumbura SSN, Hyde KD, Jones EBG, McKenzie EH et al. 2015 – Towards a natural classification and backbone tree for Sordariomycetes. Fungal Diversity 72, 199–301.
Maharachchikumbura SSN, Hyde KD, Jones EBG, McKenzie EHC et al. 2016 – Families of Sordariomycetes. Fungal Diversity 79, 1–317.
Matheny PB, Liu YJ, Ammirati JF, Hall BD. 2002 – Using RPB1 sequences to improve phylogenetic inference among mushrooms (*Inocybe*, Agaricales). American Journal of Botany 89, 688–698.
Meyers SP. 1957 – Taxonomy of marine Pyrenomycetes. Mycologia 49, 475–528.
Meyers SP. 1966 – Variability in growth and reproduction of the marine fungus, *Lulworthia floridana*. Helgolander wissenschaftliche Meeresuntersuchungen 13, 436–443.
Meyers SP, Moore RT. 1960 – Thalassiomycetes II. New genera and species of Deuteromycetes. American Journal of Botany 47, 345–349.
Meyers SP, Reynolds ES. 1959a – Cellulolytic activity in lignicolous marine Ascomycetes. Bull Mar Sci Gulf Caribb 9, 441–455.
Meyers SP, Reynolds ES. 1959b – Effects of wood and wood products on perithecial development by lignicolous marine Ascomycetes. Mycologia 53, 138–145.
Moore RT, Meyers SP. 1962 – Thalassiomycetes: III. The genus *Zalerion*. Can J Microbiol 8, 407–416.
Muller E, von Arx JA. 1962 – Die Gattungen der didymosporen Pyrenomyceten. Beiträge zur Kryptogamenflora der Schweiz 11, 1–922.
Murray MG, Thompson WF. 1980 – Rapid isolation of high molecular weight plant DNA. Nucleic Acid Research 8, 4321–4326.
Nakagiri A. 1984 – Two new species of *Lulworthia* and evaluation of genera-delimiting characters between *Lulworthia* and *Lindra* (Halosphaeriaceae). Transactions of the Mycological Society of Japan 25, 377-388.
Nakagiri A, Tubaki K. 1983 – *Lindra obtusa*, a new marine ascomycete and its *Anguillospora* anamorph. Mycologia 75, 487–497.
Nambiar R, Raveendran K. 2015 – Identification of marine mycoflora in Amini Dweep of Lakshadweep islands. BIOINFOLET 12, 518–520.
Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ. 2015 – IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology & Evolution 32, 268–274.
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.

Pang KL, Hassett BT, Shaumi A, Guo SY et al. 2021 – Pathogenic fungi of marine animals: A taxonomic perspective. Fungal Biology Reviews 38, 92–106.
Pang KL, Jheng JS, Jones EBG. 2011 – Marine mangrove fungi of Taiwan. National Taiwan Ocean University Press, Keelung.
Pang KL, Vrijmoed LLP, Kong RYC. 2003 – Polyphyly of *Halosarpheia* (Halosphaeriales, Ascomycota): implications on the use of unfurling ascospore appendage as a systematic character. Nova Hedwigia 77, 1–18.
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, 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, 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.
Raghukumar C, Ravindran J. 2012 – Fungi and their role in corals and coral reef ecosystems. In: Raghukumar C (ed) Biology of marine fungi. Springer-Verlag, Berlin Heidelberg, pp 89–113.
Raghukumar S. 2017 – Fungi in coastal and oceanic marine ecosystems. Springer, Cham
Rämä T, Nordén J, Davey ML, Mathiassen GH et al. 2014 – Fungi ahoy! Diversity on marine wooden substrata in the high North. Fungal Ecology 8, 46–58.
Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018 – Posterior summarization in bayesian phylogenetics using Tracer 1.7. Systematic Biology 67, 901–904.
Réblová M, Miller AN, Rossman AY, Seifert KA et al. 2016 – Recommendations for competing sexual-asexually typified generic names in Sordariomycetes (except Diaporthales, Hypocreales, and Magnaporthales). IMA Fungus 7, 131–153.
Rees G, Johnson RG, Jones EBG. 1979 – Lignicolous marine fungi from Danish sand dunes. Transactions of the British Mycological Society 72, 99–106.
Rees G, Jones EBG. 1984 – Observations on the attachment of spores of marine fungi. Botanica Marina 27, 145–160.
Rehner SA, Buckley E. 2005 – A *Beauveria* phylogeny inferred from nuclear ITS and EF1-α sequences: Evidence for cryptic diversification and links to *Cordyceps* teleomorphs. Mycologia 97, 84–98.
Rehner SA, Samuels GJ. 1994 – Taxonomy and phylogeny of *Gliocladium* analysed from nuclear large subunit ribosomal DNA sequences. Mycological Research 98, 625–634.
Ronquist F, Teslenko M, Van Der Mark P, Ayres DL et al. 2012 – MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61, 539–542.
Sachs J. 1874 – Lehruch der Botanik, 4th ed. Engelmann, Leipzig.
Sakayaroj J. 2005 – Phylogenetic relationships of marine Ascomycota. Dissertation, Prince of Songkla University.
Sakayaroj J, Pang KL, Jones EBG. 2011 – Multi-gene phylogeny of the Halosphaeriaceae: its ordinal status, relationships between genera and morphological character evolution. Fungal Diversity 46, 87–109.
Sayers EW, Cavanaugh M, Clark K, Pruitt KD et al. 2019 – GenBank. Nucleic Acid Research 47, D94–D99.
Schaumann K, Mulach W, Molitoris HP 1986 – Comparative studies on growth and exoenzyme of different *Lulworthia* isolates. In: Moss ST (ed) The biololgy of marine fungi. Cambridge University Press, Cambridge, pp 49–60.
Schindelin J, Arganda-Carreras I, Frise E, Kaynig V et al. 2012 – Fiji: an open-source platform for biological-image analysis. Nature Methods 9, 676–682.

Schmidt I .1974 – Hohere Meerespilze der Ostsee. Natur und naturschutz in Mecklenburg 12, 1–148
Schmidt I. 1985 – Types and type collections of new higher marine and fresh-water fungi from the Baltic coast. Mycotaxon 24, 419–421.
Schmitt I, Crespo A, Divakar PK, Fankhauser JD et al. 2009 – New primers for promising single-copy genes in fungal phylogenetics and systematics. Persoonia 23, 35–40.
Schoch CL, Crous PW, Groenewald JZ, Boehm EWA et al. 2009 – A class-wide phylogenetic assessment of Dothideomycetes. Studies in Mycology 64, 1–15.
Shearer CA, Burgos J. 1987 – Lignicolous marine fungi from Chile. Botanica Marina 30, 455–458.
Spatafora JW, Volkmann-Kohlmeyer B, Kohlmeyer J. 1998 – Independent terrestrial origins of the Halosphaeriales (marine Ascomycota). American Journal of Botany 85, 1569–1580.
Stamatakis A. 2006 – Phylogenetic models of rate heterogeneity: a high performance computing perspective. In: Proceedings 20th IEEE international parallel and distributed processing symposium. IEEE, pp 8.
Stielow JB, Lévesque CA, Seifert KA, Meyer W et al. 2015 – One fungus, which genes? Development and assessment of universal primers for potential secondary fungal DNA barcodes. Persoonia 35, 242–263.
Stiller JW, Hall BD. 1997 – The origin of red algae: implications for plastid evolution. Proceedings of the National Academy of Sciences of the United States of America 94, 4520–4525.
Sutherland GK. 1916 – Additional notes on marine pyrenomycetes. Trans Br mycol Soc 5, 257–263.
Tamura K, Stecher G, Kumar S. 2021 – MEGA11: Molecular Evolutionary Genetics Analysis Version 11. Molecular Biology & Evolution 38, 3022–3027.
Tibell S. 2016 – New records of marine fungi from Sweden. Svensk mykologisk tidskrift 37, 43–54.
Tokura R. 1982 – Arenicolous marine fungi from Japanese beaches. Transactions of the Mycological Society of Japan 23, 423–433.
Tokura R, Nakagawa K. 1983 – Studies on the proper guidance of biological marine practice. VII. Marine fungi from Hakoishi Beach of the Sea of Japan (III). Fungi occurred on sand baited with balsa wood and other substances. Annual Report of Researches in Science Education, Kyoto University of Education 12, 29–57.
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, 505–511.
Tubaki K, Nakagari A. 1982 – Marine and aquatic fungi in and around Teshio-cho. II. Human Culture and Environmental Studies in Northern Hokkaido, University of Tsukuba Japan 3, 35–46.
Velmurugan N, Lee YS. 2012 – Enzymes from marine fungi: current research and future prospects. In: Jones EBG, Pang KL (eds) Marine fungi and fungal-like organisms. De Gruyter, Berlin, Boston, pp 441–474.
Vilgalys R, Hester M. 1990 – Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. Journal of Bacteriology 172, 4239–4246.
Walker AK. 2012 – Marine fungi of U.S. Gulf of Mexico barrier island beaches: biodiversity and sampling strategy. Dissertation, University of Southern Mississippi.
Wang G. 2006 – Diversity and biotechnological potential of the sponge-associated microbial consortia. Journal of Industrial Microbiology and Biotechnology 33, 545.
Wang G, Li Q, Zhu P. 2008 – Phylogenetic diversity of culturable fungi associated with the Hawaiian sponges *Suberites zeteki* and *Gelliodes fibrosa.* Antonie van Leeuwenhoek 93, 163–174.
Wang X, Pecoraro L, Chen J, Tang Y, Lee S, Chen S, Liu H. 2024 – *Halophilomyces hongkongensis*, a novel species and genus in the Lulworthiaceae with antibacterial potential, colonizing the roots and rhizomes of the seagrass *Halophila ovalis*. Journal of Fungi 10(7), 474.

White TJ, Bruns T, Lee S, Taylor J. 1990 – Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols: a guide to methods and applications. Academic Press, San Diego, pp 315–322.
Wijayawardene NN, Hyde KD, Rajeshkumar KC, Hawksworth DL et al. 2017 – Notes for genera: Ascomycota. Fungal Diversity 86, 1–594.
Wijayawardene NN, Hyde KD, Dai DQ, Sánchez-García et al. 2022 – Outline of Fungi and fungus-like taxa – 2021. Mycosphere 13, 53–453.
Wilson IM. 1956 – Some new marine Pyrenomycetes on wood or rope: *Halophiobolus* and *Lindra*. Transactions of the British Mycological Society 39, 401–415.
Woudenberg JH, Aveskamp MM, de Gruyter J, Spiers AG et al. 2009 – Multiple *Didymella* teleomorphs are linked to the *Phoma clematidina* morphotype. Persoonia 22, 56–62.
Yusoff M, Jones EBG, Moss ST. 1995 – Ascospore ultrastructure in the marine genera *Lulworthia* Sutherland and *Lindra* Wilson. Cryptogamie Botany 5, 307–315.

Statements and Declarations

COMPETING INTERESTS

The authors declare no conflicts of interest regarding this article.

Data Availability

The datasets generated during and/or analysed during the current study are available in the TreeBASE repository, http://purl.org/phylo/treebase/phylows/study/TB2:S31313, and http://purl.org/phylo/treebase/phylows/study/TB2:S31291.