Abstract

*Alternaria*, a genus of ascomycetes, comprises major plant pathogens, saprobes and are common allergens to humans. There are more than 360 accepted species in the genus, which are currently divided into 29 sections. This paper aims to elaborate the taxonomy of *Alternaria* with multi-locus phylogenetic trees derived by analyses of a concatenated DNA sequence dataset consisting of ITS, LSU, rpb2 and GAPDH and Alt-a1 loci. Eighteen new species viz. *Alternaria arctoseptata*, *A. arundinis*, *A. baoshanensis*, *A. breviconidiophora*, *A. brevirastra*, *A. ellipsoidalis*, *A. eupatoriicola*, *A. falcata*, *A. Iathyri*, *A. macilenta*, *A. macroconidia*, *A. minimispora*, *A. nodulariconidiophora*, *A. oblongoellipsidea*, *A. orbanchae*, *A. phragmiticola*, *A. phytolaccceae* and *A. salicicola* are introduced and classified in sect. *Alternaria*, sect. *Infectoriae*, sect. *Porri* and sect. *Radicina*. *Alternaria alternata* and *A. dolichodium* are also described herein with new host and geographical records, in China, Italy, and Thailand. This study further explores the utility of divergent time estimates to gain additional insights into the evolutionary relationships of *Alternaria* in Pleosporales.

INTRODUCTION

*Alternaria* Nees is a ubiquitous dematiaceous hyphomycete genus, comprising over 790 species epithets, and approximately 368 species accepted within 29 sections. Species of *Alternaria* occupy diverse ecological niches, from endophytes on various asymptomatic plant tissues to saprobes on a wide range of hosts and substrates (i.e., dead vegetation, paper, and food), as well as plant and animal (including human) pathogens worldwide. The genus is cosmopolitan and widely distributed in Asia (e.g., India, Japan), Australia, Europe, and North America.

As invasive pathogens, *Alternaria* species are frequently isolated from different habitats such as the atmosphere, dust, indoor environments, soil, and damaged old buildings. The most prevalent diseases of plants caused by *Alternaria* are leaf spots and defoliation with typical concentric zonatic symptoms featuring brown to black necrotic lesions surrounded by chlorotic areas on leaves, but can also infect flowers, fruits, roots, seedlings, and stems with different kinds of lesions. These diseases reduce their market value and result in financial losses of important economic crops, such as cabbage, cucumber, fava bean, onion, potato, tomato and ornamental plants. Most causal agents are restricted to *Alternaria* sects. *Alternanthae* D.P. Lawr. et al., *Alternaria* D.P. Lawr. et al., *Brassicicolae* D.P. Lawr. et al., *Crivellia* (Shoemaker & Inderb.) Woudenb. & Crous, *Gypsophilae* D.P. Lawr. et al., *Nimbya* (E.G. Simmons) Woudenb. & Crous, *Porri* D.P. Lawr. et al., *Radicina* D.P. Lawr. et al., and *Sonchi* D.P. Lawr. et al. and occur on over 4,000 host and non-host specific plants. Jayawardena et al. showed that the majority of pathogenic *Alternaria* species infected a vast array...
of host species. Effective implementation of control strategies is generally hampered by misidentification. As an important plant pathogen, further details on phylogeny, diseases and symptoms, as well as morphological characters of Alternaria were also discussed by Jayawardena et al.[25,26].

Alternaria species have the ability to produce a wide spectrum of secondary metabolites. Potential phytotoxins produced by Alternaria are beneficial for biotechnological applications as biocontrol agents or mycoherbicides of innumerable plant species under diverse habitats[11,12,13]. Furthermore, Alternaria species also produced mycotoxins and are implicated in opportunistic animal and human diseases (e.g., alternariosis) that significantly affect the health of victims and can also contaminate food products. Alternaria alternata (Fr.) Keissl. and A. infectoria E.G. Simmons have frequently been reported as causative agents of phaeohyphomycosis in immuno-compromised patients and kidney transplant patients or airborne allergens[11,15,29–34].

Alternaria, currently belongs to Pleosporaceae of Pleosporales, Dothideomycetes[1,2], and was introduced by von Nees & Daniel[35], with A. tenuis Nees as the type species. von Keissler[36] considered A. tenuis to be conspecific with Torula alternata Fr.[37] and synonymized both A. tenuis and T. alternata with A. alternata which is currently designated as the generic type. Extensive morphology-based taxonomy of Alternaria was mainly dealt with by Simmons (1920–2013), who provided a monograph of Alternaria and recognized 275 species in the genus based on the patterns of sporulation and conidial morphology[38]. The latest taxonomic treatment of Alternaria was carried out by Lawrence et al.[13,15], Lawrence et al.[13,15] described the asexual morph of Alternaria as alternarioid dematiaceous hyphomycetes with effuse, pigmented colonies, colorless hyphae, mononematous to caespitose, macronema tous, simple or branched, pale brown to brown conidiophores, monotretic or polytretic, sympodial, conidigenous cells, and dark pigmented, multi-celled, typically dictyosporous, or rarely phragmosporous conidia, some borne singly and most catenate chains. The sexual morph of Alternaria has only been reported for species in sects. Alternaria, Crivellia, Ellbesioides Woudenb. & Crous, Eureka Woudenb. & Crous, Infectoriae Woudenb. & Crous, Nimbya and Panax D.P. Lawr. et al., and is characterized by small, dark brown, erumpent to superficial, globose to ovoid, glabrous, uni-loculate ascocoma, with papillate ostioles, composed of thin-walled peridia, containing fissitunicate, cylindrical to cylindric-clavate ascii, embedded in broad cellular pseudoparaphyses and muriform, ellipsoidal to fusoid, pigmented ascospores[11,15,24].

Over the course of taxonomic discussions of Alternaria, many genera have been considered to be the sexual morph of Alternaria, including Allewia E.G. Simmons, Crivellia Shoemaker & Inderb., Lewia M.E. Barr & E.G. Simmons, and Macrospora Fuckel[15,24]. Moreover, some sexual genera (viz. Clathrospora Rabenh., Comoclatrichis Clem., Leptosphaeria Ces. & De Not., and Pleospora Rabenh. ex Ces. & De Not.) have also been described with alternarioid asexual morphs, of which Pleospora were usually mentioned as the sexual morph of Alternaria[15]. However, Simmons[42] linked Pleospora with the asexual genus Stemphylium Wallr. Hitherto, Pleospora and Stemphylium were considered as congeneric, and Stemphylium was recommended to be used over Pleospora due to its wider use and earlier introduction[29]. Woudenberg et al.[71] demonstrated that Alternaria, Brachyladium Corda, Chalastospora E.G. Simmons, Chmelia Svob.-Pol., Crivellia, Ellbesioides E.G. Simmons, Lewia, Nimbya E.G. Simmons, synonymizes Yong Wang bis & X.G. Zhang, Teretispora E.G. Simmons, Ulocladium Preuss, Undifilium B.M. Pryor et al. and Ybotromyces Rulamort formed internalclades within Alternaria sensu stricto and thus these genera were synonymized and treated as sections of Alternaria. Macrospora was also considered as the sexual morph of sect. Nimbya and thus the genus was treated as a synonym of Alternaria[11,15]. The type species of Macrospora, M. scirpivora E.G. Simmons & D.A. Johnson, was synonymized under Alternaria as A. scirpivora (E.G. Simmons & D.A. Johnson), Woudenb. & Crous by Woudenberg et al.[13]. Based on the prior introduction of Alternaria, widespread use and number of the species, Rossman et al.[39] proposed to use Alternaria rather than Allewia, Crivellia and Lewia.

The DNA-based classification of the genus Alternaria has so far relied on over ten gene loci, including nuclear ribosomal DNA (LSU, SSU), the intervening ITS regions, mtSSU, protein-coding genes such as ACT, Alt-a1, CAL, GAPDH, RPB2, TEF1-α, THN, Tsr1, and the plasma membrane ATPase gene[7,11,15,25,26]. Multiple molecular methods have been investigated or proposed for distinguishing Alternaria species, including random amplified polymorphic DNA[41], amplified fragment length polymorphism[42], selective subtractive hybridization[43] and sequence characterized amplified genomic regions[44]. However, the standard gene regions and other protein-coding loci (e.g., ACT, CAM, RPB2, TEF1-α, Tsr1, TUB2 and chitin synthase) are not able to delineate species within all the sections of Alternaria, such as small spore species-groups like sect. Alternaria and sect. Infectoriae[12,45–48], Hong et al.[49] illustrated that the Alt-a1 locus is reliable for Alternaria species identification. Lawrence et al.[14] used five protein-coding loci (viz. ACT, Alt-a1, CAM, GAPDH, and plasma membrane ATPase) for clarifying the phylogenetic hypothesis among Alternaria and revealed that the plasma membrane ATPase and CAM genes were the most suitable phylogenetic markers for molecular identification of Alternaria species. Woudenberg et al.[11] delineated phylogenetic lineages within Alternaria, and allied genera based on the multi-locus phylogeny of SSU, LSU, ITS, GAPDH, RBP2 and TEF1-α gene regions and introduced 16 new Alternaria sections. Subsequently, whole-genome sequencing has become an essential tool to delineate ambiguous species in Alternaria and other complex species[12]. Therefore, Woudenberg et al.[12] used multi-locus phylogeny based on ITS, GAPDH, RPB2, TEF1-α, Alt-a1, endoPG and OPA10-2 gene loci, coupled with whole-genome and transcriptome comparisons to discriminate species in sect. Alternaria. Lawrence et al.[15] provided a comprehensive taxonomic treatment of Alternaria with multi-locus phylogeny and accepted 27 sections in Alternaria, but later revised it to 28 accepted sections[7,15]. Recently, Gannibal et al.[16] and Ghafri et al.[7] introduced two new sections (i.e., sects. Helianthiiniciens and Omanentes) of Alternaria and thus, 29 sections were accepted[6,7,15].

Historical studies on Alternaria

The study of Alternaria and their allied genera has been debated for over 200 years. As summarized by Lawrence et al.[15], there are five chronological stages in the taxonomic studies of Alternaria. The first stage (1816–1850s) is when the genus Alternaria was first described in 1816, with A. tenuis as
the type, but it was then confused with genera such as *Macrosporum* and *Stemphylium*. However, the first validly published species name was *Torula alternata*.[97] The second stage (1850s–1930s) involved publication of numerous alternarioid species, wherein Elliott[60] first attempted to revise the taxonomy and nomenclature of *Alternaria* and *Macrosorium*, but this resulted in an increasing number of nomenclatural problems within the alternarioid hyphomycetes. The third stage (1930s–1960s) includes various revisions of *Alternaria* made by Wiltshire[51], Neergaard[52], and Joly[53]. However, their work did not follow the rules of nomenclature, and despite wide adoption, these are not in practice to date. The fourth stage (1960s–2000s) is when Emory Guy Simmons (1920–2013) presented a complete reappraisal and revision of all names and taxa related to *Alternaria*, representing the most extensive compilations in the taxonomic history of the genus. The fifth stage (2000s–2015s) involved molecular phylogenetic methods to further investigate the taxonomy of *Alternaria*. Taxonomic studies integrating both morphological and molecular data were provided by Pryor & Gilbertson[54], Hong et al.[49], Lawrence et al.[13,14,53], Woudenberg et al.[11,12,22] and Grum-Grzhimaylo et al.[56]. In subsequent studies, the utility and reliability of different genes in deciphering phylogenetic relationships have been discussed by Woudenberg et al.[12] and Lawrence et al.[15].

The *Alternaria* sections

*Alternaria* sections are recognized based on molecular phylogenies, but these do not always correlate with species-groups that were earlier delineated based on morphological characteristics (Table 1).[11,13–15,22,50] The species-groups *A. alternata*, *A. alternantherae*, *A. brassicicola*, *A. infectoria*, *A. porri*, *A. radicina* and *A. sonchi* were phylogenetically strongly supported by Chou & Wu[57], De Hoog & Hörn[50], Hong et al.[49], Indebitini et al.[58], Lawrence et al.[14,53], Pryor & Bigelow[58], Pryor & Gilbertson[54], Pryor et al.[60], Runa et al.[21], Wang et al.[61], and Woudenberg et al.[11,12]. Lawrence et al.[14] introduced *A. panax* and *A. gypsophila* as two species-groups and proposed eight species-groups to sections within *Alternaria*. The latest treatment of *Alternaria* were carried out by Lawrence et al.[15] who generalized the genus with 27 sections. Recently, Ghafri et al.[7] included sect. *Omanenses* Al Ghafri et al. to the genus. While Gannibal et al.[58] introduced a new section, sect. *Helianthiflentes*, for *A. helianthiflentes* which was previously demonstrated as a monotypic lineage in Woudenberg et al.[7] and Lawrence et al.[15].


**Section Alternantherae** was introduced by Lawrence et al.[14] for species group *Alternaria alternantherae* Holcomb & Antonop., comprising three species previously described as *Nimbya* species viz. *A. celosicola* Jun. Nishikawa & C. Nakash., *A. gomphephora* Togashi and *A. perpunctulata* (E.G. Simmons) D.P. Lawr., M.S. Park & B.M. Pryor, and the type species of the section, *A. alternantherae*.[11,15]. Subsequently, the other three species were included in the sect. *Alternantherae* viz. *A. crossoidea* (Davis) Gannibal, *A. pimpriana* V.G. Rao, and *A. anomalous* Jun. Nishikawa & C. Nakash. that *A. crossoidea* and *A. pimpriana* were previously accommodated in *Nimbya*.[62–64]. Currently, seven species are accepted in this section.

**Section Alternaria** was introduced by Lawrence et al.[14] to accommodate *Alternaria* species, commonly referred to small-spored *Alternaria* groups. The main morphological feature that can be used to distinguish *Alternaria* sect. *Alternaria* from other sections is the short conidia produced in chains (frequently less than 60 μm in vitro).[11,14,65]. The sexual morph is known from *A. alternata* and described as typically small-sized, erumpent, globose to ovoid, smooth, dark brown, papillate ascomata, cylindrical to cylindric-clavate asci, and ellipsoid to fusoid, brown, eguttulate, smooth-walled ascospores, with 3–7 transverse septa, 1–2 longitudinal septa.[15,24]. There were approximately 60 species accommodated in section *Alternaria* based on ITS sequence data.[11]. However, Woudenberg et al.[12] accepted only 11 phylogenetic species and one species complex in this section. Gannibal[65] re-circumscribed and amended the section based on morphological assessments by Simmons.[58]. Gannibal[65] included the other 37 morpho-species and accepted 59 species in this section. Subsequently, the other four species were included in this section by Gannibal & Lawrence[62] viz. *A. calystegiae* Nelen, *A. diversispora* (Thum.) E.G. Simmons, *A. guarantica* (Spec.) E.G. Simmons and *A. macalpinei* E.G. Simmons. Wanasinghe et al.[68] introduced *A. dolicioidum* J.F. Li, Camporesi & K.D. Hyde on *Rosa canina* in Italy. Jayawardena et al.[67] also introduced *A. italica* J.F. Li, Camporesi & K.D. Hyde on *Vitis vinifera* in Italy. Nishikawa & Nakashima[63] also included *A. iridicola* (Ellis & Everh.) J.A. Elliott in this section. In 2022, Li et al.[68] introduced six saprobic species from Italy in this section (i.e., *A. muiformispora* J.F. Li et al., *A. obpyricynida* J.F. Li et al., *A. ovoidesa* J.F. Li et al., *A. pseudooinfectoria* J.F. Li et al., *A. rostroconidia* J.F. Li et al., and *A. tortilis* J.F. Li et al.). In addition, Gou et al.[69] also introduced two *Alternaria* species as pathogens causing leaf spot or blight symptoms on *Iris* plants in China viz. *A. setosae* Y.N. Gou & J.X. Deng, and *A. tectorum* Y.N. Gou & J.X. Deng. Therefore, 73 species are now accommodated in this section.

**Section Brassicicola** was introduced by Lawrence et al.[14] for the species-group *Alternaria brassicicola* (Schwein.) Wiltshire. The section comprises five species viz. *A. brassicicola*, *A. conoidea* (E.G. Simmons) D.P. Lawr. et al., *A. mimicula* E.G. Simmons, *A. septoriaeides* (Westend.) E.G. Simmons, and *A. solidaccana* E.G. Simmons.[11,15]. Multi-locus phylogenetic analyses demonstrated that sect. *Brassicicola* has close phylogenetic relationships with sects. *Sonchi*, *Radicina*, *Gysophila*, *Porri*, *Alternaria*, and *Alternanthera*.[11,14,15]. However, the conidial morphology of sect. *Brassicicola* is different from these sections in producing extremely small phragmosporous conidia with heavily melanized transverse septa.[11,14,15].

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Table 1. Synopsis of Alternaria sections based on the asexual morphs.

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<tr>
<td>Sect. Alternantherae</td>
<td>Conidiophores Short to moderately long, with slightly enlarged conidiogenous tip. Large, ellipsoidal to ovoid, or subcylindrical, rarely narrow ellipsoidal, solitary or rarely paired, disto- and euseptate, transversely septate with no or 1–2 longitudinal or oblique septa, slightly constricted near some septa, with a long apical narrow beak, conidiobial beak unbranched, septate or aseptate, long filiform, sometimes swollen at the end, internal compartmentation occurs, with cell bright at end, with hexagonal, octagonal or rounded transverse sections lumina. Conidia</td>
<td>Species in this section are reported as plant pathogens that mainly cause leaf spots.</td>
<td>[11,13,15,55]</td>
</tr>
<tr>
<td>Sect. Alternaria</td>
<td>Conidiophores Short to long, straight or curved, simple or branched, with one or several apical conidiogenous loci. Conidia Oblong to long ellipsoidal, small or moderate in size, septate, slightly constricted near some septa, with few longitudinal septa, in moderately long to long, simple or branched chains, form tapered beak or secondary conidiophore with one or a few conidiogenous loci.</td>
<td>Species in this section are reported as plant pathogens on leaves, stems, fruits, and vegetables. Some species cause opportunistic infections of humans. Species in this section are also reported as resources of potential toxins and secondary metabolites.</td>
<td>[11,12,15,100]</td>
</tr>
<tr>
<td>Sect. Brassicicola</td>
<td>Conidiophores Short to moderately long, simple or branched, with one or several apical conidiogenous loci. Conidia Ellipsoidal, ovoid or somewhat obclavate, small or moderate in size, septate, slightly or strongly constricted at most of the transverse septa, or with or without longitudinal septa, in moderately long to long, simple or branched chains, with dark septa and cell walls. Apically or laterally form secondary conidiophores with one or a few conidiogenous loci. Sometimes produced chlamydospores.</td>
<td>Species in this section mainly cause black spot disease on a wide range of hosts, particularly on Brassica spp. such as cabbage, Chinese cabbage, cauliflower, oilseeds, broccoli and canola. Species in this section are also reported as resources of antibiotic masses.</td>
<td>[11,14,100–103]</td>
</tr>
<tr>
<td>Sect. Chlastospora</td>
<td>Conidiophores Short to long, simple or branched, with one or several conidiogenous loci. Conidia Pale to medium brown, narrowly ellipsoidal to ellipsoidal or ovoid, beakless, with no or multiple transverse eusepta and rarely longitudinal septa, solitary or in chains. Apically or laterally form secondary conidiophores with one or a few conidiogenous loci.</td>
<td>Species in this section are primarily reported as saprobes and causal agents of human diseases.</td>
<td>[11,30,38]</td>
</tr>
<tr>
<td>Sect. Cheiranthus</td>
<td>Conidiophores Short to moderately long, simple or branched, with one or several conidiogenous loci. Conidia Ovoid, broadly ellipsoid with transverse and longitudinal septa, slightly or strongly constricted at the septa, in short to long, simple or branched chains.</td>
<td>Species in this section are primarily saprobes and pathogens on various plant hosts.</td>
<td>[11,38,55]</td>
</tr>
<tr>
<td>Sect. Crivella</td>
<td>Conidiophores Straight or curved, simple or branched, with geniculate, sympodial proliferations. Conidia Cylindrical, straight or curved to inequilateral, with transverse septa, rarely constricted at septa, simple or branched chains. Apically or laterally form secondary conidiophores. Sometimes produced microsclerotia or chlamydospores.</td>
<td>Species in this section are mainly known as pathogens on opium poppy (Papaver somniferum L.), the sexual morph of which links with genus Crivella.</td>
<td>[11,58]</td>
</tr>
<tr>
<td>Sect. Dianthica</td>
<td>Conidiophores Simple or branched, with or without apical geniculate proliferations. Conidia Narrowly ovoid or narrowly ellipsoidal with transverse and few longitudinal septa, slightly constricted at the septa, with a long (filamentous) beak or apical secondary conidiophore, solitary or in short chains.</td>
<td>Species in this section mainly cause leaf spot and blight on economic vegetation hosts such as carnation (Dianthus sp.) and sesame (Sesamum indicum L.).</td>
<td>[11,104,105]</td>
</tr>
<tr>
<td>Sect. Embellisia</td>
<td>Conidiophores Simple, septate, straight or with geniculate sympodial proliferation. Conidia Simple, septate conidiophores, straight or with multiple, geniculate, sympodial proliferations.</td>
<td>Species in this section are reported as pathogens on vegetable crops such as tomato and garlic.</td>
<td>[11,106,107]</td>
</tr>
<tr>
<td>Sect. Embellisoides</td>
<td>Conidiophores Simple, septate conidiophores, straight or with multiple, geniculate, sympodial proliferations. Conidia Solitary or in short chains, obovoid to ellipsoid, with transverse and longitudinal septa, transverse conidiophore can be thick, dark and rigid in contrast to the external wall. Apical or lateral, short secondary conidiophores may occur. Sometimes produced sexual morph and chlamydospores.</td>
<td>Species in this section are mainly reported as saprobes in soil and pathogen on plant hosts.</td>
<td>[9,108,109]</td>
</tr>
<tr>
<td>Sect. Eureka</td>
<td>Conidiophores Simple, septate conidiophores, straight or with geniculate, sympodial proliferations. Conidia Solitary or in short chains, narrowly ellipsoidal to cylindrical, with transverse and longitudinal septa, slightly constricted at the septum, with a blunt rounded apex. Sometimes form apical or lateral, short secondary conidiophores and sporeulated sexual morph and chlamydospores.</td>
<td>Species in this section are reported as pathogens and endophytes that are active in the biotransformation of some secondary metabolites.</td>
<td>[11,110,111]</td>
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Table 1. (continued)

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<td><strong>Sect. Euphorbiolae</strong></td>
<td>Conidiophores: Short to long, broad, apical and sometimes lateral, secondary conidiophores. Conidia: Medium to large-sized, in short to moderately long chains, ovoid, obclavate, disto- and eusepta, with multiple transverse and some longitudinal septa, slightly constricted near some transverse septa, with or a simple long beak in the terminal conidia.</td>
<td>Species in this section served as pathogens on economic plants such as Euphorbiolae sp. and Citrus sp. and also produced secondary metabolites.</td>
<td>[11,112]</td>
</tr>
<tr>
<td><strong>Sect. Gypsophilae</strong></td>
<td>Conidiophores: Simple, or occasionally branched, with one or a few conidiogenous loci. Conidia: Solitary or in short chains, ellipsoid to long ovoid, with multiple transverse and longitudinal septa, conspicuously constricted near some transverse septa. Apically form secondary conidiophores with one or two conidiogenous loci or laterally with a single conidiogenous locus.</td>
<td>Species in this section is well-known as a pathogen on sunflower and cosmos, and also associated with some other species in Asteraceae (i.e., Arctium sp. and Sonchus sp.).</td>
<td>[6]</td>
</tr>
<tr>
<td><strong>Sect. Helianthiiiflentes</strong></td>
<td>Conidiophores: Simple, or branched, with one or a few conidiogenous loci. Conidia: Solitary or in short chains, large, narrowly or broadly ovoid, or ellipsoidal, with several transverse and longitudinal septa, constricted near septa, sometimes non-beaked. Apically form secondary conidiophores, or a few lateral secondary conidiophores, or short to very long filiform beak.</td>
<td>Species in this section occur on the host family Caryophyllaceae.</td>
<td>[1,14,38]</td>
</tr>
<tr>
<td><strong>Sect. Infectoriae</strong></td>
<td>Conidiophores: Short to long, simple or branched, with one or several conidiogenous loci. Conidia: Moderately long to long, branched chains, small or moderate sized, obclavate to long ellipsoidal, septate, slightly constricted near some septa, with few longitudinal septa.</td>
<td>Species in this section are known as saprobes as well as plant and human pathogens.</td>
<td>[11,14,38,70]</td>
</tr>
<tr>
<td><strong>Sect. Japonicae</strong></td>
<td>Conidiophores: Short to long, simple or occasionally branched, with a single conidiogenous locus. Conidia: Short to long ovoid with transverse and longitudinal septa, conspicuously constricted at most of the transverse septa, in short chains. Apically formed secondary conidiophores with single conidiogenous locus.</td>
<td>Species in this section particularly occur on hosts in Brassicaceae.</td>
<td>[11,14]</td>
</tr>
<tr>
<td><strong>Sect. Nimbya</strong></td>
<td>Conidiophores: Simple, short to form moderately long, sometimes one to a few short to long, geniculate, sympodial metastasis. Conidia: Solitary or in short chains, narrowly elongate-obclavate, gradually tapering apically, with transverse disto- and eusepta, sometimes slightly constricted near eusepta.</td>
<td>Species in this section are known as saprobes and plant pathogens. Species in this section produce phytotoxins</td>
<td>[11,15,5,85,113,114]</td>
</tr>
<tr>
<td><strong>Sect. Omanenses</strong></td>
<td>Conidiophores: Long, simple, with multiple geniculate, sympodial metastasis or short conidiogenous loci normally with a terminal cluster of three conidia. Conidia: Solitary, obvoid and sphaeroid, non-beaked, with transverse and longitudinal septa.</td>
<td>Species in this section consist of a core taxon A. omanensis which is saprobid on dead woods.</td>
<td>[7]</td>
</tr>
<tr>
<td><strong>Sect. Panax</strong></td>
<td>Conidiophores: Simple or branched, short to moderately long, with one or a few conidiogenous loci. Conidia: Solitary, simple or branched, in short chains, obclavate to ovoid, with multiple transverse and longitudinal septa, conspicuously constricted near several transverse septa, apically formed secondary conidiophores with or several conidiogenous loci, multiple lateral secondary conidiophores with a single conidiogenous locus.</td>
<td>Species in this section are known as pathogens causing blight on economic plants such as ginseng and American ginseng (Araliaceae).</td>
<td>[11,14,115]</td>
</tr>
<tr>
<td><strong>Sect. Phragmosporae</strong></td>
<td>Conidiophores: Simple, short to moderately long, with one or multiple geniculate, sympodial metastasis. Conidia: Solitary or in simple short chains, broadly ovoid to long ovoid, ellipsoidal, curved, or limaciform, with multiple transverse and few to multiple longitudinal septa, some septa darkened, slightly to conspicuously constricted near several transverse septa, apically formed secondary conidiophores with one or several conidiogenous loci.</td>
<td>Species in this section are mainly known as saprobes from soil and marine environments.</td>
<td>[11]</td>
</tr>
<tr>
<td><strong>Sect. Porri</strong></td>
<td>Conidiophores: Short to long, simple, with one or several conidiogenous loci. Conidia: Solitary or in short to moderately long chains, with a simple or branched, long to filamentous beak, medium or large size, broadly ovoid, obclavate, ellipsoidal, subcylindrical or obovoid, disto- and eusepta, with multiple transverse and longitudinal septa, slightly constricted near some transverse septa, apically or laterally formed secondary conidiophores.</td>
<td>Species in this section consist of some important phytopathogens and produce phytotoxins.</td>
<td>[11,14,22,6,117]</td>
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<tr>
<td>Sect. Pseudoalternaria</td>
<td>Conidiophores: Simple or branched, septate, smooth, medium brown, simple with a single apical pore, with short to long, simple to multi-geniculate secondary conidiophores with one to many conidiogenous loci.</td>
<td>Species in this section are known as pathogens on plant hosts.</td>
<td>[15]</td>
</tr>
<tr>
<td></td>
<td>Conidia: Mostly catenulate, ellipsoid to obclavate, medium brown to golden brown, with several transverse and longitudinal septa, smooth, secondary conidiophore may occur as a false beak.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sect. Pseudoulocladium</td>
<td>Conidiophores: Simple or branched, with short, geniculate, sympodial metastaatis.</td>
<td>Species in this section are reported as phytopathogens for human infection.</td>
<td>[11]</td>
</tr>
<tr>
<td></td>
<td>Conidia: Obovoid, non-beaked with a narrow base, in simple or mostly branched chains, apically formed secondary conidiophores with multiple conidiogenous loci and laterally secondary conidiophores may occur with a single conidiogenous locus.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sect. Radicina</td>
<td>Conidiophores: Straight, simple or branched, short or long, with multiple, short geniculate, sympodial proliferations, with one to a few conidiogenous loci at the apex.</td>
<td>Species in this section mainly occur on hosts in family Apiaceae.</td>
<td>[11]</td>
</tr>
<tr>
<td></td>
<td>Conidia: Solitary or in short chains, moderate in size, broadly ovoid to narrowly ellipsoidal, beakless, with several transverse and longitudinal septa, apically formed solitary, short, secondary conidiophores.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sect. Soda</td>
<td>Conidiophores: Simple or occasionally branched, short to moderately long, with one conidiogenous locus.</td>
<td>Species in this section are isolated from soda lake environments (Western Siberia, Russia).</td>
<td>[56]</td>
</tr>
<tr>
<td></td>
<td>Conidia: Solitary or in short to long, simple or branched chains, moderate to very large in size, narrowly ellipsoid to elongate-ovoid or somewhat obclavate, septate, with transverse and longitudinal septa, conspicuously constricted at most of the transverse septa, produced microsclerotia or chlamydospores, apical or lateral short secondary conidiophores with a single conidiogenous locus may occur, and conidiogenous tip can be enlarged.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sect. Sonchi</td>
<td>Conidiophores: Simple or branched, with short, geniculate, with one or several conidiogenous loci.</td>
<td>Species in this section mainly occur on a wide range of hosts within Asteraceae (Compositae).</td>
<td>[14]</td>
</tr>
<tr>
<td></td>
<td>Conidia: Single or in short chains, medium to large size, subcylindrical, broadly ovoid, broadly ellipsoid or obclavate, with multiple transverse and few longitudinal septa, slightly constricted at the septa.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sect. Teretispora</td>
<td>Conidiophores: Simple, sometimes extending at the apex with one or two, geniculate, sympodial proliferations.</td>
<td>Species in this section consist of a core species, <em>Alternaria leucanthemi</em>, which is a phytopathogen causing plant blight disease.</td>
<td>[11,38]</td>
</tr>
<tr>
<td></td>
<td>Conidia: Single, long cylindrical, lacking a beakportion, with many transverse and a few longitudinal septa, constricted at most of the transverse septa, secondary conidiophores with single conidium from the base of primary conidium and rarely formed apically.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sect. Ulocladioides</td>
<td>Conidiophores: Short, geniculate, sympodial proliferations.</td>
<td>Species in this section are mainly known as phytopathogens causing leaf spot disease and can be saprobes on a variety of host substrates as well as a causal agent of keratitis.</td>
<td>[11,15]</td>
</tr>
<tr>
<td></td>
<td>Conidia: Obovoid, non-beaked with a narrow base, single or in chains, with apical secondary conidiophores.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sect. Ulocladium</td>
<td>Conidiophores: Simple, with one or two short, geniculate, sympodial proliferations.</td>
<td>Species in this section are mainly isolated from plant litter and rarely from marine environments. Potential bioactivities were also reported.</td>
<td>[11,118]</td>
</tr>
<tr>
<td></td>
<td>Conidia: Single, obvoid, non-beaked, with a narrow base.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sect. Undifilum</td>
<td>Conidiophores: Simple, septate, straight, or with geniculate sympodial proliferation.</td>
<td>Species in this section mainly occur on hosts in family Fabaceae.</td>
<td>[11]</td>
</tr>
<tr>
<td></td>
<td>Conidia: Ovate to obclavate to long ellipsoid, straight to inequilateral, single, transverse septa, septa can be thick, dark and rigid, and form unique germ tubes, which are wavy or undulate until branching.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Section Chalastospora was introduced by Woudenberg et al.[11] for a species group that was previously described as Chalastospora species. The section is typified by Alternaria cetera E.G. Simmons, and the other five species were also initially accommodated in this section, including A. abundans (E.G. Simmons) Woudemb. & Crous, A.armoraciae E.G. Simmons & C.F. Hill, A. breviramosa Woudemb. & Crous, A. malorum (Ruehle) U. Braun, Crous & Dugan, and A. obclavata (Crous & U. Braun) Woudemb. & Crous[11]. Interestingly, A. abundans and A. armoraciae can be distinguished from the other species in sect. Chalastospora by having mostly phragmoconidia that are short and not elongated as in other species of this section[15]. Marin-Felix et al.[70] included A. poblestenis Iturrieta-González, Dania García & Gené in this section and thus, seven species are listed in sect. Chalastospora.

Section Cheiranthus was introduced by Woudenberg et al.[11] to accommodate Alternaria cheiranthi (Lib.) P.C. Bolle, and A. indefessa (E.G. Simmons) Woudemb & Crous (= Embellisia indefessa E.G. Simmons). Woudenberg et al.[11] treated a non-sporulating strain CBS 115.44 which was formally identified as A. resedae Neerg., in this section. However, A. resedae was treated as a synonym of A. septoriiodes E.G. Simmons in sect. Brassicicola. Thus, Woudenberg et al.[11] treated the strain CBS 115.44 as ‘Alternaria sp.’ Gannibal & Lawrence[62] assigned A. latifluida E.G. Simmons to this section based on morphology with conidia having many longitudinal septa. Hence, three species are accepted in this section[62]. Phylogenetic analyses demonstrated this section is sister to sects. Pseudoaulocladioides[14,15], and Ulocladioides[14,15].

Section Crivella was introduced by Woudenberg et al.[11] to accommodate the type species of Crivella, C. papaveraeae (De Not.) Shoemaker & Inderb. (asexual morph known as Brachycladium penicillatum Corda), and B. papaveris (Sawada) Shoemaker & Inderb. Both species are important pathogens of opium poppy[13]. Phylogenetic analyses based on ITS, GAPDH and TEF1-α sequences revealed that these two species clustered with the Alternaria-complex instead of Pleospora sensu stricto. Hence, Woudenberg et al.[11] transferred these two species to the new section of Alternaria as A. papavericola Woudemb. & Crous and A. penicillata (Corda) Woudemb. & Crous. However, Lawrence et al.[15] mentioned that the phylogenetic status of this section is uncertain. The sexual morph of A. penicillata was interdispersed with dark microsclerotia and macroconidiophores, forming medium-sized (320–400 × 220–300 µm), globose to depressed globose ascomata, with ellipsoidal ascospores (20–25 × 6–9 µm)[15].

Section Dianthica was introduced by Woudenberg et al.[11] and is typified by Alternaria dianthica Neerg. Three species were accommodated in this section, including A. dianthica, A. elegans E.G. Simmons & J.C. David, and A. simsimi E.G. Simmons[11]. Xu et al.[71] introduced another pathogenic species, A. kareliniae B. Xu & Z.D. Jiang, causing leaf spot on Karelinia caspia (Pall.) Less. in China. However, the name was validly listed in Index Fungorum[72]. Thus, four phylogenetic species are known in this section. Phylogenetic analyses based on protein-coding genes showed that sect. Dianthica has a close relationship with sect. Ulocladioides[11,15].

Section Embellisia was introduced by Woudenberg et al.[11] and is typified by Alternaria embelisitia Woudemb. & Crous (= Helminthosporium allii Campman.). The section was established for the species previously described in Embellisia, including three species viz. E. allii E.G. Simmons, E. chlamydospora (Hoes, G.W. Bruehl & C.G. Shaw) E.G. Simmons, and E. tellustris E.G. Simmons. Embellisia was initially introduced to separate an atypical species of Helminthosporium Link[73] based on conidial and conidiophore morphology which is characterized by successive sympodial proliferations conidiophores and phragmoconidia, with distinctly dark, rigid and thickened transverse septa[15]. Phylogenetic analyses based on GAPDH, ITS and Alt-a1 genes demonstrated that the section has close relationships with sects. Phragmospora, Soda, Chalastospora, Pseudoalternia, and Infectionae[11,15]. Woudenberg et al.[11] therefore, designated the new name for these three Embellisia species and transferred them to Alternaria sect. Embellisia, namely Alternaria chlamydosporigena Woudemb. & Crous, A. embelisitia Woudemb. & Crous, and A. tellustris (E.G. Simmons) Woudemb. & Crous.

Section Euphoribiicola was introduced by Woudenberg et al.[11] to accommodate six species previously described as Embellisia species and named as Embellisia group III in Lawrence et al.[55]. The section consists of Alternaria botryospora Woudemb. & Crous, A. hyacinthi de Hoog & P.J. Mull. bis Woudemb. & Crous (type species), A. lolii (E.G. Simmons & C.F. Hill) Woudemb. & Crous, A. planifunda (E.G. Simmons) Woudemb. & Crous, A. proteae (E.G. Simmons) Woudemb. & Crous, and A. tumida (E.G. Simmons) Woudemb. & Crous[11,15]. These species were obtained from plants or the rhizosphere[15]. The sexual morph of species in this section was regarded as Allewia species and characterized by ovoid to spherical, dark, thin-walled, pseudeothelial, papillate ascomata with markedly setose, subellipsoidal to subcylindrical ascus and slightly inequilateral subellipsoidal immature ascospores. Mature ascospores are ellipsoidal to subclavate, with multiple transverse septa and a discontinuous series of longitudinal septa[15]. Phylogenetic analyses supported the section as a sister group with sect. Eureka[11,15].

Section Euphoribiicola was introduced by Woudenberg et al.[22] and is typified by Alternaria euphorbiicola E.G. Simmons & Engelhard. Two species are currently accommodated in this section viz. A. euphorbiicola and A. limicola E.G. Simmons & M.E. Palm[22]. These two species were obtained from plant host families Euphorbiaceae and Rutaceae as saprobes and pathogens[17,22]. Woudenberg et al.[22] established sect. Euphoribiicola as a separate section with sect. Porri based on the formation of conidia in chains. Multi-locus phylogenetic analyses clearly separated the section from other species in sect. Porri[22].

Section Eureka was introduced by Woudenberg et al.[11] to accommodate four Alternaria species and the other two species previously described as Embellisia species which was mentioned as Embellisia group IV in Lawrence et al.[55]. Six species are currently known for this section, including Alternaria angozanthi Priest, A. cumini E.G. Simmons, A. eureka E.G. Simmons (type species), A. geniostomatis E.G. Simmons & C.F. Hill, A. leptinellae (E.G. Simmons & C.F. Hill) Woudemb. & Crous, and A. triglochinicola Alcorn & S.M. Francis. These species were commonly isolated from plants and the rhizosphere[11,15]. The sexual morph is known for the type species of the section was regarded as Allewia species and characterized by spherical to ovoid, thin-walled, dark, papillate ascomata, with conspicuously setose, subcylindrical to subellipsoid ascus, somewhat inequilateral, with subellipsoidal and slightly
inequilateral juvenile ascospores. Ascospores are subclavate to ellipsoid, with transverse septa, discontinuous series of longitudinal septa when mature\([53]\). Multi-locus phylogenetic analyses based on the protein-coding genes demonstrated that the section has a close relationship with the morphologically similar sect. *Emblessioides*\([11,13]\).

**Section Gypsophila** was introduced by Lawrence et al.\([14]\) to accommodate four *Alternaria* species, comprising *A. gypsophila* Neerg. (type species), *A. nobilis* (Vize) E.G. Simmons, *A. vaccariae* (Sævul. & Sandu) E.G. Simmons & S.T. Koike and *A. vaccaricola* E.G. Simmons. Woudenberg et al.\([13]\) recommended the other four species viz. *A. axiaeriisporifera* E.G. Simmons & C.F. Hill, *A. ellipsioidea* E.G. Simmons, *A. juxseptata* E.G. Simmons, and *A. saponarinae* (Peck) Neerg. to this section based on multi-locus phylogeny. Based on morphological examination of *Alternaria* species producing conidia with many longitudinal septa, Gannibal & Lawrence\([62]\) included *A. longispora* McAlpine in the sect. *Gypsophila*. Consequently, Gannibal\([74]\) introduced *A. kamtschatcica* Gannibal from leaves of *Dianthus barbatus* in Russia. He et al.\([3]\) introduced the other two new species in this section viz. *A. barbata* L. He & J.X. Deng and *A. hispanica* L. He & J.X. Deng from China. Currently, there are 12 species accommodated in this section that are restricted to the host family Caryophyllaceae.\([3,17,74]\). The section has a close relationship with sects. *Alternaria, Alternanthera, Euphorbicola*, and *Porri*\([11,14,13]\).

**Section Helianthiiniciens** was introduced by Gannibal et al.\([8]\) to accommodate *Alternaria helianthiiniciens* E.G. Simmons, Walcz & R.G. Roberts which was previously treated as a monotypic lineage in Woudenberg et al.\([11]\) and Lawrence et al.\([13]\). Currently, only a single species is represented in this section.\([6]\) The species was previously well-known as a causative pathogen on sunflower (*Helianthus annuus* L.) and cosmos (*Cosmos bipinnatus* Cav.) in Asia, Europe, and North America.\([6]\). Gannibal et al.\([6]\) reported the species on other hosts (i.e., *Arctium* sp. and *Sonchus* sp.) from Russia, suggesting that *A. helianthiiniciens* may also occur on other plant species in Asteraceae. Morphologically, *A. helianthiiniciens* resembles many species in sect. *Porri* in having large conidial size.\([6]\). However, multi-locus phylogenies analyzed by Woudenberg et al.\([11]\) and Ghafari et al.\([11]\) demonstrated that *A. helianthiiniciens* formed an independent lineage within *Alternaria* but could not be assigned to any other known sections. Therefore, Gannibal et al.\([6]\) established this new section.

**Section Infectoriae** was introduced by Woudenberg et al.\([11]\) for *Alternaria infectoria* E.G. Simmons species-group, comprising approximately 45 accepted species in the sect. *Infectoriae*\([1,24,27,75–80]\). The human pathogenic genera *Ybtromyces* Rulmont (as *Alternaria caespitosa* (de Hoog & C. Rubio) Woudenb. & Crous) and *Chmelia* (as *Alternaria slovaca* (Svob.-Pol.) Woudenb. & Crous) were also embedded in sect. *Infectoriae*.\([11]\). The section is typified by *A. infectoria* and taxa in this section are common saprobes and human pathogens as well as endophytes on apple leaves.\([15,27,80]\). The sexual morph of sect. *Infectoriae* was linked to species in *Lewia* and is characterized by smooth-walled ascomata, subcylindrical or subellipsoid asci and muriform ascospores with 5–7 transverse septa and 1–2 longitudinal septa in central segments, with or without longitudinal or oblique septum in terminal cells.\([15]\). The main refined morphological features of taxa in sect. *Infectoriae* are small conidia (usually less than 60 μm in vitro) and long secondary conidiophores.\([11,15,77]\). Members of sect. *Infectoriae* are presumed to be homothallic mating-type genes that can produce pseudoascomata in axenic culture.\([15,81]\). Phylogenetic analyses revealed the section as the sister group to sect. *Pseudoalternaria* and the most suitable genetic markers for 45 distinguishing species in the sect. *Infectoriae* are ATPase and cmdA genes.\([14,15,70]\).

**Section Japonicae** was introduced by Woudenberg et al.\([11]\) with the type species of the section as *Alternaria japonica* Yoshii. The section was established to accommodate *A. japonica* together with *A. nepalensis* E.G. Simmons based on multi-locus phylogeny. *Alternaria japonica* was previously connected to the *A. brassicicola* species-group\([14,34,59]\) but this connection was questioned by Hong et al.\([49]\). Bessadat et al.\([82]\) included an additional species *A. telliensis* N. Bessadat, D. Ayad & P. Simonneau in this section; however, this species was invalidly introduced. Species in sect. *Japonicae* are frequently isolated from Brassicaceae hosts.\([11,15]\). The phylogenetic status of the sect. *Japonicae* is uncertain within *Alternaria*.\([15]\).

**Section Nimbya** was introduced by Woudenberg et al.\([11]\) and is typified by *Alternaria scirpicola* (Fuckland) Sivan. The section initially contained four species previously described as *Nimbya* species viz. *A. caricos* (E.G. Simmons) Woudenberg & Crous, *A. scirpicola*, *A. scirpinestans* (E.G. Simmons & D.A. Johnson) Woudenberg & Crous, and *A. scirpivora* (E.G. Simmons & D.A. Johnson), Woudenberg & Crous. Gannibal\([83]\) included the other two species, *A. hetro schemos* (Fautrey) Gannibal and *A. juncicola* (E.G. Simmons) Gannibal in this section. In addition, Ahmadpour\([84]\) and Ahmadpour et al.\([85]\) also introduced *A. caricos* Ahmadp., *A. cypericola* Ahmadp., Poursafar & Ghosta, *A. heyranica* Ahmadp., Poursafar & Ghosta, and *A. junci-acutic* Ahmadp., Poursafar & Ghosta to this section. Hence, there are currently ten species accommodated in sect. *Nimbya*. It sounds that sect. *Nimbya* are restricted to Cyperaceae and Juncaceae host plant families.\([85]\). The sexual morph of the section was referred to *Macrospora* Fuckland and is characterized by immersed to superficial, subglobose, ostiolate ascoma, with broadly cylindrical or clavate to obovoid asci and broadly ellipsoidal, brown to dark brown, multi-septate ascospores.\([15,24,28]\). Section *Nimbya* is closely related to sects. *Embellisia, Phragmospora, Chalostospora* and *Infectoriae* based on phylogenetic analyses of the combined SSU, RPB2 and TEF-1α sequence dataset.\([11]\).

**Section Omanenses** was introduced by Ghafari et al.\([27]\), with the single species *Alternaria omanensis* as the type species of the section. *Alternaria omanensis* was isolated from dead wood in Oman as a saprobe and is known for both sexual and asexual morphs. The sexual morph of the section is characterized by superficial, subglobose to globose, or ovoid to cup-shaped (when dry), dark brown to black, carbonaceous ascoma, with a blunt ostiole, cylindrical to subcylindrical asci and pale brown to dark brown, muriform, subclavate to broadly obovoid or ellipsoid ascospores, with 3 transverse septa, 1–2 longitudinal septa in the central segments, without septa at the end cells, and constricted at the central septum (asexual morph see Table 1). Multi-locus phylogenetic analyses of a combined SSU, LSU, ITS1, GAPDH, TEF1-α and RPB2 sequence dataset demonstrated that the section has a close relationship with sects. *Emblessioides, Eureka* and *Ulocladium*\([7]\).
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Alternaria

eringii (Pers.) S. Hughes & E.G. Simmons and A. panax Whetzel
(as A. panaxis in Deng et al.[86] and Lawrence et al.[113]; type
species). Woudenberg et al.[111] included A. avenirica E.G.
Simmons and A. photostica E.G. Simmons to this section and the
sexual morphs of these two species were known as Lewia
avernicola Kosiak & Kwasańska[38] and L. photostica E.G. Simmons[80],
respectively. Deng et al.[86] reported two pathogenic species in
this section viz. A. aralae H.C. Greene and A. dendropanaxis S.H.
Yu & J.X. Deng that were associated with leaf spot and blight
disease on Araiaceae in Korea, while Gannibal & Lawrence[62]
included A. prasonis E.G. Simmons based on morphology.
Recently, Hashemlou et al.[87] described A. haydariae Y.
Ghosta et al. on stems of Serratula coriaceae Fisch. & C.A. Mey.
from Iran in the sect. Panax. Thus, there are currently nine
species accommodated in this section. PCR assays of mating-
type genes indicated that members in sect. Panax are both
homothallic and heterothallic species that are either capable of
sporulating as sexual morphs in vitro or without an identified
sexual morph. Phylogenetic analyses based on the GAPDH,
RPB2 and TEF-1α sequences suggested that sect. Panax has a
close relationship with A. thalictrigena and sect. Teretispora[11,13].

Section Phragmospora was introduced by Woudenberg et al.[111]
and is typified by Alternaria phragmospora Emden. The section
contains six species viz. A. chlamydospora Mouch., A.
didymospora (Munt.-Cvetk.) Woudemb. & Crous, A. limaciformis
E.G. Simmons, A. molestia E.G. Simmons, A. mouchacca E.G.
Simmons, and A. phragmospora. These species are known from
soil, seawater, seawater plants and animals, excluding A.
didymospora which was found in equine nasal mucosa. There
are no species associated with land plants in this section[13].
Phylogenetic results indicated the section is sister to sect.
Embellisia, with A. didymospora and A. phragmospora were
linked[11,15].

Section Porri was introduced by Lawrence et al.[114] and is
typified by Alternaria porri (Ellis) Cif. Section Porri has been
reported as the largest section of Alternaria with approximately
63 species revealed in the section based on multi-locus
phylogenies[14,15,22]. A detailed study of this large-spored section
was carried out by Woudenberg et al.[22]. The section displays a
high level of genetic variation and contains many important
plant pathogens, such as A. bataticola Ikata ex W. Yamam., A.
porri, A. solani Sorauer and A. tomatophila E.G. Simmons,
causing leaf and stem blight of sweet potato, purple blotch of
onion and early blight of potato and tomato, respectively[22],
Gannibal[83] included A. rhapontici (Nelen) Gannibal in the
from Physalis alkekengi L. (Solanaceae) in China. Cai et al.[89]
also introduced a pathogenic species A. yunnanensis Z.Y. Cai et al.,
which causes leaf spots on rubber trees in China.Poursafar et al.[90]
introduced a pathogenic species A. guilanica Poursafar et al.,
on Solanum melongena L. with leaf spot and blight symptoms from Iran. Hence, 67 species are known in this
section, making this section the second-largest section after sect.
Alternaria. Multi-locus phylogeny demonstrated that the section is sister to sect. Euphorbiicola, and clustered with sects.
Alternaria and Alternanthera[11,14,15,22].

Section Pseudotemaria was introduced by Lawrence et al.[115]
and is typified by Alternaria arhenatheri D.P. Lawr.,
Rotondo & Gannibal. The section initially consisted of two
species viz. A. arhenatheri and A. rosae E.G. Simmons & C.F. Hill
based on both phylogeny and morphology. Based on
morphological examination, Gannibal & Lawrence[97] described
a new taxon, A. parvicaespitosa Gannibal & D.P. Lawr. as a
misidentified isolate previously identified as A. rosae by Zhu &
Xiao[91]. Deng et al.[92] accommodated a new pathogenic
species, A. brassicifoli S.H. Yu & J.X. Deng, causing necrotic leaf
spots of Brassica rapa L. (Brassicaceae) in Korea in the section.
However, Deng et al.[92] did not validly indicate the type
specimens for their new species, and thus, the species is treated
as invalid (nom. inval.) based on nomenclature article 40.1 (Shenzhen, China) that ‘Publication on or after 1 January 1958 of
the name of a new taxon at the rank of genus or below is valid only
when the type of the name is indicated’[93]. Subsequently, four
other species were included in the section viz. A. alticamnia
Iturrieta-González, Dania García & Gené, A. ershadii A. Poursafar,
Ghosta & M. Javan-Nikkhah, A. inflata Iturrieta-González, Dania
García & Gené., and A. kordkuyana A. Poursafar et al.[70,94,95],
Currently, eight species are known in sect. Pseudoalternaria, all
of which were confirmed using multi-locus phylogeny. Sect.
Pseudoalternaria was shown to be closely related to sects.
Infectoria and Chalastospora[15,70].

Section Pseudoulocladium was introduced by Woudenberg et al.[111] to accommodate species previously described as
Ulocladium species and is typified by Alternaria chartarum
Preuss. Four species were initially included in the section viz. A.
aspera Woudemb. & Crous, A. chartarum, A. concatenata
Woudemb. & Crous, and A. septospora (Preuss) Woudemb. &
Crous[111]. Based on morphology, Gannibal & Lawrence[60]
included A. lanuginosus (Harz) Sacc. and A. sylvestris Gannibal &
D.P. Lawr. Section Pseudoulocladium morphological resembles
sects. Ulocladioides and Ulocladium but differs in simple or
branched chains of conidia, whereas sect. Ulocladioides usually
have densely geniculate conidiophores with clustered, short
conidial chains, and secondary conidiophores are short with
several conidigenous loci. Section Ulocladium typically
produces small, clustered, single conidia without chains[96],
Phylogenetic analyses of protein-coding genes revealed that
the section has a sister relationship with sect. Dianthicola and

Section Radicina was recognized by Pryor & Gilbertson[54]
and formally established by Lawrence et al.[114]. The section was
introduced to accommodate the radicina species-group and is
typified by Alternaria radicina Meier, Drechsler & E.D. Eddy.
Species in this section are pathogens occurring on
Apaicinaceae[11,15], Woudenberg et al.[111] and Lawrence et al.[15]
listed five species in this section, including A. carotinulenta E.G.
Simmons, A. petroselini (Neerg.) E.G. Simmons, A. radicina, A.
selini E.G. Simmons and A. smyrnii (P. Crouan & H. Crouan)
E.G. Simmons based on multi-locus phylogeny. Subsequently,
Marin-Felix et al.[70] introduced A. chlamydosporifera Iturrieta-
González, Dania García & Gené, isolated from rabbit dung in
Spain, to the section. He et al.[15] described two new species in
this section viz. A. divaricatae He & J.X. Deng and A. vulgaris L.
He & J.X. Deng, both isolated from Umbelliferae (Apiaceae) in
China. Hence, there are currently eight species accommodated in
this section. Phylogenetic analyses demonstrated that the
section has a close relationship with sect. Gyropophila[15].

Section Soda was introduced by Grum-Grzhimaylo et al.[56]
 to contain three species isolated from soils at the different
highly alkaline soda lakes in Russia, comprising Alternaria
kuldunae Bilanenko, Georgieva & Grum-Grzhim. (type species),
A. petuchovskoi Bilanenko, Georgieva & Grum-Grzhim., and A. shukurtuzi Bilanenko, Georgieva & Grum-Grzhim. Species in this section showed a potential alkali-tolerant to facultative alkaliophilic type of the adaptation. The sexual morph for the section is unknown. Multi-focus phylogeny of SSU, LSU, RPB2, ITS, and GAPDH showed that the section clustered with sects. *Infectoriae*, *Chalastospora*, and *Embellisidia*.[96]

**Section Sonchi** was described as the species-group by Hong et al.[49] and validly introduced by Lawrence et al.[14]. Only two species are accommodated in this section viz. *Alternaria cinerariae* Horii & Enjoji and the type species of the section *A. sonchi* Davis. Species in this section occur on a wide range of hosts in family Asteraceae.[15,17]. The sexual morph of the section is unknown. Phylogenetic analyses based on the *GAPDH*, *RPB2* and *TF1-α* sequences showed that sect. *Sonchi* forms a sister clade with two monotypic lineages, *A. brassicaceae* (Berk.) Sacc. and *A. helianthinficiens*. EG. Simmons, Walcz & R.G Roberts.[11]. Currently, *A. helianthinficiens* was raised to the section rank of *Alternaria* by Gannibal et al.[60]. Ferreira & Barreto[97] designated the neotype of *Acroconidiella tropoeoli* (T.E.T. Bond) J.C. Lindq. & Alippi (≡ *Heterosporum tropoeoli* T.E.T. Bond) and proposed the new name for the species as *Alternaria obtusa* B.W. Ferreira & R.W. Barreto. The species is sister to sect. *Sonchi*.[97]

**Section Teretispora** was introduced by Woudenberg et al.[11] to accommodate a single species, *Alternaria lecanthemi* Nelen, as the type of the section. The species was isolated from *Leucanthemum maximum* (Ramond) DC. (Asteraceae) and is characterized by simple primary conidiophores bearing 1–3 conidiogenous loci and generally solitary, cylindrical conidia, with 7–14(–17) transverse septa, and 3–7 longitudinal septa.[15,13]. The sexual morph has not yet been described for the section. Phylogenetic analyses showed that sect. *Teretispora* is sister to *A. thalictrigena*, and clustered with sect. *Panax*. Thus, Woudenberg et al.[11] proposed to raise this species as a section, rather than a monotypic lineage.

**Section Ulocladioides** was introduced by Woudenberg et al.[11] and is typified by *Alternaria cucurbiteae* Letendre & Roum. The section was introduced to accommodate ten species previously described as *Ulocladium* species based on phylogeny, place it distant from sect. *Ulocladium*. Section *Ulocladioides* is similar to the sect. *Ulocladium*, and is characterized by short, geniculate conidiophores, with sympodial proliferations and obovoid, non-beaked conidia, with a narrow base, single or in chains.[11]. Gannibal & Lawrence[96] included the other ten species and thus, 20 species are currently known for this section. Phylogenetic analyses based on the *GAPDH*, *RPB2* and *TF1-α* sequences showed that sect. *Ulocladioides* has a close relationship with sects. *Pseudoulocladium* and *Dianthicola*.[11].

**Section Ulocladium** was introduced by Woudenberg et al.[11] and is typified by *Alternaria botryitis* (Preuss) Woudenh. & Crous. The section is introduced to accommodate the epitype of the former *Ulocladium* as *Alternaria botryitis* (CBS 197.67) and additional three species viz. *A. alternariae* (Cook) Woudenh. & Crous, *A. capsici-annul Sävul. & Sandu, and A. oudeemansii* (E.G. Simmons) Woudenh. Gannibal & Lawrence[96] included *A. manihotica* (J.M. Yen) Gannibal & D.P. Law in the section based on morphological study and thus, five species are known for the section. Phylogenetic analyses based on the *GAPDH*, *RPB2* and *TF1-α* sequences showed that sect. *Ulocladium* is sister to the monotypic lineage *A. argyranthemi*.[11].

**Section Undifilum** was introduced by Woudenberg et al.[11] and is typified by *Alternaria bornmuelleri* (Magnus) Woudenh. & Crous. The section consists of five species viz. *A. bornmuelleri*, *A. cinerea* (Baumk & Creamer) Woudenh., *A. fulva* (Baumk & Creamer) Woudenh. & Crous, *A. gansuensis* J. Li Liu & Y.Z. Li, and *A. oxytropis* (Q. Wang, Nagao & Kakish.) Woudenh. & Crous.[11,98]. Section *Undifilum* resembles sect. *Embellisia*, but can be distinguished by conidial germination with the germ tube being wavy and unbranched.[11,60]. Species in this section were isolated from Fabaceae as endophytes and produced a swaisione toxic compound, causing a neurological disease of grazing animals.[98]. Phylogenetic analyses of the *GAPDH*, *RPB2* and *TF1-α* sequences showed that the section forms an independent lineage closely related to a monotypic lineage *Embellisia dennisi* (M.B. Ellis) E.G. Simmons, (CBS 110533, CBS 476.90), which was resurrected as *Alternaria dennisi* M.B. Ellis in Woudenberg et al.[11].

**Evolutionary and fossil studies of Alternaria**

The study of fossil fungi has become an essential tool to understanding fungal evolution and diversification, as well as the correlation of fungi with other organisms coupled with historical functions in the ecosystem.[119,120]. The detailed study of fungal fossils was limited in the early stages due to the technical factors used to study fossil fungi and visual matching for identifying similar extant species as well as poor preservation and unclear morphological characteristics.[119–121]. Furthermore, the study of fossil fungi received little attention because of lack of interest, expertise and collaboration.[119,120], Samarakoone et al.[120] mentioned that although the study of fossil fungi is not an essential tool for fungal taxonomy, it is important for understanding the paleoecological conditions and calibrating divergent times of fungal evolution based on molecular clock studies. Hence, Samarakoone et al.[120] assimilated 16 selected fossil fungi in Ascomycota and provided detailed information based on descriptions, illustrations, minimum age estimations, and phylogenetic affinity, mostly regarding the epiphytic Dothideomycetes and Sordariomycetes.

The fossil record of *Alternaria* has also not been determined in the Kalgotkar and Jansonius database of fossil fungi.[122]. However, there is a fossil record referred to *Alternaria* described as *Polycyellasporonites alternariatus* (Kalgotkar & Sigler) Kalgotkar & Janson (≡ *Piriurella alternariata* Kalgotkar & Sigler). *Polycyellasporonites alternariatus* was first described as *Piriurella alternariata* by Kalgotkar & Sigler[123] for the fossil-fossil-produced dictyosporae spore group. The species was referred to *Alternaria* in forming muriform, ovoid to obclavate, rostrate, pale brown to brown conidia, arising singly or in clusters, with transverse septa more prominent and thicker than the longitudinal or oblique septa. The broader basal region distally tapered to a short or cylindrical beak with or without a dark thickened tip.[123]. The species was found from iceberg Bay formation at Kanguk Peninsula, Axel Heiberg Island and Northwest Territories, Canada with an estimated age during the late Paleocene or early Eocene (40.4–58.7 MYA).[123]. However, the link between *P. alternariatus* and *Alternaria* has not yet been confirmed due to *Alternaria* being variable in shape, size and septation of conidium and was shown to be a species complex.[117–14,22,35,123].
Evolutionary estimates based on molecular clocks have been increasingly common in fungal taxonomy in recent years,[124–130] with some works including the Pleosporales[130–132]. Hyde et al.[128] proposed Kingdom Fungi as evolving during the Stenian to Calymmian era (1000–1600 MYA), the phylo evolved between Devonian to Cambrian (358–541 MYA), the classes evolved during Jurassic to Carboniferous (145–358 MYA) and the orders evolved during Cretaceous to Carboniferous (66–358 MYA). They also determined higher ranks of fungi based on the divergence time estimations of Sordariomycetes, of which the familial rank would correspond to 50–150 MYA. Liu et al.[129] recommended that the orders of Dothideomycetes should have evolved between 100 and 220 MYA (crown age) and 130 and 310 MYA (stem age), and the families are ranked between 20–100 MYA (crown age). However, the divergence time estimations of Alternaria based on DNA sequence evidence remain unexplored.

In this research, we isolated Alternaria species from 65 specimens, collected from different plant hosts in Yunnan, China, Italy, Russia and Thailand from 2014 to 2019 and introduce 18 novel Alternaria species, all of which are represented by the hyphomycetous asexual morphs as saprobes on dead plant tissues. We also provide updated phylogenetic relationships for the sections in Alternaria based on phylogenetic analyses of a concatenated dataset from seven gene regions (ITS, LSU, SSU, TEF1-α, RPB2, GAPDH and Alt-a1 loci) and have estimated evolutionary divergence time for Alternaria.

**MATERIALS AND METHODS**

**Sample collection, examination and isolation**

Alternaria species, isolated from various hosts, were mainly collected in Italy, and partly from China (Yunnan), Russia and Thailand, during 2014–2019. Materials were brought to the laboratory in Zip-loc plastic bags and examined under a Motic SMZ 168 stereomicroscope. Morphological studies were conducted following the guidelines by Senanayake et al.[133]. Micromorphological characters of Alternaria species were examined under a Nikon ECLIPSE 80i compound microscope and images were captured using a Nikon ECLIPSE 80i compound microscope with a Canon EOS 550D digital camera. Measurements were made with the Tarosoft (R) Image Frame Work and images used for figures were processed with Adobe Photoshop CS3 Extended version 10.0 software. New species were justified based on Jeewon & Hyde[134] and registered in Faces of Fungi[135] and Index Fungorum[5].

Isolates were derived via single spore isolation following the method of Chomnunti et al.[136] and Senanayake et al.[133]. Germinating spores were transferred to potato dextrose agar (PDA; 39 g/L distilled water, Difco™ potato dextrose, Montreal, Canada) or malt extract agar (MEA; 33.6 g/L sterile distilled water, Difco™ malt extract, Montreal, Canada) media and incubated at 18–25°C. The cultural characteristics such as mycelium color, shape, texture and growth rate were determined after 1–8 weeks. The sporation in vitro was induced on potato carrot agar (PCA; 20 g potato + 25 g carrot + 15 g agar/1 L) and observed after 8 weeks. The living cultures were preserved in PDA, the sterilized 10% glycerol, and double-distilled water (ddH₂O) and deposited at the Mae Fah Luang University Culture Collection (MFLUCC), and duplicated at the Culture Collection of Kunming Institute of Botany (KUMCC/KUNCC) and China General Microbiological Culture Collection Center (CGMCCC). The type and other collected specimens were deposited in the herbarium of Mae Fah Luang University (MFLU), Chiang Rai, Thailand and Herbarium of Cryptogams Kunming Institute of Botany, Academia Sinica (KUN-HKAS), China.

**DNA extraction, PCR amplification and sequencing**

Fungal isolates cultured on PDA or MEA at 25–28°C for 25–30 d were used for genomic DNA extraction following the guidelines by Dissanayake et al.[137]. Fungal mycelium was scraped off and stored in a sterilized 1.5-ml microcentrifuge for further DNA extraction. Fungal genomic DNA was extracted using the Biospin Fungus Genomic DNA Extraction Kit (BSC1451, Bioflux®, China), following the manufacturer’s instructions.

DNA amplifications were conducted by polymerase chain reaction (PCR) with seven genes as listed in Table 2. Polymerase chain reaction (PCR) was performed in an ABI Veriti gradient PCR machine (Applied Biosystem, USA) with the total 25 µl reaction volume, containing 1 µl of DNA template, 1 µl of each forward and reverse primers, 12.5 µl of 2× Power Taq PCR Master Mix (mixture of EasyTaqTMDNA Polymerase, dNTPs, and optimized buffer, Beijing BioTeke Corporation, P.R. China) and 9.5 µl of sterilized double-distilled water (ddH₂O). PCR thermal cycling conditions of each locus were set up following Woudenberg et al.[11] but adjusted as: for ITS, LSU, SSU, and TEF1-α was set up at initially, 94 °C for 3 min, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C for 30 s, elongation at 72 °C for 1 min; for RPB2 was set up at initially 95 °C for 2.30 min, followed by 35 cycles of denaturation at 95 °C for 30 s, annealing at 52 °C for 1 min, elongation at 72 °C for 1 min; for GAPDH was set up at initially 94 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 57 °C for 1 min, elongation at 72 °C for 90 sec; for Alt-a1 was set up at initially 94 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 57 °C for 30 s, elongation at 72 °C for 1 min; a final extension at 72 °C for 10 min, and finally hold at 4 °C. The PCR fragments were then checked on 1% agarose electrophoresis gels stained with ethidium bromide and visualized under the UV light using the Molecular Imager Gel Doc XR + Imaging system (BIO-RAD, USA). The amplified PCR fragments were sent to a commercial sequencing provider (TsingKe Biological Technology (Beijing) Co., Ltd, P.R. China) for purification and sequencing in both forward and reverse directions. Consensus sequences were incorporated with both forward and reverse sequences, computed by Bioedit v.7.1.3.0[138]. All acquired nucleotide sequences were deposited in GenBank (Supplemental Tables S2, S3).

**Fossil calibration, divergence time and evolutionary rate estimations**

Fossil calibrations used in the analyses followed the methodology described in Phukhamsakda et al.[111]. Two fossil and one secondary calibration were applied to estimate all other nodes in the tree. Fossil 1, *Metacapnodium succinum*...
Table 2. Gene loci and primers used in this study.

<table>
<thead>
<tr>
<th>Gene loci</th>
<th>Primers</th>
<th>Sequence 5’–3’</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Internal transcribed spacer region (ITS, including the 5.8S gene)</td>
<td>ITSS</td>
<td>GGA AGT AAA AGT CGT AAC AAG G</td>
<td>[139]</td>
</tr>
<tr>
<td></td>
<td>ITS4</td>
<td>TCC TCC GCT TAT TGA TAT GC</td>
<td></td>
</tr>
<tr>
<td>28S large subunit rDNA (LSU)</td>
<td>LR0R</td>
<td>GAA CCC GCT GAA CTT AAG C</td>
<td>[140]</td>
</tr>
<tr>
<td></td>
<td>LRS</td>
<td>ATC CTG AGG GAA ACT TC</td>
<td></td>
</tr>
<tr>
<td>18S small subunit rDNA (SSU)</td>
<td>NS1</td>
<td>GTA GTC ATA TGC TTG TCT C</td>
<td>[139]</td>
</tr>
<tr>
<td></td>
<td>NS4</td>
<td>CTT CGG TCA ATT CCT TTA AG</td>
<td></td>
</tr>
<tr>
<td>Alternaria major allergen (Alt-α1)</td>
<td>Alt-for</td>
<td>ATG CAG TTC ACC ACC ATC GC</td>
<td>[49]</td>
</tr>
<tr>
<td></td>
<td>Alt-rev</td>
<td>AGG AGG GTG AYG TAG GCG TC</td>
<td></td>
</tr>
<tr>
<td>Glyceraldehyde 3-phosphate Dehydrogenase (GAPDH)</td>
<td>GDP-1</td>
<td>CAA CGG CCT CGG TCG CAT TG</td>
<td>[141]</td>
</tr>
<tr>
<td></td>
<td>GDP-2</td>
<td>GCC AAG CAG TTG GTG TTG C</td>
<td>[14]</td>
</tr>
<tr>
<td>Plasma membrane ATPase (ATPase)</td>
<td>ATPDF1</td>
<td>ATC GTC TCC ATG ACC GAG TTC G</td>
<td>[14]</td>
</tr>
<tr>
<td></td>
<td>ATPDRI</td>
<td>TCC GAT GGA GAT CAT GAT ACC C</td>
<td></td>
</tr>
<tr>
<td>The second largest subunit of RNA polymerase II (RPB2)</td>
<td>fRPB2-5f</td>
<td>GAY GAY MGW GAT CAT TTY GG CCC</td>
<td>[142]</td>
</tr>
<tr>
<td></td>
<td>fRPB2-7CR</td>
<td>ATR GCT TGY TTR CCC AT</td>
<td></td>
</tr>
<tr>
<td>Translation elongation factor 1-α (TEF1-α)</td>
<td>EF1-983F</td>
<td>GCC CYY GHG CAY CGT GAY TTY AT</td>
<td>[143]</td>
</tr>
<tr>
<td></td>
<td>EF1-2218R</td>
<td>ATG ACACCR ACR ACR ACR GTY TGY</td>
<td></td>
</tr>
<tr>
<td></td>
<td>EF1-728F</td>
<td>CATCGAAGTTCCGAGAGG</td>
<td>[144]</td>
</tr>
<tr>
<td></td>
<td>EF1-986R</td>
<td>TACTTGAAGAACCCTTACC</td>
<td></td>
</tr>
</tbody>
</table>

(Metacapnodiaceae) was used to calibrate the minimum age of Capnodiales (normal distribution, mean = 100, SD = 150, providing 95% credibility interval of 346 MYA)\(^{126,131,145-147}\) and fossil 2, *Margaretbarromyces dictyosporus* was used to calibrate the crown age of Aigialus (Aigialaceae) (gamma distribution, offset = 35, shape = 1, scale = 25, providing 95% credibility interval of 110 MYA)\(^{313,148}\). The split between Arthoniomycetes and Dothideomycetes was calibrated using the results from Phukhamsakda et al.\(^{131}\) as the secondary calibration (normal distribution, mean = 300, SD = 50, providing 95% credibility interval of 382 MYA).

Evolutionary estimation based on molecular clock analysis was performed by BEAST 1.8.4\(^{149}\). Aligned sequence data were partitioned separately for each ITS, LSU, SSU, TEF1-α and RPB2 dataset, and were loaded to prepare an XML file constructed with BEAUti v1.8.4. Clock and substitution models were set to be independently estimated for each gene partition, while the tree prior parameters were set to be linked across partitions. A lognormal distribution, mean = 300, SD = 50, providing 95% credibility interval of 382 MYA).

Phylogenetic analyses

The quality of the generated ITS, LSU, SSU, TEF1-α, RPB2, GAPDH, Alt-α1 and ATPase sequences was checked using Bioedit v. 7.1.3.0\(^{130}\) and subjected to the nucleotide BLAST search engine via the NCBI (www.ncbi.nlm.nih.gov) for checking potential contaminants or erroneous sequences as well as delineating the closely related taxa. All reference sequences were downloaded from GenBank (Supplemental Tables S1, S2, S3) based on recent publications\(^{4,12,47,63,70,78,79,88,89}\).

The multiple sequence alignments were automatically generated by MAFFT v. 7.452\(^{[153]}\) (https://mafft.cbrc.jp/alignment/software/), and manual improvements were made where necessary using BioEdit v. 7.2.\(^{[138]}\) Individual gene alignments were separately analyzed by maximum likelihood (ML) in order to check the congruence of tree topology and thus the combined multi-locus phylogenetic trees were inferred based on Bayesian inference (BI) and maximum likelihood (ML) analyses. Five different datasets were generated to estimate phylogenetic relationships of *Alternaria* sections (analysis 1), intraspecific variation of *A. alternata* (analysis 2), sect. *Infectoriae* (analysis 3), sect. *Porri* (analysis 4), and sect. *Radicina* (analysis 5).

Maximum likelihood (ML) analyses were performed by RAxML\(^{[154]}\) implemented in raxmlGUI 1.3\(^{[155]}\) with 1000 bootstrap replicates and GAMMAI model of nucleotide substitution. MrModeltest v. 2.3\(^{[156]}\) was used to determine the best-fit model of nucleotide substitution for each locus and incorporated into the analyses (Table 3). Bayesian inference (BI) analyses were performed by MrBayes v.3.1.2\(^{[157]}\). Markov Chain Monte Carlo (MCMC) of six simultaneous Markov chains were run with 1–5 million generations to determine posterior probabilities (PP)\(^{[158,159]}\) and started from a random tree topology. Trees were frequently sampled at 100\(^{4}\) generation and the temperature value of heated chain was set to 0.15. The extra runs were required when the average standard deviation of split frequencies was not lower than 0.01 after one million generations. The first 25% trees represented the burn-in phase of the analyses, were discarded and the remaining trees were used for calculating posterior probabilities (PP) in the majority rule consensus tree. The phylogram were visualized in FigTree v. 1.4.0\(^{[152]}\) and edited in Microsoft Office PowerPoint 2016 (Microsoft Inc., USA). The final alignments and trees were submitted in TreeBASE (www.treebase.org) following the submission ID: 258523–258527.
RESULTS

Phylogeny of Pleosporales and divergence time estimations

Representative strains of taxa in Pleosporales were analyzed based on a combined ITS, LSU, SSU, TEF1-α and RPB2 DNA sequence dataset comprised 227 strains of ingroup taxa. Four species in Arthoniomycetes (Arthonia dispersa UPSC2583, Dendrographa leucophaea f-minor, Roccella fuciformis Tehler 8171 and Schismatoma decolorans Ertz 5003) were selected as the outgroup taxa. The best scoring RAxML tree is presented in Fig. 1 with final ML optimization likelihood value of −61934.763756 (ln). RAxML analysis yielded 1,831 distinct alignment patterns and 19.69% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.252569, C = 0.228251, G = 0.283442, T = 0.235738, with substitution rates AC = 1.554349, AG = 4.323993, AT = 1.241832, CG = 1.108361, CT = 8.993327, GT = 1.000000. The gamma distribution shape parameter alpha = 0.307857 and the Tree-Length = 19.058776. Bayesian posterior probabilities (PP) from MCMC were evaluated with the final average standard deviation of split frequencies = 0.009034. The final alignment and tree were submitted in TreeBASE as submission ID: 258527.

The phylogenetic results of Pleosporales (Fig. 1) showed an overall similar tree topology with maximum clade credibility (MCC) tree (Fig. 2). Alternaria sections formed well-resolved and stable clades (up to 80% ML, 0.95 PP; Fig. 1) within Pleosporaceae; while the phylogenetic status of sects. Embellisioides and Eureka (Fig. 1: phylogenetic tree of Pleosporales) are not well-resolved, concuring with phylogenetic results of Alternaria sections (Analysis 1; Fig. 3: phylogenetic tree of Alternaria sections).

According to divergence time estimates (Fig. 2), the stem and crown ages of Dothideomycetes are 358 (266–492) Mya and 310 (230–392) Mya in the Permian Period, respectively (Fig. 2). Pleosporales diverged with other orders roughly 253 (184–326) Mya in the Triassic Period. The crown age of Pleosporales is around 233 (168–301) Mya in the Late Triassic. The crown and stem ages of Dothideomycetes and Pleosporales in the MCC tree (Fig. 2) are well-supported, falling in the recommended divergence time classes for method and order status by Liu et al.[29] and Hongshan et al.[31]. In Pleosporales, Pleosporinae diverged approximately 120 (84–159) Mya in Cretaceous. The stem age of Alternaria is at 62 (42–85) Mya and the crown age of Alternaria is at 53 (36–72) Mya in the age of late Paleocene to early Eocene. The species occurred in the sections that diverged earlier than other sections in Alternaria with beakless, rare multi and longitudinal septate conidia, less forming secondary conidiophores such as the species in sects. Crivelia, Phragmospora, Ulocladium, and Undifilium, while later diverged sections mostly comprise species with beaks or multi-septate conidia forming secondary conidiophores with conidiogenous loci[11,12,14,15,22]. Divergence times of other sections in the analysis are shown in Table 4.

Phylogenetic analyses of Alternaria sections

In this study, five phylogenetic trees were inferred to define the phylogenetic placements of the novel Alternaria species and relationships of taxa in Alternaria sections. The multi-locus phylogenetic tree (Fig. 3) demonstrated that 18 novel species were delineated in sects. Alternaria, Infectoriae, Porri and Radicina. Fourteen new species and two new records on host and geography are introduced in sect. Alternaria and two novel species are introduced to sect. Infectoriae, and the other two new species are introduced in sects. Porri and Radicina, respectively.

Analyses 1 revealed phylogenetic relationships of the representative Alternaria taxa in 29 sections and the novel species introduced in this study. The combined ITS, LSU, SSU, TEF1-α, RPB2, GAPDH and Alt-α1 sequence dataset comprises 189 taxa with Stempylhum vescarium (CBS 191.86) and Pleospora tarda (CBS 714.68) as the outgroup taxa. Bayesian inference (BI) and maximum likelihood (ML) analyses of the combined dataset resulted in phylogenetic reconstructions with largely similar topologies. The best scoring RAxML tree is shown in Fig. 3, with the final ML optimization likelihood value of −42167.053232 (ln). The dataset consists of 4,385 total characters, including gaps (ITS: 1–679 bp, LSU: 680–1,532 bp, SSU: 1,533–2,459 bp, TEF1-α: 2,460–2,740 bp, RPB2: 2,741–3,314 bp, GAPDH: 3,315–3,908 bp, Alt-α1: 3,909–4,385 bp). RAxML analysis yielded 1,623 distinct alignment patterns and 15.42% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.248242, C = 0.254002, G = 0.257113, T = 0.240642, with substitution rates AC = 1.284821, AG = 4.323993, AT = 1.081773, CG = 0.849184, CT = 5.615040, GT = 0.240642, with substitution rates AC = 1.284821, AG = 4.323993, AT = 1.081773, CG = 0.849184, CT = 5.615040, GT = 0.240642. The gamma distribution shape parameter alpha = 0.184966 and the Tree-Length = 2.767524. Bayesian posterior probabilities (PP) from MCMC were evaluated with the final average standard deviation of split frequencies = 0.008657.

Present multi-locus analyses (Fig. 3) demonstrated that most Alternaria sections formed well-resolved clades with high support values (up to 70% ML, 0.95 PP), excluding sects. Cheiranthus, Omanenses, and Undifilium. Section Cheiranthus clustered with sects. Dianthicola and Pseudoulocladium with significant support in BI analysis (0.96 PP) but low support in ML analysis. Three representative species in sect. Cheiranthus (A. cheiranthi, A. indefessa and Alternaria sp.) grouped together with significant support in ML analysis (74% ML) but low support in BI analysis; while the clades of sect. Eureka and sect. Embellisioides were not well separated, and grouped together with high support values (85% ML, 0.99 PP). Alternaria cuminii

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CBS 121329 formed an independent lineage basal to sect. *Eureka* and sect. *Embellisioides* with high support (93% ML, 0.99 PP). Three representative strains of *A. omanensis* formed a robust clade (100% ML, 1.00 PP), basal to sect. *Eureka* and sect. *Embellisioides* with significant support in BI analysis (0.95 PP), but low support in ML analysis. The putative strain of *A. bornmuelleri* (DAOM 231361), represented sect. *Undifilum* and formed an independent lineage (0.95 PP) with *A. dennisii* (CBS 476.90, CBS 110533).

Fourteen new species are introduced in sect. *Alternaria*, including *A. arctoseptata*, *A. baoshanensis*, *A. breviconidiophora*, *A. ellipsoidialis*, *A. eupatoriicola*, *A. falcata*, *A. lathyri*, *A. macilenta*, *A. macroconidia*, *A. minimispora*, *A. oblongoellipsoidea*, *A. orobanches*, *A. phragmiticola* and *A. salicicola*. These novel species formed independent well-supported subclades (up to 80% ML and 0.95 PP; Fig. 3) within sect. *Alternaria*. The new collection, *A. doliconidium* (MFLUCC 14-0020), clustered with the type strains (HKAS 100840, MFLUCC 17-0263) of *A.
Fig. 1 (continued)
doliconidium with high support values (99% ML, 100 PP; Fig. 3). However, the species did not form a well-resolved clade and clustered with other strains of Alternaria alternata and A. italica.

Analyses 2 represented the intraspecific variation of Alternaria alternata corresponding with their hosts. Phylogenetic construction of A. alternata based on a combined ITS, LSU, SSU, TEF1-α, RPB2, GAPDH and Alt-a1 DNA sequence dataset comprised 110 strains with A. eichhorniae Nag Raj & Ponnappa (CBS 489.92, CBS 119778) as the outgroup. The best scoring RAxML tree is shown in Fig. 4, with the final ML optimization likelihood value of −6848.962092 (ln). The dataset consists of 4,377 total characters including gaps (ITS: 1–514 bp,
LSU: 515–1,368 bp, SSU: 1,369–2,295 bp, TEF1-α: 2,296–2,540 bp, RPB2: 2,541–3,311 bp, GAPDH: 3,312–3,897 bp, Alt-a1: 3,898–4,377 bp). RAxML analysis yielded 74 distinct alignment patterns and 1.54% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.246749, C = 0.253377, G = 0.260395, T = 0.239479, with substitution rates AC = 5.780289, AG = 13.046393, AT = 1.475727, CG = 0.816872, CT = 36.600039, GT = 1.000000. The gamma distribution shape parameter alpha = 0.020000 and the Tree-Length = 0.029480. Bayesian posterior probabilities (BYPP) from MCMC were evaluated with final average standard deviation of split frequencies = 0.008559. The final alignment and tree were

![Fig. 3](image-url)  

Phylogenetic construction of genus *Alternaria* using RAxML-based maximum likelihood analysis of a combined ITS, LSU, SSU, TEF1-α, RPB2, GAPDH and Alt-a1 DNA sequence dataset. Bootstrap support values for maximum likelihood (ML, black) equal to or greater than 70% and Bayesian posterior probabilities (PP, red) equal to or greater than 0.95 PP are shown above the nodes. The tree is rooted to *Stemphylium vesicarium* (CBS 191.86) and *Pleospora tarda* (CBS 714.68). Newly generated strains are in blue. The type strains obtained from ex-type cultures are indicated by ‘T’ and the type strains obtained from specimens are indicated by ‘H’.
Fig. 3 (continued)
Fig. 3 (continued)
submitted in TreeBASE as submission ID: 258523. *Alternaria alternata* strains represented in this study were obtained from diverse plant hosts and humans. Forty-five new collections of *A. alternata* were included in the present analyses and are reported for different hosts and geography from China, Italy and Thailand. Multi-locus phylogenetic analyses (Fig. 4) showed a high intraspecific genetic variation of *A. alternata*. This phylogenetic result concurs with Woudenberg et al.[13]. However, the strains of *A. alternata* can be distinguished into five main subclades with significant support (up to 80% ML, 0.95 PP) in this study. Hence, existing strains of *A. alternata* may represent five species rather than a single species, and further work is needed to clarify the phylogeny.

Analyses 3 represented phylogenetic relationships of two novel taxa, *Alternaria arundinis* and *A. nodulariconidiophora*, with other representative species in sect. *Infectoriae* and sect. *Pseudoalteraria*. Phylogenetic construction of sect. *Infectoriae* is based on a combined ITS, GAPDH and ATPase DNA sequence dataset comprising 68 strains of ingroup taxa and two taxa in sect. *Chalastospora* (*A. malorum* CBS 135.31 and *A. abundans* CBS 534.83) were selected as the outgroup taxa. The best scoring RAxML tree is shown in Fig. 5 with the final ML optimization likelihood value of −8,122.101740 (ln). The dataset consists of 2,280 total characters, including gaps (ITS: 1–561 bp, GAPDH: 562–1,081 bp, ATPase: 1,082–2,280 bp). RAxML analysis yielded 428 distinct alignment patterns and 7.89% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.221370, C = 0.311012, G = 0.250900, T = 0.216718, with substitution rates AC = 1.538856, AG = 2.663454, AT = 1.056408, CG = 1.258484, CT = 8.888843, GT = 1.000000. The gamma distribution shape parameter alpha = 0.122301 and the Tree-Length = 0.445658. Bayesian posterior probabilities (PP) from MCMC were evaluated with final average standard deviation of split frequencies = 0.008633. The final alignment and tree were submitted in TreeBASE as submission ID: 258524. Three strains of *A. arundinis* (MFLU 21-0313A, MFLU 21-0313B, MFLUCC 21-0128) formed a monophyletic subclade (92% ML, 0.99 PP), sister to *A. incomplexa* E.G. Simmons (CBS 121330) with significant support (89% ML, 1.00 PP), while *A. nodulariconidiophora* (MFLU 21-0315, MFLUCC 21-0131) clustered with *Alternaria* sp. (JS8-5, FA3-2) and *A. humuli* E.G. Simmons (CBS 119404) with significant support (87% ML, 1.00 PP). Many *Alternaria* spp. isolated from black head mold-affected wheat and barley in Iran were included in the present analyses and remained phylogenetically unresolved, concurring with Poursafar et al.[47]. Unfortunately, phylogenetic affinities of most species in this section are characterized by internally low support values, also in agreement with Poursafar et al.[47] and Marin-Felix et al.[70]. More informative phylogenetic markers such as ATPase and cmdA genes were suggested to use at species level identification due to species in sect. *Infectoriae* showing high genetic variation.[13,70].

Analyses 4 represented phylogenetic relationships of the novel species, *Alternaria brevirostra* with other representative species in sect. *Porri*. Phylogenetic construction of *Alternaria*

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**Table 4.** Divergence times of *Alternaria* sections indicated in MCC tree. The age value with * indicates recent results lacking key coding gene strains.

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Genus</th>
<th>Sections</th>
<th>Divergence times (crown age)</th>
<th>Divergence times (stem age)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Alternaria sect. <em>Alternaria</em></td>
<td>110 (79–148) Mya</td>
<td>120 (84–159) Mya</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Alternaria sect. <em>Chalastospora</em></td>
<td>0.4 (0–1.5) Mya</td>
<td>14 (6.7–21) Mya</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Alternaria sect. <em>Cheiranthus</em></td>
<td>5 (1.7–10) Mya</td>
<td>14 (6.7–21) Mya</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Alternaria sect. <em>Crivellia</em></td>
<td>2.3 (0.5–5.5) Mya</td>
<td>33 (22–45) Mya</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Alternaria sect. <em>Dianthicola</em></td>
<td>16 (8.8–26) Mya</td>
<td>26 (16–38) Mya</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Alternaria sect. <em>Eureke</em></td>
<td>7.6 (1.5–19) Mya</td>
<td>53 (36–71) Mya</td>
</tr>
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<td></td>
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<td></td>
<td>Alternaria sect. <em>Omanenses</em></td>
<td>14 (5.6–24) Mya</td>
<td>28 (18–44) Mya</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Alternaria sect. <em>Panax</em></td>
<td>16 (7.6–26) Mya</td>
<td>27 (18–37) Mya</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Alternaria sect. <em>Helianthiinicientes</em></td>
<td>0.11 (0–0.3) Mya</td>
<td>24 (13–36) Mya</td>
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<td></td>
<td></td>
<td></td>
<td>Alternaria sect. <em>ectionarias</em></td>
<td>–</td>
<td>31 (14–47) Mya</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Alternaria sect. <em>Omanenses</em></td>
<td>–</td>
<td>30 (14–47) Mya</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Alternaria sect. <em>Panax</em></td>
<td>14 (6.8–23) Mya</td>
<td>22 (12–33) Mya</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Alternaria sect. <em>Porri</em></td>
<td>6.7 (3–11) Mya</td>
<td>11 (5.6–17) Mya</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Alternaria sect. <em>Pseudoulcadinium</em></td>
<td>2.1 (0.4–5.8) Mya</td>
<td>17 (9.5–27) Mya</td>
</tr>
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<td></td>
<td>Alternaria sect. <em>Soda</em></td>
<td>3 (0.5–8.4) Mya</td>
<td>32 (26–54) Mya</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td>Alternaria sect. <em>Teretispora</em></td>
<td>0.2 (0–1.03) Mya</td>
<td>27 (17–40) Mya</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Alternaria sect. <em>Ulocladium</em></td>
<td>0.9 (0.1–2.5) Mya</td>
<td>44 (32–60) Mya</td>
</tr>
</tbody>
</table>
sect. Porri based on a combined ITS, GAPDH, TEF1-α, RPB2 and Alt-a1 DNA sequence dataset comprised 114 strains of 65 ingroup species. Five strains of three species in sect. Euphorbiicola (A. limicola CBS 483.90, CBS 117360 and A. euphorbiicola CBS 119460, CBS 198.86) and sect. Gypsophilae (A. gypsophilae CBS 107.41) were selected as the outgroup taxa. The best scoring RAxML tree is shown in Fig. 6 with the final ML optimization likelihood value of \(-11,626.467690\) (ln). The dataset consists of 2,715 total characters, including gaps (ITS: 1–539 bp, GAPDH: 540–1,121 bp, TEF1-α: 1,122–1,463 bp, RPB2: 1,464–2,239 bp, Alt-a1: 2,240–2,715). RAxML analysis yielded 597 distinct alignment patterns and 3.43% undetermined characters or gaps. Estimated base frequencies were as follows: \(A = 0.231369, C = 0.294521, G = 0.244128, T = 0.229982\), with substitution rates \(AC = 0.982217, AG = 4.158740, AT = 0.987304, CG = 0.590117, CT = 8.931720, GT = 1.000000\). The gamma distribution shape parameter \(\alpha = 0.207829\) and the Tree-Length = 0.669039. Bayesian posterior probabilities (PP) from MCMC were evaluated with the final average standard deviation of split frequencies = 0.008326. The final alignment and tree were submitted in TreeBASE as submission ID: 258525.

Two strains of the novel species, A. brevirostra (MFLUCC 21-...
Fig. 5  Phylogenetic construction of *Alternaria* sect. *Infectoriae* using RAxML-based analysis of a combined ITS, GAPDH and ATPase DNA sequence dataset. Bootstrap support values for maximum likelihood (ML, black) equal to or greater than 70% and Bayesian posterior probabilities (PP, red) equal to or greater than 0.95 PP are shown above the nodes. The tree is rooted with taxa in sect. *Chalastospora* (*Alternaria malorum* CBS 135.31 and *A. abundans* CBS 534.83). Newly generated strains are in blue. The type strains obtained from ex-type cultures are indicated by ‘T’ and the type strains obtained from specimens are indicated by ‘H’.

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0129, MFLUCC 21-0130), formed a sister clade with *A. rostellata* (CBS 117366) and clustered with *A. nitrimii* (CBS 109163), *A. pipionipisi* (CBS 116115), *A. crassa* (CBS 110.38) and *A. macrospora* (CBS 117128). However, phylogenetic relationships of the species in this subclade were not well-resolved. Concurring with Woudenberg et al.[11,22], sect. *Porri* displayed a

![Phylogenetic construction of *Alternaria* sect. *Porri* using RAxML-based analysis of a combined ITS, GAPDH, TEF1-α, RPB2 and Alt-a1 DNA sequence dataset. Bootstrap support values for maximum likelihood (ML, black) equal to or greater than 70% and Bayesian posterior probabilities (PP, red) equal to or greater than 0.95 PP are shown at the nodes. The tree is rooted to sect. *Gypsophilae* (*Alternaria gypsophilae* CBS 107.41). Newly generated strains are in blue and the type strains are indicated by 'T'.](image-url)
high degree of genetic variation, and the phylogenetic status of many species remain unresolved in this study.

Analyses 5 represented phylogenetic relationships of the new taxon, *Alternaria phytolaccæ*, with other species in sect. *Radicina* and the closely related sect. *Gypsophilæ*. Phylogenetic construction of sect. *Radicina* based on a combined ITS, TEF1-α, RPB2, and GAPDH DNA sequence dataset comprised 18 strains of ingroup taxa and *A. helianthi-inficiens* (CBS 208.86, CBS 117370) was selected as the outgroup. The best scoring RAxML tree is shown in Fig. 7 with the final ML optimization likelihood value of –5,160.537105 (ln). The dataset consists of 2,209 total characters, including gaps (ITS: 1–521 bp, TEF1-α: 522–767 bp, RPB2: 768–1,636 bp, GAPDH: 1,637–2,209 bp). RAxML analysis yielded 220 distinct alignment patterns and 8.90% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.246820, C = 0.276063, G = 0.242024, T = 0.235092, with substitution rates AC = 1.221528, AG = 4.038587, AT = 0.589501, CG = 0.595656, CT = 9.444647, GT = 1.000000. The gamma distribution shape parameter alpha = 0.191394 and the Tree-Length = 0.206922. Bayesian posterior probabilities (PP) from MCMC were evaluated with final average standard deviation of split frequencies = 0.008477. The final alignment and tree were submitted in TreeBASE as submission ID: 258526. Two strains of the novel species, *A. phytolaccæ* (MFLU 21-0314, MFLUCC 21-0135), formed a strong support clade (98% ML, 1.00 PP) and clustered with *A. selini* E.G. Simmons (EGS 25-198), *A. petroselini* (Neerg.) E.G. Simmons (CBS 112.41) and *A. vulgaris* L. He & J.X. Deng (YZU161234, YZU161235), with significant support (60% ML, 0.97 PP).

**Taxonomy**

The current morphology-based taxonomy of *Alternaria* followed the treatment of Emory G. Simmons (1920–2013), who provided a monograph of *Alternaria* based on the patterns of sporulation and conidial morphology[38]. In addition, a comprehensive treatment with multi-locus phylogeny-based taxonomy was carried on by Woudenberg et al.[11,12,22]. In the present study, 18 saprobic species have been introduced into
sects. *Alternaria, infectoriae, Porri* and *Radicina* based on morphological characteristics on host substrates, coupled with multi-locus phylogenetic evidence. In addition, the sporulation of novel species was also induced on OA, PCA and PDA following Emory G. Simmons’s criterion, of which *A. arctoseptata*, *A. baoshanensis*, *A. breviconidiophora*, *A. ellipsoidalis*, *A. eupatoriicola*, *A. falcata*, *A. lathyri*, *A. macilenta*, *A. minimispora*, *A. oblongoellipsoidea*, *A. phragmiticola* and *A. salicicola* in sect. *Alternaria*, *A. arundinis* and *A. nodulariconidiophora* in sect. *infectoriae* and *A. phytolaccae* in sect. *Radicina*, were sporulated on PCA (Fig. 8). Besides, *A. alternata*, *A. doliconidium* and *A. macroconidia* were sporulated on OA. While *A. orobanches* (sect. *Alternaria*) and *A. brevirostra* (sect. *Porri*) did not sporulate on any agar media.
Section *Alternaria* D.P. Lawr., Gannibal, Peever & B.M. Pryor

Type species – *Alternaria alternata* (Fr.) Keissl.

Notes – Simmons\(^{[160]}\) described the species-groups of *Alternaria alternata*, *A. tenuissima*, *A. cheiranthi* and *A. brassicicola* based on the morphological characteristics of sporulation. Lawrence et al.\(^{[14]}\) revealed eight distinct asexual lineages of *Alternaria* based on a molecular phylogenetic approach using ten protein-coding loci incorporated extensive taxon sampling (176 species) and proposed eight novel sections for *Alternaria*, in which sect. *Alternaria* introduced by Woudenberg et al.\(^{[11]}\) assigned an orthographic variant ‘*Alternata*’ for sect. *Alternaria* that is contradictory to ICBN Arts. 22.1 and 22.2. Thus, Lawrence et al.\(^{[15]}\) resurrected the section named *Alternaria*. Most species in this section are small-spored, with concatenated conidia that can be found as saprobes and as pre- or post-harvest diseases in over 100 host plants as well as human pathogens\(^{[12,15]}\). Some important plant pathogens in this section such as *A. arborescens* can cause stem canker on tomato, and *A. longipes* caused brown spot disease on tobacco\(^{[12]}\). Major updated taxonomic treatment of sect. *Alternaria* was circumscribed by Woudenberg et al.\(^{[12]}\). The generic type of *Alternaria*, *A. alternata* is also accommodated in this section. *Alternaria alternata* displays high genetic variation, and thus, Woudenberg et al.\(^{[12]}\) synonymized 35 morpho-species under *A. alternata*, of which three formae speciales and two pathotypes of *A. alternata* were recognized according to the detection of host-specific toxins. Woudenberg et al.\(^{[12]}\) mentioned that the genome assembly showed high similarity between the isolates within sect. *Alternaria* (96.7%–98.2% genome identity) compared with isolates from other sections (85.1%–89.3% genome identity), while the synonymized morpho-species under *A. alternata* showed 1.4%–1.5% SNPs in

their whole-genome reads. As *Alternaria* isolates were highly polymorphic, the low informative genes of the ITS, LSU and SSU were the least successful in separating the species in sect. *Alternaria*, while GAPDH was commonly used to distinguish all species in the section, except for distinguishing the *A. arborescens* species complex (AASC) from *A. alternata*. The other genes viz. Alt-a1, endoPG, KOG1058, OPA10-2 and RPB2 could separate all species in the section from *A. alternata* but could not separate different pairs of other species from one another [12].

*Alternaria alternata* (Fr.) Keissl., Beih. bot. Zbl., Abt. 2 29: 434 (1912)

Index Fungorum number: IF 119834, Facesoffungi number: FoF 03825; Fig. 9


Synonyms: See Woudenberg et al. [12] and Index Fungorum [5]

Type details – India, on *Arachis hypogaea* (Fabaceae), 1 December 1980, E.G. Simmons, IMI 254138 [epitype; designated by de Hoog & Horré [20]], ex-epitype living culture, CBS 916.96 = ATCC 66981 = EGS 34.01; Germany, on fragments of a pithy stem, C.G.D. Nees von Esenbeck, No. 910, 262-129, a [neotype; designated by Simmons] [161].

Saprobic on dead branches of *Reseda* sp. Sexual morph Undetermined. Asexual morph Mycelium superficial on the substrate, composed of septate, branched, smooth, thin-walled, pale white to grey hyphae. Conidiophores 

\[(160.5–)179.5–184(–188) \times (9–)12–14(–15.5) \mu m \quad (\bar{x} = 181.4 \times 13.2 \mu m, n = 100),\] 

macronematous, mononematous, flexuous, cylindrical, versicolorous, brown to dark brown, septate, unbranched, smooth to rough, with small granules, thick-walled. Conidiogenous cells 

\[(12–)13–15.5(–16) \times \] 

Fig. 9 *Alternaria alternata* (MFLU 21-0302). (a), (b) Colonies on dead branch. (c)–(i) Conidiophores. (j)–(u) Conidia. Scale bars: (a) = 0.1 cm, (b) = 300 \mu m, (c)–(u) = 20 \mu m.
(10–)11.5–13(–14) µm (± = 14.3 × 12.2 µm, n = 100), mono- to polytretic, integrated, terminal, determinate, percurrent, subhyaline to pale brown, smooth, thin-walled, rounded or doliform at apex, with 1–3 apical conidiogenous loci. Conidia (76–)82.5–91.5(–98) × (22.5–)29–37(–39) µm (± = 86.4 × 32.4 µm, n = 100) acrogenous, sometimes catenate, dry, muriform, straight, sometimes curved, ovoid to clavate or obpyriform, sometimes formed short, narrow, unbranched beak, grey-brown to brown, 3–4(–8) transverse septa, and 1–2 longitudinal septa, with asceptate or 1 longitudinal or oblique septum or Y-shaped at the end cell, smooth or verrucose, thin-walled. Conidial secession schizolytic.

Culture characteristics – Conidia germinating on PDA within 14 h and germ tubes produced from all cells. Colonies growing on PDA, cottony, pale white to grey, reaching 5 cm in 7 d at 25 °C, mycelium superficial, effuse, radially striate, with irregular edge, subhyaline hyphae. Conidia sporulated on OA media within 15 d, phragmosporous to muriform, obclavate to obpyriform, light brown to brown, with branched or unbranched acicular or doliform, asceptate, apical beak, formed branched, apically or laterally secondary conidiophores with 1–2 conidiogenous loci, olivaceous-brown to brown, 1–4 transversely euseptate, 1–3 longitudinal or oblique or Y-shaped septa in transverse divisions, borne in chains with at least 3 conidia, smooth to minutely verruculose.

Material examined – Italy, Province of Arezzo [AR], near Passo la Calla, on dead aerial stem of Reseda sp. (Resedaceae), 13 July 2014, E. Camporesi, IT1994 (MFLU1 21-0302), living culture = MFLUCC 21-0797.

Notes – In this study, we obtained 45 new collections of Alternaria alternata from China, Italy and Thailand. Multi-locus phylogeny of ITS, LSU, SSU, TEF1-α, RPB2, GAPDH and Alt-α loci confirmed species identification of these 45 strains as A. alternata. These 45 strains formed various internal subclades within A. alternata and can be separated into five main subclades with 80% ML, 0.95 PP support (Fig. 4). These 45 collections showed a diverse range of host occurrences in families Adoxaceae, Arecaceae, Asteraeae, Betulaceae Brassicaceae, Caprifoliaceae, Fagaceae, Lamiaceae, Malvaceae, Orobanchaceae, Pinaceae, Poaceae, Rubiaceae, Rosaceae, Sapindaceae, Solanaceae, Urticaceae and some unidentified plant litter (Table 5).

The major subclade A formed a significant subclade with 81% ML, 0.98 PP support containing 62 strains with several internal branches. Newly generated strains HWP-01, IT2144, IT2145, IT3598, and IT3651 formed a single lineage with strains CBS 965.95 and CBS 966.95; these isolates occurred on host families Asteraceae, Adoxaceae, Fagaceae, Poaceae and Solanaceae as pathogens and saprobes. The saporic strains H-71, IT2143, and IT3556 formed a single lineage with strain CBS 130254 (isolated from human sputum in India), and CBS 911.97 (isolated from Artemisia brevifolia (Asteraceae) in India) and clustered with CBS 130262, CBS 130265 (isolated from human sputum in India) and CBS 121492 (isolated from Cucumis melo (Cucurbitaceae) in China). Six strains isolated from human sputum and sinustis in India (CBS 877.95, CBS 130255, CBS 130258, CBS 130259, CBS 130261, CBS 130263) clustered with three strains isolated from Malus domestica (Rosaceae) in South Africa (CBS 113013, CBS 113014, CBS 113015), strains isolated from Citrus jamhiri (CBS 102596), C. reticulata (CBS 102600) and Minneola tangelo (CBS 119399) in the USA, three new strains isolated from Aster sp. (IT2115), Orobanche sp. (IT3504) in Italy and unidentified grass (DMS 15) in Thailand. At the same time, the strain CBS 117143 (isolated from Capsicum annum (Solanaceae) in Italy) formed a significant subclade (79% ML, 0.96 PP) with CBS 113054 (isolated from M. domestica in South Africa), and clustered with the two new isolates IT 1994 and IT 2166.

The strain CBS 120829 (isolated from Punica granatum (Punicaceae) in Greece), formed a single lineage with CBS 124277 (isolated from Prunus sp. (Rosaceae) in Denmark) and clustered with CBS 117130 (isolated from Arbutus unedo (Ericaceae) in Italy) with significant support in BI analyses (0.98 PP). Five strains isolated from Minneola tangelo in Israel, South Africa and Turkey (CBS 102559, CBS 102602, CBS 102603, CBS 121344, and CBS 121346) also formed a single lineage (66% ML, 0.99 PP) within subclade A. The strain CBS 124278 (isolated from Prunus sp. in Denmark) formed a single lineage with CBS 102604 (isolated from Minneola tangelo in Israel) with significant support (68% ML, 0.96 PP), while at the same time, the new isolate IT2900 formed a single lineage with CBS 195.86 (isolated from Euphorbia esula (Euphorbiaceae) in Canada) with high support (100% ML, 1.00 PP). Three new isolates (HAM 02, IT 2087, IT 3426) formed a single lineage with CBS 603.78 (isolated from the air in USA) and clustered with CBS 113024 (isolated from Minneola tangelo in South Africa). Two new isolates (IT 2063, IT 3168) formed a significant branch with 87% ML, 1.00 PP support clustered with CBS 447.86 (isolated from Malva sp. (Malvaceae) in Morocco). Three new isolates (HXB 08, IT3419, IT2064) also formed a significant support lineage (73% ML, 0.99 PP) with CBS 479.90 (isolated from Citrus unshiu in Japan) and clustered with IT2347, HKM 1 and CBS 126071 (isolated from soil in Namibia) with significant support (87% ML, 1.00 PP). The strain CBS 112252 formed an independent single lineage basal to subclade A with significant support (81% ML, 1.00 PP).

Subclade B was represented by five strains, including the ex-type strain of Alternaria alternata (CBS 916.96). Two new isolates (H-49, IT2162) formed a single lineage with the type strain of A. alternata (CBS 916.96) and CBS 116749 with 96% ML, 1.00 PP support, clustering with CBS 106.34 (isolated from Linum usitatissimum, Linaceae) with 81% ML, 0.99 PP support.

Subclade C contained seven new isolates from China and Italy (IT2053, KIB-H2, IT2277, IT3160, IT3439, IT2090 and HAM-03), clustering with strain CBS 119115 (isolated from Prunus sp. in Greece), two strains from South Africa (CBS 115069, CBS113025), four strains from USA (CBS 127672, CBS 267.77, CBS 119543, CBS 127671), two strains from India (CBS 130260, CBS 125606), CBS 686.68 (from Sahara Desert sand) and CBS 104.26, with 96% ML, 1.00 PP support.

Subclade D formed a high support subclade (99% ML, 0.95 PP) containing five strains that include two new strains (IT 3048, IT2454) isolated from Acer opalus and Urtica sp. in Italy. The two new strains (IT 3048, IT2454) formed a single lineage with CBS 117.44 (isolated from Godetia sp. in Denmark) with 89% ML, 1.00 PP support, clustering with CBS 106.24 (isolated from Malus sylvestris in USA) and CBS 121544 (isolated from Cucumis sativus in USA).

Subclade E formed a basal lineage with 86% ML, 1.00 PP support, including ten new isolates (IT2103, IT 3442, IT 3449, IT 2114, IT 2427, HSH-01, PB-12, HTWD-01, IT 2125, HMRC-51), two isolates from soil (CBS 127334, CBS 126910) and from Plantago
<table>
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In vitro with irregular edge, white to brown hyphae; conidia not on PDA, hairy, fluffy, brown to dark brown, reaching 5 cm within 7 d at 25 °C, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, hyaline to subhyaline hyphae, 2–5 μm diam; conidia formed in vitro within 30 d, borne in chains with at least two conidia, yellow to light brown, subglobose to ellipsoidal, 55 × 20 μm (Fig. 8h).

Material examined – Italy, Province of Forlì-Cesena, Predappio, Fiuman, on dead standing stem of Lathyrus sp. (Fabaceae), 2 September 2014, E. Camporesi, IT2088 (MFLU 21-0308, holotype), ex-type living culture = MFLUCC 21-0139.

Notes – Alternaria arctoseptata was isolated from the same host genus Lathyrus sp. as A. lathyr i. Alternaria arctoseptata can be distinguished from A. lathyr i. having paler conidia, with short narrow apical beak or formed secondary conidiophores. Furthermore, the conidiophores of A. arctoseptata are shorter, pale brown to light brown conidiophores with apically swollen knots, arising from stromatic base, which are darker in A. lathyr i. Phylogenetically two strains of A. arctoseptata (MFLUCC 21-0139, MFLU 21-0308) formed a high support clade (100% ML, 0.99 PP) that clustered with A. baoshanensis and A. ovoidea with 86% ML, 0.99 PP support (Fig. 3), and distant from A. lathyr i. Alternaria arctoseptata differs from A. baoshanensis in having apical beak, and larger conidia (60 × 25 μm vs. 38 × 18 μm) that are rather constricted at some septa as well as having rather monotropic, larger conidiogenous cells (11.5 × 12 μm vs. 6.2 × 7.5 μm). Alternaria arctoseptata also differs from A. ovoidea in having paler brown conidia that are rather constricted at some septa(10). A comparison of RPB2 nucleotide pairwise shows that A. arctoseptata differs from A. baoshanensis in 10/559 bp (1.8% difference, no gap) and differs from A. ovoidea in 12/565 bp (2.1% difference, no gap). A comparison of Alt-a1 nucleotide pairwise shows that A. arctoseptata differs from A. baoshanensis in 8/474 bp (1.7% difference, no gap) and differs from A. ovoidea in 18/520 bp (3.5% difference, no gap). Based on distinct morphological characteristics and phylogenetic support, A. arctoseptata is introduced as a new species in this study.

Alternaria baoshanensis J.F. Li, Phookamsak & Jeewon, sp. nov.

Index Fungorum number: IF 558435; Facesoffungi number: FoF 12653; Fig. 11.

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(*continued*)
Etymology: Named after the locality, Baoshan (Yunnan, China), where the species was collected.

Holotype: MFLU 21-0296

Saprobic on rattan of Curcubita moschata (Duch ex Lam.) Duch ex Poiret (Cucurbitaceae). Sexual morph Undetermined.

Asexual morph Mycelium superficial on the substrate, composed of septate, branched, smooth, thin-walled, composed of dark hyphae. Conidiophores 80–100 × 12–20 µm (\(\bar{x} = 48 \times 14 \mu m, n = 20\)), macronematous, straight or flexuous, unequally cylindrical, versicolorous, light brown to dark brown, smooth, thick-walled, septate, sometimes branched, with several aggregated at the base. Conidiogenous cells 5–7 × 6–10 µm (\(\bar{x} = 6.2 \times 7.5 \mu m, n = 20\)), mono- to polytretic, integrated, terminal, determinate or percurrent, cylindrical, subhyaline to light brown, doliform apex, with apically or laterally 1–2 conidiogenous loci, smooth, thin-walled, with a distinctive conidiogenous hilum. Conidia 25–60 × 12–22 µm (\(\bar{x} = 38 \times 18 \mu m, n = 30\)) acrogenous, solitary or borne in chain with at least 1–3 conidia, straight, curved, varied in shapes, usually subglobose to ellipsoidal, or subcylindrical to obpyriform, occasionally irregular in shape, sometimes formed a short beak, light brown to yellowish brown, 3–6 transverse septa, with 1–2 longitudinal or oblique septa in some transverse divisions, smooth, sometimes verrucose, thin-walled. Conidial secession schizolytic.

Culture characteristics – Conidia germinating on PDA within 14 h and germ tubes produced from all cells. Colonies growing on PDA, hairy fluffy, brown, reaching 5 mm in 10 d at 25 ºC, mycelium superficial, effuse, radially striate, with irregular edge, brown hyphae; conidia not formed in vitro within 60 days. Colonies growing on PCA, white to light brown colored, cottony, fluffy, reaching 5 cm within 7 d at 25 ºC, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, subhyaline to light brown hyphae, 2–5 µm diam; conidia formed in vitro within 60 d, borne in chains with at least 2 conidia, light brown to brown, ovoid to ellipsoidal, 40 × 15 µm (Fig. 8e).

Material examined – China, Yunnan, Baoshan, Shuizhai County, on dead rattan of Curcubita moschata (Cucurbitaceae), 25 October 2015, J.F. Li, H-50 (MFLU 21-0296, holotype), ex-type living culture = MFLUCC 21-0124.

Notes – Alternaria baoshanensis can be distinguished from other related species (A. actroseptata and A. ovoidea) in having

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![Fig. 10 Alternaria arctoseptata (MFLU 21-0308, holotype). (a) Colonies on dead stem of Lathyrus sp. (Fabaceae). (b)–(g) Conidiophores bearing conidiogenous cells. (h), (i) Immature conidia. (j), (o) Conidia formed secondary conidiophores. (k)–(n) Mature conidia. Scale bars: (a) = 200 µm, (b)–(o) = 20 µm.](image-url)
versicolorous conidiophores\textsuperscript{[68]}. Multi-locus phylogeny demonstrated that two strains of \textit{A. baoshanensis} (MFLUCC 21-0124, MFLU 21-0296) form a robust clade (100\% ML, 1.00 PP), sister to \textit{A. ovoidea} with 67\% ML, 0.96 PP support (Fig. 3). \textit{Alternaria baoshanensis} differs from \textit{A. ovoidea} in having shorter conidiogenous cells, with apically or laterally 1–2 conidiogenous loci (5–7 × 6–10 μm vs. 9–13 × 8.5–15 μm), while \textit{A. ovoidea} has conidiogenous loci cicatrized on conidial secession\textsuperscript{[68]}. Furthermore, \textit{A. baoshanensis} has slightly smaller conidia (25–60 × 6–10 μm vs. 48–65 × 15.5–30 μm)\textsuperscript{[68]}. Conidia of \textit{A. baoshanensis} are varied in shapes, usually subglobose to ellipsoidal, solitary or borne in chain (at least 1–3 conidia), light brown to yellowish brown, 3–6 transverse septa, with 1–2 longitudinal or oblique septa in some transverse divisions. Whereas, conidia of \textit{A. ovoidea} are solitary, ovoid, orangish brown to copper brown, with 1–3 transverse septa, and 1 longitudinal septum in transverse divisions\textsuperscript{[68]}.

\textbf{Alternaria breviconidiophora} J.F. Li, Camporesi, Phookamsak & Jeewon, \textit{sp. nov.}

\textit{Index Fungorum} number: IF 558436; \textit{Facesoffungi} number: FoF 12654; Fig. 12

\textbf{Etymology}: Named after its short conidiophores and small conidial structures.

\textbf{Holotype}: MFLU 21-0317

Saprobic on dead hanging branches of \textit{Digitalis} sp. (Scrophulariaceae). \textbf{Sexual morph} Undetermined. \textbf{Asexual morph} Mycelium superficial on the substrate, composed of brown to dark brown hyphae. \textit{Conidiophores} 25–88 × 6–10 μm (\(\bar{x} = 45 \times 9 \text{ μm, } n = 40\)), macronematous, straight or flexuous, cylindrical, dark brown, smooth, thick-walled, septate, unbranched, arising from stromatic base. \textit{Conidiogenous cells} 8–11 × 8–9 μm (\(\bar{x} = 9.5 \times 8 \text{ μm, } n = 20\)), mono- to polytretic, integrated, terminal, determinate or percurrent, cylindrical, paler light brown, apically doliform, with one or a few conidiogenous loci. \textit{Conidia} 8.6–12 × 7–10 μm (\(\bar{x} = 10 \times 8 \text{ μm, } n = 30\)) acrogenous, solitary or borne in chains with at least 2–3 conidia, globose or subglobose, sometimes slightly quadrilateral or ovoid, yellowish brown to brown or dark brown, sectored, 1–2 transverse disto- or eusepta, with 1 longitudinal or oblique or Y-shaped septum, smooth to verruculose, thick-walled. \textit{Conidial secession} schizolytic.
Culture characteristics – Conidia germinating on PDA within 14 h and germ tubes produced from all cells. Colonies growing on PDA, cottony, brown to dark brown, reaching 5 mm in 10 d at 25 ºC, mycelium superficial, effuse, radially striate, light brown hyphae; conidia not formed in vitro within 60 d. Colonies growing on PCA, light brown colored, hairy, fluffy, reaching 5 cm within 7 d at 25 ºC, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, subhyaline to light brown hyphae, 2–5 µm diam; conidia formed in vitro within 60 d, borne in chains with at least 2 conidia, light brown to brown, globose or subglobose, 12 × 10 µm (Fig. 8l).

Material examined – Italy, Province of Forlì-Cesena, Rocca San Casciano, on dead hanging branch of Digitalis sp. (Scrophulariaceae), 7 April 2017, E. Camporesi, IT3308 (MFLU 21-0317, holotype), ex-type living culture = MFLUCC 22-0075.

Notes – Multi-locus phylogeny showed that two strains of Alternaria breviconidiophora form a robust subclade (100% ML, 1.00 PP; Fig. 3) basal to A. lathyri, A. muriformispora, and A. pseudoinfectoria with 100% ML and 1.00 PP support (Fig. 3). However, A. breviconidiophora differs from these three species in having small (= 10 × 8 µm), globose or subglobose, non-beaked, 1–2 transversely disto- or euseptate conidia and tiny conidiophores arising from a stomatic base. A RPB2 nucleotide pairwise comparison showed that A. breviconidiophora differs from A. lathyri in 12/570 bp (2.1% difference, no gap), and differs from A. pseudoinfectoria in 9/550 bp (1.5% difference, no gap). An Alt-a1 nucleotides comparison showed that A. breviconidiophora differs from A. lathyri in 9/500 bp (1.8% difference, no gap), differs from A. muriformispora in 10/462 bp (2.2% difference, no gap), and differs from A. pseudoinfectoria in 7/480 bp (1.5% difference, no gap). These tally along with recommendations outlined in Jeewon & Hyde[134] establish A. breviconidiophora as a new species.


Index Fungorum number: IF554202; Facesoffungi number: FoF 04041; Fig. 13

Type details – ITALY, Province of Forli-Cesena [FC], Raggio di Santa Sofia, on dead aerial spines of Rosa canina L. (Rosaceae), 16 October 2014, E. Camporesi, IT2165 (KUN-HKAS100840, holotype), ex-type living culture = KUMCC 17-0263.

Saprobic on dead stems of Reseda sp. Sexual morph Undetermined. Asexual morph Mycelium superficial on the substrate, with dark brown hyphae. Conidiophores (140–)167–176(–189.5) × 8–10(–10.5) µm (µ = 172.4 × 9.5 µm, n = 100), macronematous, mononematous, straight or flexuous, cylindrical, dark brown, paler towards the apex, septate, unbranched, smooth, thick-walled. Conidiogenous cells (7.5–)9–10(–12) × (5.5–)8–12.5(–13) µm (µ = 9.6 × 10.2 µm, n = 100), mono- to polytretic, sympodial, integrated, terminal,

Fig. 12 Alternaria breviconidiophora (MFLU 21-0317, holotype). (a) Colonies on dead branch. (b) Conidiophores arising on stomatic base. (c)–(g) Conidiophores. (h)–(q) Conidia. Scale bars: (a) = 50 µm, (b)–(g) = 20 µm, (h)–(q) = 10 µm.
determinate or percurrent, cylindrical, subhyaline to paler brown, thick-walled, apically doliiform, with 1–3 conidiogenous cicatrized loci on conidial secession. Conidia (56.5–)65.5–71(–79) × (22–)26–30(–34) µm ($\bar{x} = 67.3 \times 27.8$ µm, $n = 100$) acrogenous, solitary or borne in chains with at least 2 conidia, dry, curved, obclavate to ellipsoidal, or obpyriform, with short, unbranched, aseptate apical beak, or non-beaked, brown to dark brown, 3–5 transverse disto- or eusepta, with 1 longitudinal or oblique or Y-shaped septum in transverse divisions, verruculose to verrucose, thick-walled. Conidial secession schizolytic.

**Fig. 13** *Alternaria doliconidium* (MFLU 21-0294). (a) Dead stem of *Reseda* sp. (Resdaceae). (b) Colonies on dead stem. (c)–(j) Conidiophores on natural substrate. (k)–(m) Conidiogenesis sporulated in vitro. (n) Germinated conidium. (o)–(r) Conidia ((q), (r) on natural substrate)). Scale bars: (a) = 0.1 cm, (b) = 500 µm, (c)–(r) = 20 µm.
Culture characteristics – Conidia germinating on PDA within 14 h and germ tubes produced from lateral cells. Colonies growing on PDA, hairy fluffy or cottony, grey to brown, reaching 5 cm in 15 d at 25 ºC; mycelium superficial, effuse, radially striate, with irregular edge, grey to light brown hyphae. Conidia sporulated on OA within 30 d, phragmosporous to muriiform, oblong to subglobose, with short, branched or unbranched, aseptate apical beak, formed apically, or laterally secondary conidiophores with 1 conidiogenous locus, olivaceous-brown to golden brown, sectored, 2–3 transversely eusepta, with 0–1 longitudinal or oblique or Y-shaped septum in transverse divisions, borne in chains with at least 2–4 conidia, verruculose to verrucose.

Material examined – China, Yunnan Province, Kunming, Kunyang Town, on dead stem of Reseda sp. (Resedaceae), 18 September 2014, J.F. Li, H-11B (MFLU 21-0294, new geographical and host record), living culture MFLUCC 14-0020.

Notes – Wanasinghe et al. described *Alternaria doliconidium* on Rosa canina L. (Rosaceae) from Italy. In this study, we collected *A. doliconidium* on Reseda sp. as the first record on this host from China. *Alternaria conidionis* was isolated from the same host species as *A. alternata* (MFLU 21-0302, MFLUCC 21-0797) collected in Italy. A nucleotide pairwise comparison showed that our strain MFLUCC 14-0020 differs from *A. alternata* (MFLU 21-0797) in 10/520 bp (1.9% difference, no gap) of GAPDH and 8/500 bp (1.6% difference, no gap) of *Alt-a1* gene locus. Multi-locus phylogeny (Fig. 3) showed that our strain (MFLUCC 14-0020) forms a high support clade (99% ML, 1.00 PP; Fig. 3) with the ex-type strains of *A. doliconidium* (KUN-HKAS 100840, MFLUCC 17-0263) and clustered with *A. italic* (KUMCC 17-0123, MFLUCC 14-0421) and *A. alternata* (CBS 102595, CBS 175.52, YL1, YL2, CBS 916.96) with significant support in ML analysis (71% ML; Fig. 3). A comparison of nucleotide pairwise similarities showed that *A. doliconidium* is distinct from *A. italic* and *A. alternata* (CBS 102595, CBS 175.52, YL1, YL2, CBS 916.96) in *Alt-a1*, GAPDH, RBP2, and *TEF1*-α (Table 6). However, the phylogenetic relationship between *A. doliconidium* and *A. italic* with *A. alternata* is unresolved in this study, pending further study.

*Alternaria ellipsoidalis* J.F. Li, Camporesi, Phookamsak & Jeewon, sp. nov.

Index Fungorum number: IF 558437; Facesoffungi number: FoF12655; Fig. 14

Etymology: Named after its ellipsoidal conidia.

Holotype: MFLU 21-0307

Sporobic on dead hanging hulls of Brassica sp. (Brassicaceae).

Sexual morph Undetermined. Asexual morph *Mycelium* superficial on the substrate, with dark brown hyphae. *Conidiophores* 65–188 × 5–8 µm (± 145 × 6.5 µm, n = 30), macronematous, solitary, straight or flexuous, cylindrical, light brown to brown, septate, smooth or verrucose, thick-walled, gynecia near conidiogenous loci. *Conidiogenous cells* 6–9 × 5–7 µm (± 7.5 × 5.5 µm, n = 20), polytretic, sympodial, integrated, terminal, determinate or percurrent, cylindrical, subhyaline to light brown, smooth, thin-walled, apically doliiform, with 1–4 conidiogenous loci. *Conidia* 45–70 × 15–30 µm (± 60 × 28 µm, n = 30) acrogenous, solitary or borne in chains with at least 2 conidia, straight, curved, ellipsoidial to ovoid, or opphyrifom, with short to long, aseptate, unbranched apical beak, sometimes lacking beak, pale to yellow-brown, 3–6 transverse disto- or eusepta, with 1 longitudinal or oblique or Y-shaped septum in some transverse divisions, verruculose to verrucose, thick-walled. *Conidial secession* schizolytic.

Culture characteristics – Conidia germinating on PDA within 14 h and germ tubes produced from all cells. Colonies growing on PDA, hairy fluffy, brown to dark brown, reaching 5 cm in 10 d at 25 ºC, mycelium superficial, effuse, radially striate, with irregular edge, white to grey-white hyphae; conidia not formed *in vitro* within 60 d. Colonies growing on PCA, white to light brown colored, hairy, fluffy, reaching 5 cm within 7 d at 25 ºC, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, light brown hyphae, 2–5 µm diam; conidia formed *in vitro* within 60 d, borne in chains with at least 2 conidia, light brown to brown, ellipsoidial to ovoid, or opphyrifom, 60 × 30 µm (Fig. 8g).

Material examined – Italy, Province of Averso, Stia, Papiano, on dead hanging hulls of Brassica sp. (Brassicaceae), 1 September 2014, E. Camporesi, IT2086 (MFLU 21-0307, holotype), ex-type living culture = MFLUCC 21-0132.

Notes – *Alternaria ellipsoidalis* resembles *A. falcata* due to its ellipsoidial conidia with short beak and curved conidiophores. However, *A. ellipsoidalis* differs from *A. falcata* in having solitary conidiophores with several gynecia conidiogenous loci proliferations at apex, which is rather polytretic than *A. falcata*. In multi-locus phylogenetic analyses (Fig. 3), *A. ellipsoidalis* formed an independent subclade closely related with *A. eupatoriicola* and distant from *A. falcata*. *Alternaria ellipsoidalis* can be distinguished from *A. eupatoriicola* in having larger (60 × 28 µm vs. 48 × 20 µm), pale to yellowish brown conidia, and the conidiophores are more twisted at the apex in *A. ellipsoidalis*. A *RBP2* nucleotide base comparison showed that *A. ellipsoidalis* differs from *A. eupatoriicola* in 9/550 bp (1.6% difference, no gap). In *GAPDH*, *A. ellipsoidalis* differs from *A. eupatoriicola* in 13/520 bp (2.5% difference, no gap), and in *Alt-a1* the species
differs from *A. eupatoriicola* in 10/480 bp (2.1% difference, no gap). Therefore, the new species *A. ellipsoidialis* is established.

*Alternaria eupatoriicola* J.F. Li, Camporesi, Phookamsak & Jeewon, *sp. nov.*

Index Fungorum number: IF 558438; Facesoffungi number: FoF 12656; Fig. 15

**Etymology**: Named after the host genus 'Eupatorium cannabinum'.

**Holotype**: MFLU 21-0319

Saprobic on standing dead stem of *Eupatorium cannabinum* L. (Asteraceae). **Sexual morph** Undetermined. **Asexual morph** Mycelium superficial on the substrate, thick-walled, with dark hyphae. Conidiophores 50–160 × 5–8 µm (x = 115 × 7 µm, n = 30), macronematous, mononematous, solitary, straight or flexuous, cylindrical, light brown to brown, septate, unbranched, smooth, thick-walled. Conidiogenous cells 6–8 × 4–7 µm (x = 7 × 5 µm, n = 20), mono- to polytretic, integrated, terminal, determinate or percurrent, cylindrical, subhyaline to light brown, smooth, thin-walled, apically doliiform, with 1–5 conidiogenous loci, sometimes swollen near conidiogenous loci. Conidia 40–65 × 15–30 µm (x = 48 × 20 µm, n = 30) acrogenous, straight to curved, ovoid to obpyriform, sometimes with obtuse or coniform, paler brown, short, aseptate, unbranched apical beak, reddish brown to brown, 2–5 transverse septa, with 1 longitudinal or oblique or Y-shaped septum in some transverse divisions, aseptate at the end cells, sometimes constricted at middle transverse septa, borne in chain with at least 2 conidia, verruculose or verrucose, thick-walled. **Conidial secession** schizolytic.

**Culture characteristics** – Conidia germinating on PDA within 14 h and germ tubes produced from both end cells. Colonies growing on PDA, hairy fluffy, brown to dark brown, reaching 5 cm in 20 d at 25 ºC, mycelium superficial, effuse, radially striated, with irregular edge, white to light dark brown hyphae; conidia not formed *in vitro* within 60 d. Colonies growing on PCA, white to brown colored, hairy, fluffy, reaching 5 cm within 7 d at 25 ºC, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, light brown hyphae, 2–5 µm diam; conidia formed *in vitro* within 30 d, borne in chains with at least 2 conidia, yellow to brown, ovoid to obpyriform, 50 × 20 µm (Fig. 8a).

**Material examined** – Italy, Province of Arezzo, Badia Prataglia, on dead standing stem of *Eupatorium cannabinum* (Asteraceae), 2 October 2017, E. Camporesi, IT3518 (MFLU 21-0319, holotype), ex-type living culture = MFLUCC 21-0122.

**Notes** – Based on multi-locus phylogenetic analyses, two strains of *Alternaria eupatoriicola* formed a robust clade (100% ML, 1.00PP; Fig. 3), distinct from other species within sect. **Fig. 14** Alternaria ellipsoidialis (MFLU 21-0307, holotype). (a) Colonies on dead hulls of *Brassica* sp. (b)–(g) Conidiophores bearing conidiogenous cells with a few apical conidiogenous loci. (h)–(q) Conidia. Scale bars: (a) = 300 µm, (b)–(g) = 30 µm, (h)–(q) = 20 µm.
Alternaria. The species is basal to A. pseudoinfectoria, A. muriformispora, A. lathyri, A. brevicinidiophora, A. torilis, A. phragmiticola, A. oblongoellipsoidea, and A. macilenta with 84% ML and 1.00 PP support.

**Alternaria falcata** J.F. Li, Camporesi, Phookamsak & Jeewon, sp. nov.

*Index Fungorum number*: IF 558439; *Facesoffungi number*: FoF 12657; Fig. 16

**Etymology**: Referring to the curve conidiophores.

**Holotype**: MFLU 21-0306

Saprobic on dead standing stem of *Atriplex* sp. (Chenopodiaceae). **Sexual morph** Undetermined. **Asexual morph** Mycelium superficial on the substrate, composed of dark, septate, branched hyphae. **Conidiophores** 70–130 × 5–8 µm (≈ 96 × 7 µm, n = 30), macronematous, mononematous, straight or flexuous, cylindrical, light brown to brown, septate, unbranched, smooth to verruculose, thick-walled. **Conidiogenous cells** 10–11 × 3–5.5 µm (≈ 10.5 × 4.5 µm, n = 20), mono- to polytretic, integrated, terminal, determinate or percurrent, cylindrical, subhyaline, apically doliform to coronal, with 1–2 conidiogenous loci, smooth, thick-walled. **Conidia** 20–50 × 12–23 µm (≈ 40 × 15 µm, n = 30) acrogenous, borne in chain with at least 2 conidia, straight or curved, subglobose to ellipsoidal or obpyriform, with paler brown, short, obtuse, narrow, asetate, unbranched beak, olivaceous-brown to brown, 2–5 transversely disto- or euseptate, with 1–3 longitudinal or oblique septa in some transverse divisions, sometimes formed Y-shaped septum at lower end cell, smooth to verrucose, thick-walled. **Conidial secession** schizolytic.

**Culture characteristics** – Conidia germinating on PDA within 14 h and germ tubes produced from all cells. Colonies growing on PDA, hairy or cottony, brown to dark brown, reaching 5 mm in 20 d at 25 ºC, mycelium superficial, effuse, radially striated, with irregular edge, white to light grey colored hyphae; conidia not formed *in vitro* within 60 d. Colonies growing on PCA, light brown colored, hairy, fluffy, reaching 5 cm within 7 d at 25 ºC, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, light brown hyphae, 2–5 µm diam; conidia formed *in vitro* within 60 d, borne in chains with at least 2 conidia, ellipsoidal or obpyriform, 45 × 15 µm (Fig. 8f).

**Material examined** – Italy, Province of Forlì-Cesena, Fiumicello di Premilcuore, on dead standing stem of *Atriplex* sp. (Chenopodiaceae), 29 August 2014, E. Camporesi, IT2079 (MFLU 21-0306, holotype), ex-type living culture = MFLUCC 21-0123.

**Notes** – In multi-locus phylogenetic analyses, two strains of *Alternaria falcata* formed an independent subclade (81% ML, 0.97 PP; Fig. 3) basal to *A. obpyriconidia* (MFLUCC 21-0121, MFLU 21-0300), *A. macroconidia* (MFLUCC 21-0134, MFLU 21-0301), *A. salicicola* (MFLUCC 22-0072, MFLU 21-0320), *A. arctoseptata* (MFLUCC 21-0139, MFLU 21-0308), *A. ovoidea* (MFLUCC 14-0427, MFLU 21-0298) and *A. baoshanensis* (MFLUCC 21-0124, MFLU 21-0296), respectively. *Alternaria falcata* differs from *A. arctoseptata* in having smaller (40 × 15...
Alternaria falcata

Alternaria lathyri J.F. Li, Camporesi, Phookamsak & Bhat, sp. nov.

Index Fungorum number: IF 558440; Facesoffungi number: FoF 12658; Fig. 17

Etymology: Named after the host genus 'Lathyrus'.

Holotype: MFLU 21-0297

Saprobic on dead stem of Lathyrus sp. (Fabaceae). Sexual morph Undetermined. Asexual morph Mycelium superficial on the substrate, with dark hyphae. Conidiophores 100–130 x 11–15 µm (\( \bar{x} = 115 \times 14 \) µm, \( n = 20 \)), macronematous, mononematous, straight or flexuous, cylindrical, dark brown to black, smooth, septate, unbranched, thick-walled. Conidigenous cells 13–15 x 8–10 µm (\( \bar{x} = 12.5 \times 9 \) µm, \( n = 20 \)), mononematous, integrated, terminal, determinate or percurrent, paler or light brown, smooth, thin-walled, apically rounded to doliform, with 2–4 conidigenous loci. Conidia 40–65 x 18–31 µm (\( \bar{x} = 55 \times 25 \) µm, \( n = 20 \)) acrogenous, borne in chain with at least 2 conidia, straight or curved, ovoid to obpyriform, occasionally formed a short beak, dark grey-brown, with 2–4 transverse eusepta, with 1–2 longitudinal septa in some transverse divisions, aseptate or with 1–2 oblique or Y-shaped septa at the lower end cell, slightly constricted at the middle transverse septa, verrucose, thick-walled. Conidial secession schizolytic.

Culture characteristics – Conidia germinating on PDA within 12 h and germ tubes produced from lateral cells. Colonies

\( \mu m \) vs. 60 x 25 µm), subglobose to ellipsoidal, olivaceous-brown to brown conidia, solitary conidiophores with a curved apex, while its conidia are rather ellipsoidal to obpyriform or obclavate, brown to dark brown, constricted at the septa and conidiophores aggregated on the stomatic base in A. arctoseptata. Alternaria falcata differs from A. baoshanensis in having larger (40 x 15 µm vs. 38 x 18 µm) and longer (96 x 7 µm vs. 48 x 14 µm) solitary concolorous conidiophores, while the species differs from A. ovoidea in having smaller (40 µm x 15 µm vs. 55 x 27 µm) and paler brown conidia, with a short beak, and shorter (96 x 7 µm vs. 280 x 8 µm), curved conidiophores. A RPB2 nucleotide pairwise comparison showed that A. falcata differs from A. arctoseptata in 10/565 bp (1.8% difference, no gap), differs from A. baoshanensis in 8/559 bp (1.4% difference, no gap) and differs from A. ovoidea in 9/565 bp (1.6% difference, no gap). A GAPDH nucleotide pairwise comparison showed that A. falcata differs from A. arctoseptata in 13/590 bp (2.2% difference, no gap), differs from A. baoshanensis in 13/578 bp (2.2% difference, no gap) and differs from A. ovoidea in 11/570 bp (1.9% difference, no gap). An Alt-a1 nucleotide pairwise comparison showed that A. falcata differs from A. arctoseptata in 11/520 bp (2.1% difference, no gap), differs from A. baoshanensis in 8/474 bp (1.7% difference, no gap) and differs from A. ovoidea in 14/520 bp (2.7% difference, no gap). Thus, the new species A. falcata is established based on morphology and phylogeny.
growing on PDA, cottony, brown to dark brown, reaching 5 cm in 10 d at 25 ºC, mycelium superficial, effuse, radially striate, with irregular edge, brown to dark brown hyphae; conidia not formed in vitro within 60 d. Colonies growing on PCA, white to brown colored, hairy, fluffy, reaching 5 cm within 7 d at 25 ºC, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, light brown hyphae, 2–5 µm diam; conidia formed in vitro within 30 d, borne in chains with at least 2 conidia, light brown to brown, ovoid to obpyriform, 55 × 20 µm (Fig 8b).

Material examined – Italy, Province of Forlì-Cesena, Galeata, Strada San Zeno, on dead aerial stem of Lathyrus sp. (Fabaceae), 11 January 2014, E. Camporesi, IT 1640 (MFLU 21-0297, holotype), ex-type living culture = MFLUCC 21-0140.

Notes – Multi-locus phylogeny demonstrated Alternaria lathyri has a close relationship with A. muriformispora (MFLUCC 22-0073, MFLU 21-0309) and A. pseudoinfectoria (MFLUCC 21-0126, MFLU 21-0311) with 87% ML and 0.99 PP support (Fig. 3). Alternaria lathyri can be distinguished from A. muriformispora in having smaller (55 × 25 µm vs. 83 × 29 µm) darker, and beakless conidia, with less conidial septation. The species also differs from A. pseudoinfectoria in having larger (55 × 25 µm vs. 33 × 19 µm), ovoid to obpyriform, dark grey-brown and beakless conidia, while A. pseudoinfectoria has subglobose to obclavate, or obpyriform, light brown conidia that usually formed long secondary conidiophores[68]. A RPB2 nucleotide pairwise comparison showed that A. lathyri differs from A. muriformispora in 9/570 bp (1.6% differences, no gap), and differs from A. pseudoinfectoria in 12/550 bp (2.2% difference, no gap). In Alt-a1, A. lathyri differs from A. muriformispora in 8/474 bp (1.7% differences, no gap) and differs from A. pseudoinfectoria in 8/480 bp (1.6% difference, no gap). In this study, A. lathyri is described herein as a new species occurring on the same host genus with A. arctoseptata.

Alternaria macilenta J.F. Li, Camporesi, Phookamsak & Bhat, sp. nov.

Index Fungorum number: IF 558441; Facesoffungi number: FoF 12659; Fig. 18

Etymology: Referring to its slender-shaped conidia.
Holotype: MFLU 21-0305

Saprobic on dead standing stem of Scabiosa sp. (Caprifoliaceae). Sexual morph Undetermined. Asexual morph Mycelium superficial on the substrate, composed of dark hyphae. Conidiophores 70–100 × 10–12 µm (± 85 × 11 µm, n = 30), macronematous, brown, straight or flexuous, cylindrical, septeate, unbranched, smooth, thick-walled, aggregated, arising from a stomatic base. Conidiogenous cells 20–25 × 8–10 µm (± 23.5 × 9 µm, n = 20), polytretic, integrated, terminal, determinate or percurrent, cylindrical, subhyaline to light brown, smooth, thin-walled, apically rounded or doliiform, with 1–3 conidiogenous loci. Conidia 20–50 × 8–12 µm (± 35 × 9.5 µm, n = 30) acrogenous, solitary or borne in chains with at least 2 conidia, light brown to brown, subcylindrical to obclavate, 0–4-distoseptate, smooth- to rough-walled, with wrinkle-like, thick-walled. Conidial secession schizolytic.

Culture characteristics – Conidia germinating on PDA within 14 h and germ tubes produced from both end cells. Colonies growing on PDA, cottony, brown to dark brown, reaching 5 cm in 10 d at 25 ºC, mycelium superficial, effuse, radially striate, with irregular edge, composed of septeate, branched, smooth, thin-walled, light brown hyphae, 2–5 µm diam; conidia formed in vitro within 30 d, borne in chains with at least 2 conidia, light brown to brown, subcylindrical to obclavate, 35 × 10 µm (Fig. 8d).

Material examined – Italy, Province of Forli-Cesena, Dovadola, on dead standing stem of Scabiosa sp., 25 August 2015, E. Camporesi, IT 2076 (MFLU 21-0305, holotype), ex-type living culture = MFLUCC 21-0138.

Notes – Multi-locus phylogeny (Fig. 3) demonstrated that Alternaria macilenta clustered with A. oblongoellipsoidea and A. phragmiticola with 80% ML and 0.99 PP support. Alternaria macilenta can be easily distinguished from A. oblongoellipsoidea and A. phragmiticola in having subcylindrical to obclavate, beakless, pale brown to light greyish brown, 0–4-distoseptate conidia, while lacking longitudinal septum and conidiophores aggregated at the base. A RPB2 nucleotide pairwise comparison showed that A. macilenta differs from A. oblongoellipsoidea 10/560 bp (1.8% difference, no gap) and differs from A. phragmiticola in 9/560 bp (1.6% difference, no gap). In Alt-a1, A. macilenta differs from A. oblongoellipsoidea in 10/470 bp (2.1% difference, no gap) and differs from A. phragmiticola in 8/492 bp (1.6% difference, no gap).

Alternaria macroconidia J.F. Li, Camporesi, Phookamsak & Jeewon, sp. nov.

Index Fungorum number: IF 558442; Facesoffungi number: FoF 12660; Fig. 19

Fig. 18  Alternaria macilenta (MFLU 21-0305, holotype). (a) Colonies on dead stem of Scabiosa sp. (b)–(g) Conidiophores. (h)–(l) Conidia. Scale bars: (a) = 150 µm, (b)–(l) = 20 µm.
**Etymology:** Named after its large conidia (up to 60 µm).

**Holotype:** MFLU 21-0301

**Saprobic** on branches of *Spartium junceum* L. (Fabaceae).

**Sexual morph** Undetermined. **Asexual morph** Mycelium superficial on host substrate, composed of septate, branched, smooth, thin-walled, white to light brown hyphae. **Conidiophores** 46–80 × 7–12 µm (μ = 55 × 8.2 µm, n = 100), mononematous, macronematous, straight or flexuous, cylindrical, brown to dark brown, septate, unbranched, smooth, thick-walled, arising from an aggregated base. **Conidiogenous cells** (6–)7–9(–10.5) × (7.5–)8–12 (–17) µm (μ = 7.9 × 9.6 µm, n = 100), mono- to polytretic, integrated, terminal, determinate or percurrent, cylindrical, subhyaline to pale brown, smooth, thin-walled, apically doliiform with 1 conidiogenous locus. **Conidia** (68.5–)77–89(–95.5) × (20–)26–28(–30.5) µm (μ = 75.6 × 27.7 µm, n = 100) acrogenous, solitary or borne in chain with at least 2 conidia, dry, curved, obclavate to ovoid, or obpyriform, with short to long, narrow, pale to greenish brown, aseptate, unbranched beak, olivaceous brown to golden brown or brown, 3–5 transversely disto- or euseptate, with 1 longitudinal or oblique or Y-shaped septum in some transverse divisions, usually rostrate apex when mature, minutely verruculose, thin-walled. **Conidial secession** schizolytic.

Culture characteristics – Conidia germinating on PDA within 12 h and germ tubes produced from lateral cells. Colonies growing on PDA, cottony, white to light brown, reaching 5 cm in 7 d at 25 ºC, mycelium superficial, effuse, radially striate, with regular edge, white to light brown hyphae. Conidia sporulated on OA media within 15 d, muriform, ovoid to obclavate, with aseptate, short, paler brown, acicular apical rostrum, light

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**Fig. 19** *Alternaria* macroconidia (MFLU 21-0301, holotype). (a) Specimen examined of *Spartium junceum* (Fabaceae). (b) Colonies on dead aerial branch of *Spartium junceum*. (c)–(j) Conidiophores bearing conidiogenous cells. (k)–(n) Immature conidia. (o)–(s) Mature conidia. (t) Germinated conidium. Scale bars: (a) = 0.5 cm, (b) = 1000 µm, (c)–(t) = 20 µm.
brown to brown, 2–4 transverse eusepta, 0–1 longitudinal septum in transverse division, borne in chains, smooth, laterally formed branched or unbranched conidiophores with 1–2 conidigenous loci. Colonies growing on PCA, pale white to light brown colored, cottony, fluffy, reaching 5 cm within 7 d at 25 °C, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, subhyaline hyphae, 2–5 μm diam; conidia not formed in vitro within 60 d.

Material examined – Italy, Province of Forli-Cesena, Santa Sofia, Collina di Pondo, on dead aerial branches of *Spathium junceum* (Fabaceae), 6 March 2014, E. Camporesi, IT1756 (MFLU 21-0301, holotype), ex-type living culture = MFLUCC 21-0134.

Notes – *Alternaria macroconidia* resembles *A. phragmiticola* in having obclavate conidia, with a short to long beak or rostrate apex when mature. However, *A. macroconidia* differs from *A. phragmiticola* in having slightly larger (75.6 × 27.7 μm vs. 70 × 25 μm), olivaceous brown to golden brown or brown conidia, rather monotetric conidigenous cells and shorter (55.8 × 2 μm vs. 90 × 6.5 μm), aggregated conidiophores at the base. In multi-locus phylogenetic analyses, *A. macroconidia* formed a separate clade and is sister to *A. salicicola* (MFLU 22-0072, MFLU 21-0320) with 61% ML, 0.95 PP support (Fig. 3).

Conidiogenous cells cylindrical, septate, minutely verruculose, thick-walled, with 2–4 apical conidiogenous loci. Colonies growing on PCA, pale greenish-brown, smooth, thin-walled, subhyaline, with 2–4 apical conidiogenous loci. Conidial secession schizolytic.

Culture characteristics – Conidia germinating on PDA within 14 h and germ tubes produced from all cells. Colonies growing on PDA, cottony, white to grey, reaching 5 cm in 10 d at 25 °C, mycelium superficial, effuse, radially striate, with irregular edge, yellow white to grey hyphae; conidia not formed in vitro within 60 d. Colonies growing on PCA, light brown to brown colored, hairy, fluffy, reaching 5 cm within 7 d at 25 °C, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, subhyaline to light brown hyphae, 2–5 μm diam; conidia formed in vitro within 30 d, borne in chains with at least 2 conidia, light brown, ovoid to obpyriform or obturbinate, 20 × 10 μm (Fig. 8n).

Material examined – Thailand, Chiang Rai Province, Mae Fah Luang University, on rotted peel of *Citrus lanatus* (Cucurbitaceae), 13 August 2016, J.F. Li, H-14 (MFLU 21-0295, holotype), ex-type living culture = MFLUCC 21-0127.

Notes – *Alternaria minimispora* resembles *A. breviconidiophora* due to small, subglobose to ovoid, dark brown conidia, with swollen knots conidiophores and paler brown conidigenous cells. However, *A. minimispora* differs from *A. breviconidiophora* in having solitary, longer (129 × 10 μm vs. 45 × 9 μm) conidiophores, lacking a stomatic base and conidia that are rather rostrate than *A. breviconidiophora*.

In multi-locus phylogenetic analyses, *A. minimispora* formed a sister clade with *A. rostroconidia* (64% ML, 0.99 PP; Fig. 3) and distant from *A. breviconidiophora*. *Alternaria minimispora* can be distinguished from *A. rostroconidia* in having smaller (20 × 9.5 μm vs. 66 × 22 μm), subglobose to ovoid, beakless conidia that conidia are rather short beak in *A. rostroconidia*.[66] A RPB2 nucleotide pairwise comparison showed that *A. minimispora* differs from *A. breviconidiophora* in 40/505 bp (7.9% difference, no gap) and differs from *A. rostroconidia* in 19/505 bp (3.8% difference, no gap). In GAPDH, *A. minimispora* differs from *A. breviconidiophora* in 12/550 bp (2.1% difference, no gap) and differs from *A. rostroconidia* in 10/545 bp (1.8% difference, no gap). In comparison, the *Alt-a1* nucleotide shows that *A. minimispora* differs from *A. breviconidiophora* in 14/474 bp (3% difference, no gap) and differs from *A. rostroconidia* in 8/474 bp (1.7% difference, no gap).

*Alternaria oblongoellipsoidea* J.F. Li, Camporesi, Phookamsak & Bhat, sp. nov.

Index Fungorum number: IF 558444; Facesoffungi number: FoF 12661; Fig. 20

Etymology: Named after its oblong to ellipsoidal conidia.

Holotype: MFLU 21-0295

Saprobic on rotten peel of *Citrus lanatus* (Thumb.) Matsum et Nakai (Cucurbitaceae). *Sexual morph* Undetermined. *Asexual morph* Mycelium superficial on the substrate, with dark hyphae. *Conidiophores* 65–175 × 8–13 μm (μ = 129 × 10 μm, n = 30), macronematous, mononematous, straight or flexuous, cylindrical, dark yellowish-brown, septate, unbranched, smooth, thick-walled. *Conidiogenous cells* 5–10 × 4–6 μm (μ = 8.5 × 5 μm, n = 20), mono- to polytretic, integrated, terminal, determinate or percurrent, cylindrical, doliiform or coronal-shaped, light brown to brown, smooth, thin-walled, with 1–3 apical conidigenous loci. *Conidia* 13–25 × 8–11 μm (μ = 20 × 9.5 μm, n = 30) acrogenous, borne in chain with 2–3 conidia, straight, curved, subglobsose to ovoid, sometimes obpyriform or obeturbinate, beakless, dark brown, 2–4 transversely euseptate, with 1–2 longitudinal or oblique or Y-shaped septa in some transverse divisions, smooth, thick-walled, formed apically secondary conidiophores with 1–2 conidigenous loci. *Conidial secession* schizolytic.

Notes – *Alternaria minimispora* resembles *A. breviconidiophora* due to small, subglobose to ovoid, dark brown conidia, with swollen knots conidiophores and paler brown conidigenous cells. However, *A. minimispora* differs from *A. breviconidiophora* in 14/474 bp (3% difference, no gap) and differs from *A. rostroconidia* in 19/505 bp (3.8% difference, no gap). In GAPDH, *A. minimispora* differs from *A. breviconidiophora* in 12/550 bp (2.1% difference, no gap) and differs from *A. rostroconidia* in 10/545 bp (1.8% difference, no gap). In comparison, the *Alt-a1* nucleotide shows that *A. minimispora* differs from *A. breviconidiophora* in 14/474 bp (3% difference, no gap) and differs from *A. rostroconidia* in 8/474 bp (1.7% difference, no gap).

*Alternaria oblongoellipsoidea* J.F. Li, Camporesi, Phookamsak & Bhat, sp. nov.

Index Fungorum number: IF 558444; Facesoffungi number: FoF 12662; Fig. 21

Etymology: Referring to its oblong to ellipsoidal conidia.

Holotype: MFLU 21-0310

Saprobic on dead stem of *Cichorium intybus* L. (Asteraceae). *Sexual morph* Undetermined. *Asexual morph* Mycelium superficial on the substrate, composed of septate, branched, smooth, thin-walled, brown to dark brown hyphae. *Conidiophores* 80–120 × 6.5–11 μm (μ = 96 × 9.5 μm, n = 30), macronematous, light brown to brown, straight or flexuous, cylindrical, septate, minutely verruculose, thick-walled, with several aggregated at the base. *Conidiogenous cells* 3.5–6 × 3–6 μm (μ = 4.3 × 3.5 μm, n = 20), polytretic, swollen, integrated, terminal, determinate or percurrent, doliiform, subhyaline to pale greenish-brown, smooth, thin-walled, with 2–4 apical conidigenous loci. *Conidia* 35–60 × 18–25 μm (μ = 52 × 22 μm, n = 30) acrogenous, borne in chain with at least 2 conidia, straight or curved, oblong to ellipsoidal, or ovoid, with short, narrow, septicate beak, pale brown to brown, sectored, 4–7
transverse eusepta, with 1–2 longitudinal, or oblique or Y-shaped septa in transverse divisions, smooth to minutely verrucose, thick-walled. Conidiom secession schizolytic.

Culture characteristics – Conidia germinating on PDA within 14 h and germ tubes produced from all cells. Colonies growing on PDA, hairy or cottony, brown to dark brown, reaching 5 cm in 7 d at 25 ºC, mycelium superficial, effuse, radially striate, with irregular edge, dark brown hyphae; conidia not formed in vitro within 60 d. Colonies growing on PCA, light brown to brown colored, hairy, fluffy, reaching 5 cm within 7 d at 25 ºC, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, light brown hyphae, 2–5 µm diam; conidia formed in vitro within 30 d, born in chains with at least 2 conidia, light brown, obclavate to obpyriform, 50 × 20 µm (Fig. 8c).

Material examined – Italy, Province of Forlì-Cesena, Meldola, on dead aerial stem of Cichorium intybus (Asteraceae), 8 September 2014, E. Camporesi, IT2102 (MFLU 21-0310, holotype), ex-type living culture = MFLUCC 22-0074.

Notes – In multi-locus phylogenetic analyses, *Alternaria oblongoellipsoidea* is sister to *A. phragmiticola* with 80% ML, 0.99 PP support and also clustered with *A. macilenta*. A RPB2 nucleotide pairwise comparison showed that *A. oblongoellipsoidea* differs from *A. phragmiticola* in 10/560 bp (1.8% difference, no gap) and also differs from *A. phragmiticola* in 8/492 bp (1.6% difference, no gap) based on an Alt-a1 nucleotide pairwise comparison. *Alternaria oblongoellipsoidea* can be distinguished from *A. phragmiticola* in having smaller (52 × 22 µm vs. 70 × 25 µm) oblong to ellipsoidal conidia, with 4–7 transverse eusepta, and 1–2 longitudinal or oblique or Y-shaped septa in transverse divisions. While *A. phragmiticola* has obclavate to obpyriform conidia, with longer rostrate beak and less conidial septation than *A. oblongoellipsoidea*.

*Alternaria orobanches* J.F. Li, Camporesi, Phookamsak & Jeewon, sp. nov.

Index Fungorum number: IF 558445; Facesoffungi number: FoF 12663; Fig. 22
Etymology: Named after its host occurrence on ‘genus Orobanche’

Holotype: MFLU 21-0303
Saprobic on dead hanging stem of Orobanche sp. (Orobanchaceae). Sexual morph Undetermined. Asexual morph Mycelium superficial on the host substrate, with dark hyphae. Conidiophores 50–90 × 15–18 µm ( = 75 × 17 µm, n = 30), macronematous, straight or flexuous, cylindrical, yellowish brown to pale green-brown, indistinct septate, unbranched, smooth to minutely verrucose, thick-walled, aggregated, arising from stromatic base. Conidiogenous cells 13–18 × 10–12 µm ( = 15 × 11 µm, n = 20), mono- to polytretic, integrated, terminal, determinate or percurrent, subglobose to doliiform, subhyaline to pale brown, minutely verrucose, thin-walled, with 2 apical conidiogenous loci. Conidia 20–50 × 10–20 µm ( = 38 × 16 µm, n = 30) acrogenous, solitary or borne in chain with 2 conidia, straight or curved, obclavate to ovoid, sometimes rostrate apex or formed short, narrow, subhyaline, septate, unbranched beak, pale yellowish-brown to pale brown, 3–6 transverse septa, with 0–1 longitudinal, or oblique or Y-shaped septum in some transverse divisions, slightly constricted at the central septum, minutely verrucose, thick-walled. Conidial secession schizolytic.

Culture characteristics – Conidia germinating on PDA within 12 h and germ tubes produced from lateral cells. Colonies growing on PDA, hairy fluffy, pale white to white, reaching 5 cm in 14 d at 25 ºC, mycelium superficial, effuse, radially striae, with irregular edge, white hyphae; conidia not formed in vitro within 60 d. Colonies growing on PCA, white to light brown colored, hairy, fluffy, reaching 5 cm within 7 d at 25 ºC, mycelium superficial, effuse, partly immersed on the media, radially striae, with irregular edge, composed of septate, branched, smooth, thin-walled, light brown hyphae, 2–5 µm diam; conidia not formed in vitro within 60 d.

Material examined – Italy, Province of Forlì-Cesena, Predappio, Monte Mirabello, on dead hanging stem of Orobanche sp. (Orobanchaceae), 16 July 2014, E. Camporesi, IT1997 (MFLU 21-0303, holotype), ex-type living culture, MFLUCC 21-0137.

Notes – Alternaria orobanches resembles A. arctoseptata in having short, colorless conidiophores arising from a stromatic base. However, A. orobanches differs from A. arctoseptata due to its shorter, wider and less septate conidiophores (75 × 17 µm, 1–3-septate vs. 82 × 9 µm, 2–4-septate). Conidia of A. orobanches are obclavate to ovoid, pale yellowish-brown to
pale brown while *A. arctoseptata* has subglobose to ovoid or pyriform, yellowish-brown to dark brown conidia. A GAPDH nucleotide pairwise comparison showed that *A. orobanches* differs from *A. arctoseptata* in 10/490 bp (2% difference, no gap) and also differs from *A. arctoseptata* in 13/480 bp (2.7% difference, no gap) based on Alt-a1 nucleotide pairwise comparison. Multi-locus phylogeny also supports the distinctiveness of these two species. *Alternaria orobanches* constitutes an independent lineage basal to other species in sect. *Alternaria* with high support (100% ML, 1.00 PP; Fig. 3).

### Alternaria phragmiticola J.F. Li, Camporesi, Bhat & Jeewon, sp. nov.

*Index Fungorum number*: IF 558446; *Facesoffungi number*: FoF 12664; *Fig. 23*

**Etymology**: Named after the host genus *Phragmites*, of which the species was collected.

**Holotype**: MFLU 21-0316

*Saprobic* on stem of *Phragmites* sp. (*Poaceae*). **Sexual morph** Undetermined. **Asexual morph** Mycelium superficial on the substrate, with dark hyphae. *Conidiophores* 50–108 × 4–8 µm (± 90 × 6.5 µm, n = 30), macronematous, straight or flexuous, cylindrical, dark brown, septate, smooth, thick-walled. *Conidiogenous cells* 6–8 × 8–10 µm (± 6.5 × 9.5 µm, n = 20), polytretic, integrated, terminal, determinate or percurrent, cylindrical, pale brown, smooth, thin-walled, apically doliiform, with 1–3 conidiogenous loci. *Conidia* 42–88 × 21–30 µm (± 70 × 25 µm, n = 30) acrogenous, borne in chain with at least 2 conidia, straight to curved, obclavate to obpyriform, with short, narrow, rostrate paler brown, septate apex, pale yellowish-brown to brown, 3–4 transverse disto- or eusepta, with 1–2 longitudinal or oblique or Y-shaped septa in some transverse divisions, smooth to verruculose, thick-walled. **Conidial secession** schizolytic.

**Culture characteristics** – Conidia germinating on PDA within 14 h and germ tubes produced from lateral cells. Colonies growing on PDA, hairy or cottony, brown to dark brown, reaching 5 mm in 20 d at 25 ºC, mycelium superficial, effuse, radially striate, with irregular edge, yellow-white to grey hyphae; conidia not formed in vitro within 60 d. Colonies growing on PCA, light brown to brown colored, hairy, fluffy, reaching 5 cm within 7 d at 25 ºC, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, light brown hyphae, 2–5 µm diam; conidia formed in vitro within 60 d, borne in chains with at least 2 conidia, brown to dark brown, verruculose, obclavate to obpyriform, 70 × 25 µm (Fig. 8m).

**Material examined** – Italy, Province of Forlì-Cesena, Meldola, San Colombano, on dead aerial stem of *Phragmites* sp. (*Poaceae*), 28 September 2015, E. Camporesi, IT2630 (MFLU 21-
0316, holotype), ex-type living culture, MFLUCC 21-0125.

Notes – Multi-locus phylogenetic analyses demonstrated that three strains of *Alternaria phragmiticola* formed a robust clade (100% ML, 1.00 PP; Fig. 3) and clustered with *A. macilenta* and *A. oblongoellipsoidea*. These three species formed a well-resolved clade together with significant support (84% ML, 1.00 PP; Fig. 3). *Alternaria phragmiticola* can be distinguished from *A. macilenta* and *A. oblongoellipsoidea* in having solitary, dark brown, conidiophores and obclavate to obpyriform, pale yellowish-brown to brown, conidia with a rostrate apex, while *A. macilenta* has brown, aggregated conidiophores, arising from a stomatic base and subcylindrical to obclavate, beakless, pale brown to light greyish brown, distoseptate conidia. *Alternaria oblongoellipsoidea* has more twisted conidiophores at the apex and oblong to ellipsoidal conidia, with more conidial eusepta.

*Alternaria salicicola* J.F. Li, Bulgakov & Phookamsak, sp. nov.

Index Fungorum number: IF 558447; Facesoffungi number: FoF 12665; Fig. 24

Etymology: Named after the host genus *Salix*, of which the species was found.

Holotype: MFLU 21-0320

Saprobic on dead twig of *Salix alba* L. (Salicaceae). Sexual morph Undetermined. Asexual morph *Mycelium* superficial on

Fig. 23  *Alternaria phragmiticola* (MFLU 21-0316, holotype). (a) Colonies on dead stem *Phragmites* sp. (b)–(g) Conidiophores bearing conidiogenous cells. (h)–(o) Conidia. Scale bars: (a) = 200 µm, (b)–(o) = 20 µm.
host substrate, with dark hyphae. **Conidiophores** 110–150 \( \times \) 10–15 \( \mu \)m (\( \bar{x} = 135 \times 13 \ \mu \)m, \( n = 30 \)), macronematous, straight or flexuous, cylindrical, light brown to brown, septate, branched at the base, smooth to verruculose, thick-walled. **Conidiogenous cells** (5–)10–13 \( \times \) 8–10(–14) \( \mu \)m (\( \bar{x} = 12.3 \times 8.5 \ \mu \)m, \( n = 20 \)), polytretic, integrated, terminal, determinate or percurrent, cylindrical, subhyaline to paler light brown, smooth, thick-walled, apically doliiform, with 1–3 conidiogenous loci. **Conidia** 10–50 \( \times \) 12–38 \( \mu \)m (\( \bar{x} = 45 \times 32 \ \mu \)m, \( n = 30 \)) acrogenous, borne in chain with at least 2 conidia, straight or curved, subglobose to obclavate or obpyriform, with short to long, narrow, acicular to doliiform, septate beak when mature, light yellowish-brown to light brown, sectored of 1–6 transverse disto- or eusepta, with 1–3 longitudinal or oblique or Y-shaped distosepta, smooth to verruculose, thick-walled. **Conidial secession** schizolytic.

Culture characteristics – Conidia germinating on PDA within 14 h and germ tubes produced from lateral cells. Colonies growing on PDA, hairy or cottony, brown to dark brown, reaching 5 cm in 10 d at 25 ºC, mycelium superficial, effuse, radially striate, with irregular edge, light brown to brown hyphae; conidia not sporulated *in vitro* within 60 d. Colonies growing on PCA, white to light brown colored, hairy, fluffy, reaching 5 cm within 7 d at 25 ºC, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, hyaline hyphae, 2–5 \( \mu \)m diam; conidia formed *in vitro* within 60 d, borne in chains with at least 2 conidia, brown to dark brown, with secondary conidiophores, acicular to doliiform, 45 \( \times \) 30 \( \mu \)m (Fig. 8i).

Material examined – Russia, Rostov Region, Krasnosulinsky District, trees near Kudryuchya River, on dead twig of *Salix alba* (Salicaceae), 18 June 2015; T.S. Bulgakov, T-504 (MFLU 21-0320, **holotype**), ex-type living culture = MFLUCC 22-0072.

Notes – **Alternaria salicicola** is the only species collected from Russia in this study. In multi-locus phylogenetic analyses, two strains of *A. salicicola* formed a robust clade (100% ML, 1.00 PP; **Fig. 3**) sister to *A. macroconidia*. 

*Fig. 24* *Alternaria salicicola* (MFLU 21-0320, holotype). (a) Colonies on dead twig of *Salix alba*. (b)–(e) Conidiophores bearing conidiogenous cells. (f)–(p) Conidia. (q) Germinated conidium. Scale bars: (a) = 150 \( \mu \)m, (b)–(q) = 20 \( \mu \)m.
**Section Infectoriae** Woudenb. & Crous, Study in Mycology 75: 194 (2013)

Type species – *Alternaria infectoria* E.G. Simmons.

Notes – Sect. *Infectoriae* is one of the largest and most complicated sections in *Alternaria*, containing approximately 50 species[11,70,77,79]. Species in this section often form white or nearly white, floccose colonies on nutrient-rich media and sporulated several conidial chains on low sugar media as extensive three-dimensional branching patterns, and the conidia usually produce long secondary conidiophores[47,162]. Although, members of sect. *Inflectoriae* are commonly known as saprobes, many species such as *A. infectoria* and *A. triticina* have been reported as important pathogens on various plant hosts as well as human infections[14,15,47,79,81,163]. Additionally, species in this section produce secondary metabolites such as novaezelandins and infectopyrone, rather than mycotoxins, which are unique to this section[47,163]. The latest updated account of species number in sect. *Infectoriae* was carried out by Marin-Felix et al.[70, who introduced six new species mostly collected from herbivore dung and plant litter and Iturrieta - González et al.[79, who introduced three novel species causing human cutaneous infections. In this study, we introduce two other novel saprobic species collected from dead plants in Italy based on typical morphology and multi-locus phylogeny (Fig. 5).

*Alternaria arundinis* J.F. Li, Camporesi, Bhat & Jeewon, *sp. nov.*

**Index Fungorum number**: IF 558448; **Facesoffungi number**: FoF 12666; **Fig. 25**

**Etymology**: Named after the host genus *Arundo*, of which the species was collected.

**Holotype**: MFLU 21-0313

*Saprobic* on dead leaf of *Arundo donax* L. (Poaceae). **Sexual morph** Undetermined. **Asexual morph** Mycelium superficial on the host substrate, with dark hyphae. *Conidiophores* 50–85 × 5–8 µm ( = 70 × 7 µm, n = 30), macronematous, straight or flexuous, cylindrical, pale brown to pale yellowish-brown, septate, smooth, thick-walled, plexiform on base. *Conidiogenous cells* 5–6 × 3–4 µm ( = 5.5 µm × 3.6 µm, n = 20), polytretic, integrated, terminal, determinate or percurrent, cylindrical, subhyaline to pale brown or light brown, smooth, thin-walled, apically rounded to doliiform, with 1–2 conidiogenous loci. *Conidia* 20–45 × 15–25 µm ( = 38 × 20 µm, n = 30) acrogenous, solitary or borne in chain with at least 2 conidia, straight or curved, ellipsoidal to ovoid, or obclavate, pale greyish-brown to pale yellowish-brown, 3(–5) transverse eusepta, with 1–2 longitudinal or oblique or Y-shaped disto- or eusepta in some transverse divisions, becoming sectored, slightly constricted near some septa, beakless or with short, acicular rostrum, apically formed long secondary conidiophores, with 1–3 apical or lateral conidiogenous loci, smooth, thick-walled. *Conidial secession* schizolytic.

Culture characteristics – Conidia germinating on PDA within 14 h and germ tubes produced from all cells. Colonies growing on PDA, cottony, white to dark grey, reaching 5 cm in 10 d at 25 ºC, mycelium superficial, effuse, radially striate, with irregular

**Fig. 25** *Alternaria arundinis* (MFLU 21-0313, holotype). (a) Colonies on dead stem of *Arundo donax*. (b)–(f) Conidiophores bearing conidiogenous cells. (g)–(i) Conidia formed secondary conidiophores. (j)–(n) Conidia. Scale bars: (a) = 150 µm, (b)–(n) = 20 µm.
edge, white to grey hyphae; conidia not sporulated in vitro within 60 d. Colonies growing on PCA, light brown to brown, hairy, fluffy, reaching 5 cm within 7 d at 25 °C, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, brown hyphae, 2–5 \( \mu \)m diam; conidia formed in vitro within 60 d, borne in chains with at least 2 conidia, brown to dark brown, with long secondary conidiophores, ellipsoidal to ovoid, or obclavate, 40 × 20 \( \mu \)m (Fig. 8j).

Material examined – Italy, Province of Forlì-Cesena, Predappio, Rocca delle Caminate, on dead aerial leaf of *Arundo donax* (Poaceae), 17 November 2014, E. Camporesi, IT2250 (MFLU 21-0313, holotype), ex-type living culture, MFLUCC 21-0128.

Notes – *Alternaria arundinis* is typical of sect. *Infectoriae* in forming secondary conidiophores, with white to dark grey colonies on PDA. Multi-locus phylogeny demonstrated that *A. arundinis* formed an independent lineage sister to *A. incomplexa* with significant support (89% ML, 1.00 PP; Fig. 5) and clustered with *Alternaria* sp. (H1-4) and *A. anthropophila* (CBS 541.94). *Alternaria arundinis* resembles *A. incomplexa* in having ellipsoidal to ovoid, or obclavate conidia, with 3(–5) transverse eusepta, and 1–2 longitudinal septa. However, *A. arundinis* can be distinguished from *A. incomplexa* in having shorter conidiophores (70 × 7 \( \mu \)m vs. 100 × 4 \( \mu \)m) and slightly larger conidia (38 × 20 \( \mu \)m vs. 18–25 × 5–8 \( \mu \)m), which formed secondary conidiophores with several conidiogenous loci, while the conidia can raise up to 30–40 × 8–13 \( \mu \)m, with 5–8 transverse septa and 0–4 longitudinal septa in *A. incomplexa*\[164\]. *Alternaria arundinis* differs from *A. anthropophila* in having shorter conidiophores (50–85 × 5–8 \( \mu \)m vs. 26–120 × 4–7 \( \mu \)m) with laterally and apically geniculate conidiogenous loci, while conidiophores are apically geniculate in *A. anthropophila*, the conidia of *A. arundinis* are shorter and wider (20–45 × 15–25 \( \mu \)m vs. 11–63 × 6–11 \( \mu \)m), and more longitudinal or oblique eusepate (1–2 vs. 0–1)\[79\]. An ITS nucleotide pairwise comparison showed that *A. arundinis* differs from *A. incomplexa* in 8/546 bp (1.5% difference, no gap) and differs from *A. anthropophila* in 10/546 bp (1.8% difference, no gap). In GAPDH, *A. arundinis* differs from *A. incomplexa* in 9/521 bp (1.7% difference, no gap) and differs from *A. anthropophila* in 14/521 bp (2.7% difference, no gap). In ATPase, *A. arundinis* differs from *A. incomplexa* in 16/1000 bp (1.6% difference, no gap) and differs from *A. anthropophila* in 21/1000 bp (2.1% difference, no gap).

*Alternaria nodulariconidiophora* J.F. Li, Camporesi, Bhat & Jeewon, sp. nov.

Index Fungorum number: IF 558449; Facesoffungi number: FoF 12667; Figs 26 & 27

Etymology: Referring to the geniculate conidiophores.

Figure 26: *Alternaria nodulariconidiophora* (MFLU 21-0315, holotype). (a) Colonies on dead stem of *Heracleum sphondylium*. (b)–(e) Geniculate conidiophores bearing conidiogenous cells. (f)–(m) Conidia. (n) Germinated conidium. Scale bars: (a) = 100 \( \mu \)m, (b)–(n) = 20 \( \mu \)m.
Alternaria

**Fig. 27** Alternarianonodulariconidiophora(MFLUCC21-0131) sporulated on PDA. (a) Conidium formed a geniculate secondary conidiophore. (b), (c) Secondary conidiophores bearing conidia with three-dimensional branching patterns. Scale bars: (a)–(c) = 30 μm.

**Holotype:** MFLU 21-0315

*Saprobic* on stem of *Heracleum sphondylium* L. (Apiaceae). **Sexual morph** Undetermined. **Asexual morph** *Mycelium* superficial on host substrate, composed of brown to dark brown hyphae. *Conidiophores* (111–)119.5–183 × (12–)15–23 μm (̅x̅ = 175.2 × 18 μm, n = 30), macronematous, aggregated on a stromatic base, straight or flexuous, nodular, cylindrical, light brown to brown, septate, smooth and thick-walled. *Conidigenous cells* (5.5–)7–9 × 8.6–10 μm (̅x̅ = 8.6 × 9.5 μm, n = 20), holo- to polytretic, integrated, terminal, determinate or percurrent, cylindrical, subhyaline to pale brown, smooth, thin-walled, apically doliform, with 1–2 conidiogenous loci on bulge. *Conidia* (36–)45–54 × 19–37 μm (̅x̅ = 48 × 29 μm, n = 30) acrogenous, solitary or borne in chain with 2 conidia, dry, simple, straight, curved, subglobose to ovoid, or obturbinate to obpyriform, sometimes with short, narrow, aseptate beak, greyish brown, 3–(5) transversely euseptate, with 1 longitudinal or oblique septum in some transverse divisions, smooth or minutely verrucose, thin-walled. *Conidial secession* schizolytic.

Culture characteristics – *Conidia* germinating on PDA within 14 h and germ tubes produced from all cells. Colonies growing on PDA, hairy or cottony, brown to dark brown, reaching 5 cm in 5 d at 25 ºC, mycelium superficial, effuse, with irregular edge, brown to dark brown hyphae. Conidia sporulated in PDA after 60 d (Fig. 27), phragmosporous to muriform, subglobose to ellipsoidal, or fusiform, yellowish brown, 1–4 transversely euseptate, with 1–2 longitudinal or oblique or Y-shaped septa in some transverse divisions, constricted at the septa, verrucose, formed apically or laterally geniculated secondary conidiophores, with 1–2 apical or lateral conidiogenous loci, with long secondary conidiophores, obturbinate to obpyriform, 50 × 30 μm.

Material examined – Italy, Province of Forlì-Cesena, Meldola, Pandispino, on dead aerial stem of *Heracleum sphondylium* (Apiaceae), 10 October 2017, E. Camporesi, IT2625A (MFLU 21-0315, holotype), ex-type living culture, MFLUCC 21-0131.

Notes – In multi-locus phylogeny, *Alternaria nodulariconidiophora* formed a separate branch and clustered with *Alternaria* sp. (JS8-5) and *A. humuli* (CBS 119404) with significant support (87% ML, 1.00 PP; Fig. 5). *Alternaria nodulariconidiophora* is characterized by subglobose to ovoid, or obturbinate to obpyriform conidia, with a rostrate apex, geniculate conidiophores with swollen knots, arising from a stromatic base, and subhyaline to pale brown conidiogenous cells, with 1–2 conidiogenous loci on bulge. While *A. humuli* (CBS 119404) is characterized by subhyaline to arachnoid to loosely, woolly colonies, simple to moderately, branched primary conidiophores, with 1–3 geniculate conidiogenous loci, elliptical or ovoid, 5–8 transverse septa, with or without a longitudinal septum[163]. A ITS nucleotide pairwise comparison showed that *A. nodulariconidiophora* differs from *A. humuli* in 8/545 bp (1.5% difference, no gap). In GAPDH, the species differs from *A. humuli* in 8/521 bp (1.5% difference, no gap) and also differs from *A. humuli* in 11/900 bp (1.5% difference, no gap) in ATPase nucleotide pairwise comparison.


Type species – *Alternaria porri* (Ellis) Cif.

Notes – The section *Porri* is characterized by medium to large conidia with a simple or branched, filamentous long beak, which is the second largest section in *Alternaria*[11,22]. This section includes many important phytopathogens, such as *A. bataticola*, *A. porri*, *A. solani*, and *A. tomatophila*. In our survey, a new species *A. brevirostra* is described on dead grass from Italy based on both morphological and phylogenetic evidence (Fig. 6).

*Alternaria brevirostra* J.F. Li, Camporesi, Bhat & Jeewon, sp. nov.

**Index Fungorum number:** IF 558450; **Facesoffungi number:** FoF 12668; **Fig. 28**

**Etymology:** Referring to the short rostrate conidia in sect. *Porri*.

**Holotype:** MFLU 21-0312

*Saprobic* on stems of *Erysimum* sp. (Brassicaceae) and *Plantago* sp. (Plantaginaceae). **Sexual morph** Undetermined. **Asexual morph** *Mycelium* superficial on host substrate, composed of septate, branched, brown to dark brown, smooth, thin-walled hyphae. *Conidiophores* 55–72 × 10–15 μm (̅x̅ = 68 × 13 μm, n = 30), macronematous, aggregated at the base, flexuous, cylindrical, pale yellowish-brown to light brown, septate, unbranched, smooth, thick-walled. *Conidigenous cells* 5–6 × 7–7.5 μm (̅x̅ = 5.5 × 7.2 μm, n = 20), polytretic, integrated, terminal, determinate or percurrent, spatulate or dolabiform, subhyaline to pale brown, smooth, thin-walled. *Conidia* 75–84 × 15–20 μm (̅x̅ = 80 × 17 μm, n = 30) acrogenous, solitary or borne in chain with 1 or 2 conidia, straight or curved, subcylindrical to obclavate, with slightly long, narrow, colorless, acicular, aseptate rostrum, light yellowish-brown to brown, distoseptate, 5–7 transverse septa, with 1–2 longitudinal or oblique septa in some transverse divisions, smooth, thin-walled. *Conidial secession* schizolytic.

Culture characteristics – *Conidia* germinating on PDA within 14 h and germ tubes produced from all cells. Colonies growing on PDA, hairy or cottony, brown to dark brown, reaching 5 mm in 20 d at 25 ºC, mycelium superficial, effuse, with irregular edge, brown to dark brown hyphae. Conidia sporulated in vitro within 60 d. Colonies growing on PCA, pale white to white, cottony, fluffy, reaching 5 cm within 7 d at 25 ºC, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, hyaline hyphae, 2–5 μm diam; conidia not formed in *vitro* within 60 d.

Material examined – Italy, Province of Forlì-Cesena, Tontola di Predappio, on dead aerial stem of *Plantago* sp. (Plantaginaceae), 20 October 2014, E. Camporesi, IT2195 (MFLU 21-0312, holotype), ex-type living culture, MFLUCC 21-0129; *ibid.*, Forlì, Via Nenni, on dead aerial stem of *Erysimum* sp. (Brassicaceae), 28 July 2014, E. Camporesi, IT2028 (MFLU 21-
Alternaria brevirostra (MFLUCC 21-0312, holotype). (a) Colonies on dead stem of Plantago sp. (b)–(f) Conidiophores bearing conidiogenous cells. (g)–(k) Conidia. (l) Germinated conidium. Scale bars: (a) = 100 µm, (b)–(l) = 20 µm.

An ITS nucleotide pairwise comparison showed that Alternaria brevirostra differed from A. rostellata by 12/530 bp (2.2% difference, no gap), differed from A. nitrimali (CBS 109163) by 10/530 bp (1.9% difference, no gap), differed from A. pipionipisi (CBS 116115) by 10/530 bp (1.9% difference, no gap), differed from A. crassa (CBS 110.38) by 11/530 bp (2% difference, no gap), and differed from A. macrospora by 10/530 bp (1.9% difference, no gap). In GAPDH, the species differed from A. rostellata by 8/570 bp (1.4% difference, no gap), differed from A. nitrimali (CBS 109163) by 8/577 bp (1.4% difference, no gap), differed from A. pipionipisi (CBS 116115) by 9/577 bp (1.6% difference, no gap), differed from A. crassa (CBS 110.38) by 10/577 bp (1.7% difference, no gap), and differed from A. macrospora by 11/577 bp (1.9% difference, no gap). In TEF1-α, A. brevirostra differed from A. rostellata by 11/337 bp (3.2% difference, no gap), differed from A. nitrimali (CBS 109163) by 9/337 bp (2.7% difference, no gap), differed from A. pipionipisi (CBS 116115) by 8/337 bp (2.4% difference, no gap), differed from A. crassa (CBS 110.38) by 12/337 bp (3.6% difference, no gap), and differed from A. macrospora by 10/337 bp (3% difference, no gap). In RPB2 nucleotide pairwise comparison, A. brevirostra differed from A. rostellata by 14/539 bp (2.6% difference, no gap), differed from A. nitrimali (CBS 109163) by 14/539 bp (2.6% difference, no gap), differed from A. pipionipisi (CBS 116115) by 13/539 bp (2.4% difference, no gap), differed from A. crassa (CBS 110.38) by 16/539 bp (3% difference, no gap).
gap), and differed from *A. macrospora* (CBS 117228) by 11/539 bp (2% difference, no gap).


Type species – *Alternaria radicina* Meier, Drechsler & E.D. Eddy

Notes – Section *Radicina* is a small section in *Alternaria* comprising only eight phylogenetic species [4,70]. Most species in this section were reported as pathogens of Apiaceae [4,15,70]. In this study, we introduced a novel species, *A. phytolaccae* as a saprobe on *Phytolacca* sp. (Phytolaccaceae) which is reported from a different host family for the first time.

*Alternaria phytolaccae* J.F. Li, Camporesi, Bhat & Jeewon, *sp. nov.*

Index Fungorum number: IF 558451; Facesoffungi number: FoF 12669; Fig. 29

Etymology: Name after the host genus *Phytolacca*.

Holotype: MFLU 21-0314

Saprobic on dead standing stem of *Phytolacca* sp. (Phytolaccaceae). **Sexual morph** Undetermined. **Asexual morph** Mycelium superficial on host substrate, with dark hyphae. Conidiophores 160–200 × 8–11 µm ( = 174 × 9 µm, n = 30), macro-nematous, straight or flexuous, cylindrical, pale brown to dark greyish brown, geniculate, normally sympodial proliferations with several conidiogenous loci at the apex, branched, clumped, septate, smooth, thick-walled, arising from stomatic base. Conidiogenous cells 10–16 × 8–9 µm ( = 14 × 8.6

Fig. 29 *Alternaria phytolaccae* (MFLUCC 21-0314, holotype). (a) Colonies on dead standing stem of *Phytolacca* sp. (b)–(e) Conidiophores bearing conidiogenous cells, with 2–3 conidiogenous loci on side of cell. (f), (g) Immature conidia. (h)–(k) Conidia. Scale bars: (a) = 150 µm, (b)–(k) = 20 µm.

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μm, n = 20), polytretic, integrated, terminal, determinate or percurrent, dolabrinform to spathulate, subhyaline, smooth, thin-walled, apically doliform, with 2–3 conidiogenous loci on side of cell. Conidia 30–65 × 20–30 μm (x = 45 × 24 μm, n = 30) acrogenous, solitary or borne in chain with 2 conidia, clustered or clumps, curved, ellipsoidial to obpyriform, with acute apex, beakless, sometimes with short, narrow, septate beak, pale yellowish-brown to dark greyish-brown, 3–7 transverse eusepta, with 1–2 longitudinal or oblique or Y-shape septa in some transverse divisions, becoming sectored, slightly constricted at the septa, smooth to minutely verrucose, thick-walled. Conidial secession schizolytic.

Culture characteristics – Conidia germinating on PDA within 14 h and germ tubes produced from all colonies. Colonies growing on PDA, cottony, brown to dark brown, reaching 5 cm in 7 d at 25 ºC, mycelium superficial, effuse, radially striate, with irregular edge, grey to dark grey hyphae; conidia not sporulated in vitro within 60 d. Colonies growing on PCA, light brown, hairy, fluffy, reaching 5 cm within 7 d at 25 ºC, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, hyaline hyphae, 2–5 μm diam; conidia formed in vitro within 60 days, borne in chains with at least 1–2 conidia, light brown, beakless, obpyriform, 37 × 20 μm (Fig. 8k).

Material examined – Italy, Province of Forlì-Cesena, Forlì, San Lorenzo in Noceto, on dead standing stem of Phytolaca sp. (Phytolaccaceae), 4 December 2014, E. Camporesi, IT2279 (MFLU 21-0314, holotype), ex-type living culture, MFLUCC 21-0135.

Notes – Alternaria phyllocladis morphologically corresponds with sect. Radicina in having branched, clumped, geniculate, sympodial proliferations conidiophores with several conidiogenous loci at the beakless apex. In multi-locus phylogenetic analyses (Fig. 7), A. phyllocladis formed a separate branch and clustered with A. petroselini, A. selini and A. vulgaris in section Radicina with 60% ML and 0.97 PP support. An ITS nucleotide pairwise comparison showed that A. phyllocladis differs from A. petroselini in 8/520 bp (1.5% difference, no gap), differs from A. selini in 8/520 bp (1.5% difference, no gap) and differs from A. vulgaris 9/520 bp (1.7% difference, no gap). In GAPDH, A. phyllocladis differs from A. selini in 9/567 bp (1.6% difference, no gap) and differs from A. vulgaris in 9/567 bp (1.6% difference, no gap).

DISCUSSION

Diversity of Alternaria species

Alternaria species have been reported on a wide range of monocotyledonous and dicotyledonous plants worldwide[1–15,16,19,22,38,70]. In this survey carried out in China, Italy, Russia and Thailand, 65 Alternaria samples were recovered from different plant species. Morphological examinations of specimens revealed that there were 18 species that could not be ascribed to any known species within the different Alternaria sections, viz. sects. Alternaria, Infectoriae, Porri and Radicina. Given that there were some noticeable differences in their morphs and with support from phylogeny, new species are established herein following the recommendations as outlined by Jeewon & Hyde[134].

Our study also reveals other taxonomic anomalies. We note that A. oblongoellipsoidea (MFLUCC 22-0074 and MFLU 21-0310) and A. ellipsoidialis (MFLUCC 21-0132, MFLU 21-0307A and MFLU 21-0307B) share meander conidiophores apex with confidential hollow conidiogenous loci, which occur rarely in sect. Alternaria. However, these two species can be differentiated based on their morphs: A. oblongoellipsoidea differs from A. ellipsoidialis in having rather common and short conidiophores (96 × 9.5 μm vs. 145 × 6.5 μm), with rather polytretic, swollen, doliform conidiogenous cells. Our multi-locus phylogenetic analyses (Fig. 3) also support their distinction and hence A. oblongoellipsoidea and A. ellipsoidialis should be considered as different species in sect. Alternaria.

Interestingly, Alternaria arctoseptata and A. lathyri were isolated from same host genus Lathyrus (Fabaceae). However, A. lathyri morphologically differs from A. arctoseptata in having darker brown, solitary, astomatic base conidiophores with less swollen knots, and dark brown conidia. Phylogenetic analyses with a combined seven gene loci (ITS, LSU, SSU, TEF1α, RPB2, GAPDH and Alt-a1) positions A. lathyri in a subclade distinct from A. arctoseptata. Furthermore, we also note that A. orobanches (MFLUCC 21-0137 and MFLU 21-0303) formed a single lineage basal to sect. Alternaria. However, A. orobanches shares similar morphological characteristics to others in sect. Alternaria (e.g., phragmosporous to umiform small-spored conidia, conidiophores with monotretic or polytretic conidiogenous loci at apex), and hence A. orobanches should be considered in sect. Alternaria based on morphology and phylogeny.

This study also reveals new host records for Alternaria doliconidium and diverse hosts species for A. alternata. While A. doliconidium has been collected from Rosa sp. in Italy[66], we discovered A. doliconidium from Reseda sp. (Resedaceae) in China, which is the first record of both host species and location for this species. Another important and novel finding herein that we observed and describe for the first time, is the cultural characteristics of A. doliconidium which successfully sporulated on OA medium within 30 d (with conidia borne in chains, oblong to subglobose, verruculose to verrucose with short, branched or unbranched, asepitate apical beak, apical or lateral secondary conidiophores were formed). Moreover, in this study, 45 new collections of A. alternata were isolated from diverse plant hosts (Table 5) in China, Italy and Thailand. These 45 new collections were compared with other A. alternata strains (mainly from CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands) and our phylogenetic analyses, revealed our A. alternata complex could be phylogenetically arranged in several internal subclades (Fig. 4). For example, strains HWP-01, IT2144, IT2145, IT3598, and IT3651 formed the internal subclade A with strains CBS 965.95 and CBS 966.95 (pathogen and saprobe); saprobic strains H-71, IT2143, and IT3556 formed the internal subclade with strain CBS 130254 (isolated from human sputum in India), and CBS 911.97 (isolated from Arthemisia brevifolia (Asteraceae) in India) and clustered with CBS 130262, CBS 130265 (isolated from human sputum in India) and CBS 121492 (isolated from Cucumis melo (Cucurbitaceae) in China) (pathogen and saprobe). These results also indicate that A. alternata and A. doliconidium occur on a wide range of hosts as either pathogens or saprobes.

Our phylogeny also reveals higher species diversity from one particular host. For example, A. alternata have been recovered from diverse plant hosts (Fig. 4)[67] while A. doliconidium colonizes Rosa sp. and Reseda sp.[66]. It is also worth pointing
out that our study here also reveals an unexpected higher diversity of Alternaria species, with over 30% (20 out of 65 specimens) from diverse host plants which are new to science and more than one species are associated with one host. This finding has important implications on nomenclature of Alternaria species and it would be erroneous to name species based on host without any additional information, especially for specioclé genera, a phenomenon already reported for Pestalotiopsis-like species\textsuperscript{[166]}. 

**Phylogenetic concepts of Alternaria**

DNA sequence data is very important in Alternaria taxonomy. Characters of conidia in some sections are not informative, as conidia are mostly dictyosporous in sects. Alternaria and Japonicae; some are mostly phragmosporous, such as in sects. Alternantherae and Nimbya. Species in sects. Alternantherae, Dianthicola and Porri have long apical narrow beaks or secondary conidiophores and these characteristics are absent in sects. Chalastospora, Gyposophiae and Ulocladium, while dictyosporous and phragmosporous can be found in sects. Infectoriae and Phragmosporae\textsuperscript{[18,19,38]}. In our phylogenetic analyses (Fig. 3), the topology of the phylogenetic tree for the Alternaria complex corresponds with previous ones. However, many sections that even share common morphs are usually phylogenetically distinct based on DNA sequence analyses\textsuperscript{[15,25,26]}. In addition, it is also noted that single gene analyses show that the ITS, RPB2 and Alt-a1 genes could resolve the taxonomy of most Alternaria sections, while TEF1-α and GAPDH genes could be informative at the species level but not for section levels.

It is interesting to note that RPB2 regions do provide reliable nucleotide differences for species comparison. However, this region should be analyzed and used properly before any taxonomic assumption is made. In our single gene phylogeny, it has been noted that it is not informative to decipher inter and intra-species relationships. It can be observed that the Alternaria alternata complex in section Alternaria was separated into at least five subsclades. Species in the sects. Porri and Euphorbicola are also dispersed in one subclade while taxa in the sects. Embellia and Pseudoalternaria were also unresolved in their positions. We therefore recommend precautions when using this region alone to clarify species relationships.

Although Woudenberg et al.\textsuperscript{[22]} assigned 35 morpho-species as synonyms of Alternaria alternata, their affinities are still unclear due to inconsistencies, lack of morphological details and a comparison of single nucleotide polymorphisms. However, further studies based on combined multi-locus phylogeny showed that recent A. alternata species may not constitute a monophyletic group in DNA sequence-based phylogenies\textsuperscript{[67,167]} (present study). We compared our recent collections based on morphology and phylogeny. Interestingly, our phylogenetic analyses show that the phylogenetic strains of A. alternata can be separated to a minimum five different clades (Fig. 4) while the novel taxa from various host species are both morphologically and phylogenetically distinct from A. alternata complex and other species in Alternaria sect. Alternaria (Fig. 3).

The plasma membrane ATPase and cmdA loci are suggested to be the most informative markers for delimitation of Alternaria species in sect. Infectoriae by Lawrence et al.\textsuperscript{[14,15]}, while the Alt-a1 locus is not reliable to amplify some species within this section\textsuperscript{[11,12,14,55,70]}. However, the cmdA locus has seldom been used for the phylogeny of most Alternaria sections and species\textsuperscript{[70]}. The ITS barcode is also considered a good phylogenetic marker to define the Alternaria sections. However, it has limited discriminatory power to distinguish species\textsuperscript{[11,12,14,15,55,70]}.

In our study, two new taxa are accommodated in Alternaria sect. Infectoriae, based on phylogenetic analyses of a combined ITS, GAPDH and ATPase nucleotide sequences. Our new taxa A. arundinis (MFLUCC 21-0128, MFLU 21-0313A and MFLU 21-0313B) and A. nodulariconidiophora (MFLUCC 21-0131 and MFLU 21-0315) have oblong-ellipsoidal or obclavate conidia can apically or laterally formed long, geniculate, multi-locus secondary conidiophores. These morphological characters typically tally with those in sect. Infectoriae. However, A. nodulariconidiophora was observed as developing less secondary conidiophores on the natural substrate, but secondary conidiophores were heavily produced in culture incubated on PDA media.

Woudenberg et al.\textsuperscript{[22]} indicated that ITS, Alt-a1, GAPDH, RPB2 and TEF1-α are the effective phylogenetic markers to determine relationships and species delineation for Alternaria sect. Porri. However, many strains of species in this section could not be resolved in the present study, concurring with previous studies\textsuperscript{[11,12,22]}. In our study, more than 40 phylogenetic identified species in sect. Porri with one new taxon were confirmed based on phylogenetic analyses of combined ITS, Alt-a1, GAPDH, RPB2 and TEF1-α. Our new taxon A. brevirostra (MFLUCC 21-0129 and MFLUCC 21-0130) produces a relatively short filamentous beak on conidia and this warrants further verification as to whether A. brevirostra could grow longer apical beak at a mature stage or in different cultured media and also investigate the formation of short conidial filamentous beak occur on species in sect. Porri.

Species in Alternaria sect. Racidina are less phylogenetically resolved and share some similar morphological characters, with respect to conidiophores, sporulation, conidial shape and others. The recent phylogenetic studies of this section were reported by He et al.\textsuperscript{[4]}, Marin-Felix et al.\textsuperscript{[70]} and Tao et al.\textsuperscript{[168]} where they described novel species based on the multi-locus phylogenetic analyses of ITS, GAPDH, RPB2 and TEF1-α nucleotide sequences. In our survey, based on phylogenetic analyses of a combined ITS, GAPDH, RPB2 and TEF1-α nucleotide sequences, in our study, two new taxa are accommodated in Alternaria sect. Infectoriae (MFLUCC 21-0128 and MFLU 21-0313) have oblong-ellipsoidal or obclavate conidia can apically or laterally formed long, geniculate, multi-locus secondary conidiophores. These morphological characters typically tally with those in sect. Infectoriae. However, A. nodulariconidiophora was observed as developing less secondary conidiophores on the natural substrate, but secondary conidiophores were heavily produced in culture incubated on PDA media.

On the other hand, our analyses clearly show that species are phylogenetically diverse in Alternaria complex (Figs 3 & 4). The studies of Alternaria from various samples used in the present show that the genus Alternaria is speciose, which is in agreement with previous studies\textsuperscript{[4,7,11–15,18,19,22,25,26,28,40,55,66,67,70,78,108,113,165,168,169]}. Additional novel species/sections are expected if more hosts/habitats are explored. However, there is a need to standardize the taxonomy at different levels. At lower taxonomic levels (intraspecies), one can compare the morph and nucleotide differences with one or two morphologically similar taxa, or phylogenetically close species. Chemotaxonomy can be recommended and can undoubtedly be useful,
however, even though the discipline is still in its infancy, it could be explored for such a genus.

Application of molecular dating to solve taxonomy of *Alternaria*

Divergence time estimation of fungi at higher rank has been explored based on multocus analyses mainly with combined LSU, SSU and TEF1-α regions\(^\text{[128–130,132,170]}\). However, to resolve divergence time estimation of *Alternaria* with higher rank fungal strains, we combined ITS and RPB2 regions into our phylogenetic and divergence analyses (Figs 1 & 2), which are informative markers for *Alternaria* species based on previous studies. The divergence time estimation in our study shows that *Alternaria* diverged approximately at 62 (42–85) Mya, while the crown age of *Alternaria* is around 53 (36–72) Mya as well as the divergence time of sect. *Crivella* in Late Paleocene to early Eocene. Although this divergence time estimate corresponds to those reported by Kalugtutar & Sigler\(^\text{[123]}\) where a fossil species *Piriurella alternariata* was obtained from late Palaeocene or early Eocene (56±5 Mya). However, affinity with *Alternaria* could be properly documented due to a lack of morphs and DNA sequence. On the other hand, *Alternaria* sections diverged early, such as species in sects. *Crivella*, *Phragmosporae*, *Ulocladium* and *Undifilum* are morphologically beakless, round, mostly with transverse eusepta, rarely constricted at the septa, while the type section, sect. *Alternaria* with mostly distinct characters of *Alternaria* occurred with a late divergence time as 13 (6–20) Mya\(^\text{[11,58]}\). Moreover, the sect. *Phragmosporae* diverged with other sections in age as 43 (28–58) Mya in Eocene, and crown age of this section is around 28 Mya which is in an early crown age of *Alternaria*. *Alternaria* species in sections diverged at an early age have mostly beakless conidia with transverse septate and rarely constricted, less or 0–1 longitudinal or oblique septum in some transverse divisions and these can be considered to be the primitive structures of ancient *Alternaria* species.

Both phylogenetic and evolutionary estimate analyses based on multigene data show that some *Alternaria* sections bear close relationships and share the same divergence time. Section *Porri* and sect. *Euphorbicola* diverged from a clade with a divergence time at 10 (5.6–17.4) Mya. Species in sect. *Euphorbicola* are characterized with conidia with beak not distinct from the spore body, and they differ from the characters in sect. *Porri*. *Alternaria cumini* in sect. *Eureka* formed a separate subclade from sect. *Eureka* in both phylogenetic and divergence analyses (Figs 1 & 2). Section *Eureka* and sect. *Embellisiaoides* share a divergence time as 24 (14–35) Mya and these two sections and *A. cumini* share common morphological structures in having ovoid to subcylindrical, straight to inequilateral, transseptate and less longitudinal septa\(^\text{[11,38]}\) and possibly these can be expected to be one section. *Alternaria thalictrigena*, sect. *Panax*, and sect. *Teretispora* share a divergence time as 27 (17–40) Mya and species in this two sections and *A. thalictrigena* share the same characteristics in having paler and lanky conidia, and results support their establishment as a section. Strains in sect. *Pseudoaellotormia* in our divergence analyses lack informative DNA sequences from databases and hence we use only LSU gene of the type strain *A. arrhenatheri* (CBS 133068) [ITS, SSU, TEF1-α and RPB2 genes are not available] and hence the divergence results of sect. *Pseudoaellotormia* may not be as reliable. Species in sect. *Crivella* are characterized by cylindrical, straight to curved to inequilateral, with transverse eusepta, rarely constricted at septa\(^\text{[11]}\), and they are morphologically distinct from species in other *Alternaria* sections, while sect. *Crivella* is not well-resolved in ML and BI analyses (Fig. 3) despite the fact that they constitute distinct lineages from other *Alternaria* sections in divergence time estimation analyses.

We note that the age for the crown of most sections (24 out of 29, 85.7%) in *Alternaria* are between 0.1 to 20 Mya, while the genus *Alternaria* (53 Mya), sect. *Nimbya* (24 Mya) and sect. *Phragmosporae* (28 Mya) evolved in the range for family (20–100 Mya, crown age) as proposed by Liu et al.\(^\text{[129]}\). However, the branch length between stem ancestor and crown clades could be affected by species richness of the group, net diversification rate, timescale and model setup\(^\text{[129,170]}\). Our study only explored divergence time of *Alternaria* and each section (not familial relationships) but given that divergence time (stem age) of most sections in *Alternaria* are between 10 and 50 Mya, we can argue that these time estimates can be the supplementary evidence for acceptance of sections in *Alternaria*.

**ACKNOWLEDGMENTS**

The authors are grateful to Yunnan Provincial Science and Technology Department (Grant no. 202003AD150004) and the Mushroom Research Foundation, Chiang Mai, Thailand for supporting this research. We also acknowledge that Biology Experimental Center, Germplasm Bank of Wild Species, Kunming Institute of Botany, Chinese Academy of Sciences provided molecular laboratory facilities for molecular work. We express our sincere acknowledgement to Emeritus Prof. Dr. Kevin D. Hyde for his valuable comments and suggestions. Rungtiwa Phookamsak is grateful to CAS President’s International Fellowship Initiative (PIFI) for young staff (grant no. 2019FYC0003), Post–Doctoral Fellowship 2022 from Chiang Mai University, Thailand (Grant No. R000031743) and Reinventing University System 2021, Mae Fah Luang University for providing visiting scholarship. Jianchu Xu thanks Yunnan Provincial Science and Technology Department, Key Project (Grant No. 202101AS070045) and NSFC-CGIAR Project ‘Characterization of roots and their associated rhizosphere microbes in agroforestry systems: ecological restoration in high-phosphorous environment’ (Grant No. 31861143002). Rajesh Jeewon would like to thank University of Mauritius for research support. Sinang Hongsanan would like to thank National Natural Science Foundation of China (grant no. 31950410548) for financial support. Hong-Bo Jiang would like to thank Mae Fah Luang University for Ph.D scholarship. Timur S. Bulgakov would like to thank the Federal Research Center “Subtropical Scientific Center of the Russian Academy of Sciences” (the State Task research, theme no. FGRW-2022-0006). Jun-Fu Li thanks Daping Wei, Dan-Feng Bao, Er-Fu Yang, Dr. Shaun Pennycook, Dr. Dhanushka Wanasinghe, Milan C. SamarakoOn, Dr. Mingkwon Doilom, Ningguo Liu and Qing Tian for their suggestions and assistance. Austin G. Smith at World Agroforestry (ICRAF), Kunming Institute of Botany, China, is thanked for English editing.

**Conflict of interest**

Jun-Fu Li, Rajesh Jeewon, Darbhe Jarayama Bhat, Peter Edward Mortimer, Rungtiwa Phookamsak and Nakarin...
Suwannarach are the Editorial Board members of Journal Studies in Fungi. They are blinded from reviewing or making decisions on the manuscript. The article was subject to the journal’s standard procedures, with peer-review handled independently of these Editorial Board members and their research groups.

**Dates**

Received 8 July 2022; Accepted 23 December 2022; Published online 31 January 2023

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