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Alternaria: update on species limits, evolution, multi-locus phylogeny, and classification

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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, *TEF1-α*, *RPB2*, *GAPDH* and *Alt-a1* loci. Eighteen new species viz. *Alternaria arctoseptata*, *A. arundinis*, *A. baoshanensis*, *A. breviconidiophora*, *A. brevirostra*, *A. ellipsoidialis*, *A. eupatoriicola*, *A. falcata*, *A. lathyri*, *A. macilenta*, *A. macroconidia*, *A. minimispora*, *A. nodulariconidiophora*, *A. oblongoellipsoidea*, *A. orobanches*, *A. phragmiticola*, *A. phytolaccae* and *A. salicicola* are introduced and classified in sect. *Alternaria*, sect. *Infectoriae*, sect. *Porri* and sect. *Radicina*. *Alternaria alternata* and *A. doliconidium* 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.

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INTRODUCTION

Alternaria Nees is a ubiquitous dematiaceous hyphomycete genus, comprising over 790 species epithets, and approximately 368 species accepted within 29 sections[1–7]. 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[8–16]. The genus is cosmopolitan and widely distributed in Asia (e.g., India, Japan), Australia, Europe, and North America[17].

As invasive pathogens, *Alternaria* species are frequently isolated from different habitats such as the atmosphere, dust, indoor environments, soil, and damaged old buildings[11,12,18–22]. 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[23], but can also infect flowers, fruits, roots, seedlings, and stems with different kinds of lesions[8,12,15]. 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[8,11,12,15,22,24–26]. Most causal agents are restricted to *Alternaria* sects. *Alternantherae* D.P. Lawr. et al., *Alternaria* D.P. Lawr. et al., *Brassicicola* 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[11,12,15,17,22,27,28]. Jayawardena et al.[25,26] 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 habitable regions[11,12,15]. 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, conidiogenous 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*, *Embellisioides* 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 ascomata, with papillate ostioles, composed of thin-walled peridia, containing fissitunicate, cylindrical to cylindric-clavate asci, 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., *Comoclathris* 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[40] 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[39]. Woudenberg et al.[11] demonstrated that *Allewia*, *Brachycladium* Corda, *Chalastospora* E.G. Simmons, *Chmelia* Svob.-Pol., *Crivellia*, *Embellisia* E.G. Simmons, *Lewia*, *Nimbya* E.G. Simmons, *Sinomyces* Yong Wang bis & X.G. Zhang, *Teretispora* E.G. Simmons, *Ulocladium* Preuss, *Undifilum* B.M. Pryor et al. and *Ybotromyces* Rulamort formed internal clades 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.[11]. 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*, *RPB2* 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.[6] and Ghafri et al.[7] introduced two new sections (i.e., sects. *Helianthiinficiens* and *Omanenses*) 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 *Macrosporium* and *Stemphylium*. However, the first validly published species name was *Torula alternata*[37]. The second stage (1850s–1930s) involved publication of numerous alternarioid species, wherein Elliott[50] first attempted to revise the taxonomy and nomenclature of *Alternaria* and *Macrosporium*, 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.[13,14,55], 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)[11,13–15,22,56]. 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 & Horré[20], Hong et al.[49], Inderbitzin et al.[58], Lawrence et al.[14,55], Pryor & Bigelow[59], Pryor & Gilbertson[54], Pryor et al.[60], Runa et al.[21], Wang et al.[61], and Woudenburg et al.[11,12]. Lawrence et al.[14] introduced *A. panax* and *A. gypsophilae* 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.[6] introduced a new section, sect. *Helianthiinficientes*, for *A. helianthiinficiens* which was previously demonstrated as a monotypic lineage in Woudenberg et al.[11] and Lawrence et al.[15].

Presently, *Alternaria* contains 29 sections viz. sect. *Alternantherae*, sect. *Alternaria*, sect. *Brassicicola*, sect. *Chalastospora*, sect. *Cheiranthus*, sect. *Crivellia*, sect. *Dianthicola*, sect. *Embellisia*, sect. *Embellisioides*, sect. *Euphorbiicola*, sect. *Eureka*, sect. *Gypsophilae*, sect. *Helianthiinficientes*, sect. *Infectoriae*, sect. *Japonicae*, sect. *Nimbya*, sect. *Omanenses*, sect. *Panax*, sect. *Phragmosporae*, sect. *Porri*, sect. *Pseudoalternaria*, sect. *Pseudoulocladium*, sect. *Radicina*, sect. *Soda*, sect. *Sonchi*, sect. *Teretispora*, sect. *Ulocladioides*, sect. *Ulocladium*, and sect. *Undifilum*. Furthermore, seven species identified in *Alternaria* by multi-locus phylogenetic analyses and not accommodated among the 29 accepted sections of *Alternaria* are *A. argyranthemi* E.G. Simmons & C.F. Hill, *A. brassicae* (Berk.) Sacc., *A. dennisii* M.B. Ellis, *A. peucedani* S.H. Yu, *A. soliardae* E.G. Simmons, *A. thalictrigena* K. Schub. & Crous, and *A. thlaspis* (E.G. Simmons & J.C. David) D.P. Lawr., Rotondo & Gannibal[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. celosiicola* Jun. Nishikawa & C. Nakash., *A. gomphrenae* 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. crassoides* (Davis) Gannibal, *A. pimpriana* V.G. Rao, and *A. paragomphrenae* Jun. Nishikawa & C. Nakash. that *A. crassoides* 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[38]. 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* (Thüm.) E.G. Simmons, *A. guaranitica* (Speg.) E.G. Simmons and *A. macalpinei* E.G. Simmons). Wanasinghe et al.[66] introduced *A. doliconidium* 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. muriformispora* J.F. Li et al., *A. obpyriconidia* J.F. Li et al., *A. ovoidea* J.F. Li et al., *A. pseudoinfectoria* J.F. Li et al., *A. rostroconidia* J.F. Li et al., and *A. torilis* 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. septorioides* (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*, *Gypsophilae*, *Porri*, *Alternaria*, and *Alternanatherae*[11]. 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].

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

Alternaria sections		Conidiogenesis structures	Ecology and economy	References
Sect. *Alternantherae*	Conidiophores	Short to moderately long, with slightly enlarged conidiogenous tip.	Species in this section are reported as plant pathogens that mainly cause leaf spots.	[11,13,15,55]
	Conidia	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, conidial 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.		
Sect. *Alternaria*	Conidiophores	Short to long, straight or curved, simple or branched, with one or several apical conidiogenous loci.	Species in this section are reported as plant pathogens on leaves, stems and 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.	[11,12,15,100]
	Conidia	Obclavate to long ellipsoid, 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.		
Sect. *Brassicicola*	Conidiophores	Short to moderately long, simple or branched, with one or several apical conidiogenous loci.	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 sources of antibiotic masses.	[11,14,101–103]
	Conidia	Ellipsoid, ovoid or somewhat obclavate, small or moderate in size, septate, slightly or strongly constricted at most of the transverse septa, 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.		
Sect. *Chalastospora*	Conidiophores	Short to long, simple or branched, with one or several conidiogenous loci.	Species in this section are primarily reported as saprobes and causal agents of human diseases.	[11,30,38]
	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.		
Sect. *Cheiranthus*	Conidiophores	Short to moderately long, simple or branched, with one or several conidiogenous loci.	Species in this section are primarily saprobes and pathogens on various plant hosts.	[11,38,55]
	Conidia	Ovoid, broadly ellipsoid with transverse and longitudinal septa, slightly or strongly constricted at the septa, in short to long, simple or branched chains.		
Sect. *Crivellia*	Conidiophores	Straight or curved, simple or branched, with geniculate, sympodial proliferations.	Species in this section are mainly known as pathogens on opium poppy (*Papaver somniferum* L.), the sexual morph of which links with genus *Crivella*.	[11,58]
	Conidia	Cylindrical, straight to curved to inequilateral, with transverse septa, rarely constricted at septa, single or in short, simple or branched chains. Apically or laterally form secondary conidiophores. Sometimes produced microsclerotia or chlamydospores.		
Sect. *Dianthicola*	Conidiophores	Simple or branched, with or without apical geniculate proliferations.	Species in this section mainly cause leaf spot and blight on economic vegetation hosts such as carnation (*Dianthus* sp.) and sesame (*Sesamum indicum* L.).	[11,104,105]
	Conidia	Narrowly ovoid or narrowly ellipsoid 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.		
Sect. *Embellisia*	Conidiophores	Simple, septate, straight or with geniculate sympodial proliferation.	Species in this section are reported as pathogens on vegetable crops such as tomato and garlic.	[11,106,107]
	Conidia	Solitary, ovoid to subcylindrical, straight to inequilateral, with transverse septa; septa can be thick, dark and rigid in contrast to the external wall. Sometimes sporulated chlamydospores.		
Sect. *Embellisioides*	Conidiophores	Simple, septate conidiophores, straight or with multiple, geniculate, sympodial proliferations.	Species in this section are mainly reported as saprobes in soil and pathogen on plant hosts.	[9,108,109]
	Conidia	Solitary or in short chains, obovoid to ellipsoid, with transverse and longitudinal septa, transverse septa 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.		
Sect. *Eureka*	Conidiophores	Simple, septate conidiophores, straight or with geniculate, sympodial proliferations.	Species in this section are reported as pathogens and endophytes that are active in the biotransformation of some secondary metabolites.	[11,110,111]
	Conidia	Solitary or in short chains, narrowly ellipsoidal to cylindrical, with transverse and longitudinal septa, slightly constricted at the septa, with a blunt rounded apex. Sometimes form apical or lateral, short secondary conidiophores and sporulated sexual morph and chlamydospores.		

(to be continued)

Table 1. (continued)

Alternaria sections		Conidiogenesis structures	Ecology and economy	References
Sect. *Euphorbiicola*	Conidiophores	Short to long, broad, apical and sometimes lateral, secondary conidiophores.	Species in this section served as pathogens on economic plants such as *Euphorbiicola* sp. and *Citrus* sp. and also produced secondary metabolites.	[11,112]
	Conidia	Medium to large-sized, in short to moderately long chains, ovoid, obclavate, disto- and euseptate, with multiple transverse and some longitudinal septa, slightly constricted near some transverse septa, with no or a simple long beak in the terminal conidia.		
Sect. *Gypsophilae*	Conidiophores	Simple, or occasionally branched, with one or a few conidiogenous loci.	Species in this section occur on the host family Caryophyllaceae.	[11,14,38]
	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.		
Sect. *Helianthiinficientes*	Conidiophores	Simple, or branched, with one or a few conidiogenous loci.	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.).	[6]
	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.		
Sect. *Infectoriae*	Conidiophores	Short to long, simple or branched, with one or several conidiogenous loci.	Species in this section are known as saprobes as well as plant and human pathogens.	[11,14,38, 70]
	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. Apically or laterally formed long geniculate, multi-locus secondary conidiophores, with meristematic growth.		
Sect. *Japonicae*	Conidiophores	Short to long, simple or occasionally branched, with a single conidiogenous locus.	Species in this section particularly occur on hosts in Brassicaceae.	[11,14]
	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.		
Sect. *Nimbya*	Conidiophores	Simple, short to form moderately long, sometimes one to a few short to long, geniculate, sympodial metastasis.	Species in this section are known as saprobes and plant pathogens. Species in this section produce phytotoxins	[11,55,85, 113,114]
	Conidia	Solitary or in short chains, narrowly elongate-obclavate, gradually tapering apically, with transverse disto- and eusepta, sometimes slightly constricted near eusepta.		
Sect. *Omanenses*	Conidiophores	Long, simple, with multiple geniculate, sympodial metastasis or short conidiogenous loci normally with a terminal cluster of three conidia.	Species in this section consist of a core taxon *A. omanensis* which is saprobic on dead woods.	[7]
	Conidia	Solitary, obovoid and sphaeroid, non-beaked, with transverse and longitudinal septa.		
Sect. *Panax*	Conidiophores	Simple or branched, short to moderately long, with one or a few conidiogenous loci.	Species in this section are known as pathogens causing blight on economic plants such as ginseng and American ginseng (Araliaceae).	[11,14,115]
	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 one or several conidiogenous loci, multiple lateral secondary conidiophores with a single conidiogenous locus.		
Sect. *Phragmosporae*	Conidiophores	Simple, short to moderately long, with one or multiple geniculate, sympodial metastasis.	Species in this section are mainly known as saprobes from soil and marine environments.	[11]
	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.		
Sect. *Porri*	Conidiophores	Short to long, simple, with one or several conidiogenous loci.	Species in this section consist of some important phytopathogens and produce phytotoxins.	[11,14,22,11 6,117]
	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, ellipsoid, subcylindrical or obovoid, disto- and eusepta, with multiple transverse and longitudinal septa, slightly constricted near some transverse septa, apically or laterally formed secondary conidiophores.		

(to be continued)

Table 1. (continued)

Alternaria sections		Conidiogenesis structures	Ecology and economy	References
Sect. *Pseudoalternaria*	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.	Species in this section are known as pathogens on plant hosts.	[15]
	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.		
Sect. *Pseudoulocladium*	Conidiophores	Simple or branched, with short, geniculate, sympodial metastasis.	Species in this section are reported as phytopathogens for human infection.	[11]
	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.		
Sect. *Radicina*	Conidiophores	Straight, simple or branched, short or long, with multiple, short geniculate, sympodial proliferations, with one to a few conidiogenous loci at the apex.	Species in this section mainly occur on hosts in family Apiaceae.	[11]
	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.		
Sect. *Soda*	Conidiophores	Simple or occasionally branched, short to moderately long, with one conidiogenous locus.	Species in this section are isolated from soda lake environments (Western Siberia, Russia).	[56]
	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.		
Sect. *Sonchi*	Conidiophores	Simple or branched, with short, geniculate, with one or several conidiogenous loci.	Species in this section mainly occur on a wide range of hosts within Asteraceae (Compositae).	[14]
	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.		
Sect. *Teretispora*	Conidiophores	Simple, sometimes extending at the apex with one or two, geniculate, sympodial proliferations.	Species in this section consist of a core species, *Alternaria leucanthemi*, which is a phytopathogen causing plant blight disease.	[11,38]
	Conidia	Single, long cylindrical, lacking a beak portion, 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.		
Sect. *Ulocladioides*	Conidiophores	Short, geniculate, sympodial proliferations.	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.	[11,15]
	Conidia	Obovoid, non-beaked with a narrow base, single or in chains, with apical secondary conidiophores.		
Sect. *Ulocladium*	Conidiophores	Simple, with one or two short, geniculate, sympodial proliferations.	Species in this section are mainly isolated from plant litter and rarely from marine environments. Potential bioactivities were also reported.	[11,118]
	Conidia	Single, obovoid, non-beaked, with a narrow base.		
Sect. *Undifilum*	Conidiophores	Simple, septate, straight, or with geniculate sympodial proliferation.	Species in this section mainly occur on hosts in family Fabaceae.	[11]
	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.		

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) Woudenb. & Crous, *A. armoraciae* E.G. Simmons & C.F. Hill, *A. breviramosa* Woudenb. & Crous, *A. malorum* (Ruehle) U. Braun, Crous & Dugan, and *A. obclavata* (Crous & U. Braun) Woudenb. & 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. pobletensis* 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) Woudenberg & 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. septorioides* 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. latifunda* 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. *Pseudoulocladium* and *Ulocladioides*[11,14,15].

Section *Crivellia* was introduced by Woudenberg et al.[11] to accommodate the type species of *Crivellia*, *C. papaveracea* (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[15]. 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* Woudenb. & Crous and *A. penicillata* (Corda) Woudenb. & 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 *Dianthicola* was introduced by Woudenberg et al.[11] and is typified by *Alternaria dianthicola* Neerg. Three species were accommodated in this section, including *A. dianthicola*, *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. *Dianthicola* has a close relationship with sect. *Ulocladioides*[11,15].

Section *Embellisia* was introduced by Woudenberg et al.[11] and is typified by *Alternaria embellisia* Woudenb. & Crous (≡ *Helminthosporium allii* Campan.). 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. *Phragmosporae*, *Soda*, *Chalastospora*, *Pseudoalternaria*, and *Infectoriae*[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* Woudenb. & Crous, *A. embellisia* Woudenb. & Crous, and *A. tellustris* (E.G. Simmons) Woudenb. & Crous.

Section *Embellisioides* 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* Woudenb. & Crous, *A. hyacinthi* (de Hoog & P.J. Mull. bis) Woudenb. & Crous (type species), *A. lolii* (E.G. Simmons & C.F. Hill) Woudenb. & Crous, *A. planifunda* (E.G. Simmons) Woudenb. & Crous, *A. proteae* (E.G. Simmons) Woudenb. & Crous, and *A. tumida* (E.G. Simmons) Woudenb. & 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, pseudothecial, papillate ascomata with markedly setose, subellipsoidal to subcylindrical asci and slightly inequilateral subellipsoidal immature ascospores. Mature ascospores are ellipsoid 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 *Euphorbiicola* 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. *Euphorbiicola* 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 anigozanthi* 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) Woudenb. & 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 asci, somewhat inequilateral, with subellipsoidal and slightly

inequilateral juvenile ascospores. Ascospores are subclavate to ellipsoid, with transverse septa, discontinuous series of longitudinal septa when mature[15]. Multi-locus phylogenetic analyses based on the protein-coding genes demonstrated that the section has a close relationship with the morphologically similar sect. *Embellisioides*[11,15].

Section *Gypsophilae* was introduced by Lawrence et al.[14] to accommodate four *Alternaria* species, comprising *A. gypsophilae* Neerg. (type species), *A. nobilis* (Vize) E.G. Simmons, *A. vaccariae* (Săvul. & Sandu) E.G. Simmons & S.T. Koike and *A. vaccariicola* E.G. Simmons. Woudenberg et al.[11] recommended the other four species viz. *A. axiaeriisporifera* E.G. Simmons & C.F. Hill, *A. ellipsoidea* E.G. Simmons, *A. juxtiseptata* E.G. Simmons, and *A. saponariae* (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. *Gypsophilae*. Consequently, Gannibal[74] introduced *A. kamtschatica* 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[3,11,74]. The section has a close relationship with sects. *Alternaria*, *Alternantherae*, *Euphorbiicola*, and *Porri*[11,14,15].

Section *Helianthiinficientes* was introduced by Gannibal et al.[6] to accommodate *Alternaria helianthiinficiens* E.G. Simmons, Walcz & R.G. Roberts which was previously treated as a monotypic lineage in Woudenberg et al.[11] and Lawrence et al.[15]. 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. helianthiinficiens* may also occur on other plant species in Asteraceae. Morphologically, *A. helianthiinficiens* resembles many species in sect. *Porri* in having large conidia[6]. However, multi-locus phylogenies analyzed by Woudenberg et al.[11] and Ghafri et al.[7] demonstrated that *A. helianthiinficiens* formed an independent lineage within *Alternaria* but could not be assigned to 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*[15,24,70,75–80]. The human pathogenic genera *Ybotromyces* Rulamort (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[15,77,80]. The sexual morph of sect. *Infectoriae* was linked to species in *Lewia* and is characterized by smooth-walled ascomata, subcylindrical or subellipsoidal 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 protoascomata 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[14,54,59] 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. Simoneau 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* (Fuckel) Sivan. The section initially contained four species previously described as *Nimbya* species viz. *A. caricis* (E.G. Simmons) Woudenb. & Crous, *A. scirpicola*, *A. scirpinfestans* (E.G. Simmons & D.A. Johnson) Woudenb. & Crous, and *A. scirpivora* (E.G. Simmons & D.A. Johnson), Woudenb. & Crous. Gannibal[83] included the other two species, *A. heteroschemos* (Fautrey) Gannibal and *A. juncicola* (E.G. Simmons) Gannibal in this section. In addition, Ahmadpour[84] and Ahmadpour et al.[85] also introduced *A. caricicola* Ahmadp., *A. cypericola* Ahmadp., Poursafar & Ghosta, *A. heyranica* Ahmadp., Poursafar & Ghosta, and *A. junci-acuti* 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* Fuckel and is characterized by immersed to superficial, subglobose, ostiolate ascomata, with broadly cylindrical or clavate to obovoid asci and broadly ellipsoidal, brown to dark brown, multi-septate ascospores[15,24]. Section *Nimbya* is closely related to sects. *Embellisia*, *Phragmosporae*, *Chalastospora* and *Infectoriae* based on phylogenetic analyses of the combined *GAPDH*, *RPB2* and *TEF1-α* sequence dataset[11].

Section *Omanenses* was introduced by Ghafri et al.[7], 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 ascomata, 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, ITS, *GAPDH*, *TEF1-α* and *RPB2* sequence dataset demonstrated that the section has a close relationship with sects. *Embellisioides*, *Eureka* and *Ulocladium*[7].

Section *Panax* was introduced by Lawrence et al.[14] and initially consisted of *Alternaria calycipyricola* R.G. Roberts, *A.*

eryngii (Pers.) S. Hughes & E.G. Simmons and *A. panax* Whetzel (as *A. panacis* in Deng et al.[86] and Lawrence et al.[15]; type species). Woudenberg et al.[11] included *A. avenicola* E.G. Simmons and *A. photistica* E.G. Simmons to this section and the sexual morphs of these two species were known as *Lewia avenicola* Kosiak & Kwaśna[38] and *L. photistica* E.G. Simmons[40], respectively. Deng et al.[86] reported two pathogenic species in this section viz. *A. araliae* H.C. Greene and *A. dendropanacis* S.H. Yu & J.X. Deng that were associated with leaf spot and blight disease on Araliaceae in Korea, while Gannibal & Lawrence[62] included *A. prasonis* E.G. Simmons based on morphology. Recently, Hashemlou et al.[87] described *A. hedjaroudei* Y. Ghosta et al. on stems of *Serratula coriacea* 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 *TEF1-α* sequences suggested that sect. *Panax* has a close relationship with *A. thalictrigena* and sect. *Teretispora*[11,15].

Section *Phragmosporae* was introduced by Woudenberg et al.[11] and is typified by *Alternaria phragmospora* Emden. The section contains six species viz. *A. chlamydospora* Mouch., *A. didymospora* (Munt.-Cvetk.) Woudenb. & Crous, *A. limaciformis* E.G. Simmons, *A. molesta* E.G. Simmons, *A. mouchaccae* 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[15]. 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.[14] 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 phylogeny[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 section. Liu et al.[88] introduced *A. physalidis* H.F. Liu & J.X. Deng 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 *Alternantherae*[11,14,15,22].

Section *Pseudoalternaria* was introduced by Lawrence et al.[15] and is typified by *Alternaria arrhenatheri* D.P. Lawr., Rotondo & Gannibal. The section initially consisted of two species viz. *A. arrhenatheri* and *A. rosae* E.G. Simmons & C.F. Hill based on both phylogeny and morphology. Based on morphological examination, Gannibal & Lawrence[77] 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. brassicifolii* 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. altcampina* 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. *Infectoriae* and *Chalastospora*[15,70].

Section *Pseudoulocladium* was introduced by Woudenberg et al.[11] 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* Woudenb. & Crous, *A. chartarum*, *A. concatenata* Woudenb. & Crous, and *A. septospora* (Preuss) Woudenb. & Crous[11]. Based on morphology, Gannibal & Lawrence[96] included *A. lanuginosa* (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 conidiogenous 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 clusters with sect. *Ulocladioides*[11].

Section *Radicina* was recognized by Pryor & Gilbertson[54] and formally established by Lawrence et al.[14]. 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 Apiaceae[11,15]. Woudenberg et al.[11] and Lawrence et al.[15] listed five species in this section, including *A. carotiincultae* 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.[4] introduced two new species in this section viz. *A. divaricatae* L. 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. *Gypsophilae*[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 kulundae* 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 alkalitolerant to facultative alkaliphilic type of the adaptation. The sexual morph for the section is unknown. Multi-locus phylogeny of SSU, LSU, *RPB2*, ITS, and *GAPDH* showed that the section clustered with sects. *Infectoriae*, *Chalastospora*, and *Embellisia*[56].

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* Hori & 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[11,17]. The sexual morph of the section is unknown. Phylogenetic analyses based on the *GAPDH*, *RPB2* and *TEF1-α* sequences showed that sect. *Sonchi* forms a sister clade with two monotypic lineages, *A. brassicae* (Berk.) Sacc. and *A. helianthiinficiens* E.G. Simmons, Walcz & R.G. Roberts[11]. Currently, *A. helianthiinficiens* was raised to the section rank of *Alternaria* by Gannibal et al.[6]. Ferreira & Barreto[97] designated the neotype of *Acroconidiella tropaeoli* (T.E.T. Bond) J.C. Lindq. & Alippi (≡ *Heterosporium tropaeoli* 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 leucanthemi* 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]. 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 cucurbitae* 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 *TEF1-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 botrytis* (Preuss) Woudenb. & Crous. The section is introduced to accommodate the epitype of the former *Ulocladium* as *Alternaria botrytis* (CBS 197.67) and additional three species viz. *A. alternariae* (Cooke) Woudenb. & Crous, *A. capsici-annui* Săvul. & Sandu, and *A. oudemansii* (E.G. Simmons) Woudenb. Gannibal & Lawrence[96] included *A. manihoticola* (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 *TEF1-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) Woudenb. & Crous. The section consists of five species viz. *A. bornmuelleri*, *A. cinerea* (Baucom & Creamer) Woudenb., *A. fulva* (Baucom & Creamer) Woudenb. & Crous, *A. gansuensis* J. Li Liu & Y.Z. Li, and *A. oxytropis* (Q. Wang, Nagao & Kakish.) Woudenb. & 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 swaisonine toxic compound, causing a neurological disease of grazing animals[99]. Phylogenetic analyses of the *GAPDH*, *RPB2* and *TEF1-α* sequences showed that the section forms an independent lineage closely related to a monotypic lineage *Embellisia dennisii* (M.B. Ellis) E.G. Simmons, (CBS 110533, CBS 476.90), which was resurrected as *Alternaria dennisii* 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]. Samarakoon 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, Samarakoon 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 Kalgutkar and Jansonius database of fossil fungi[122]. However, there is a fossil record referred to *Alternaria* described as *Polycellaesporonites alternariatus* (Kalgutkar & Sigler) Kalgutkar & Janson (≡ *Piriurella alternariata* Kalgutkar & Sigler). *Polycellaesporonites alternariatus* was first described as *Piriurella alternariata* by Kalgutkar & Sigler[123] for the fungal 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 Palaeocene 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[11–14,22,55,123].

Evolutionary estimates based on molecular clocks have been increasingly common in fungal taxonomy in recent years[1,124–130], 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 phyla 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 the 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 sporulation *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 (ddH_2O) 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 (CGMCC). 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 (BSC14S1, 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 a 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 EasyTaqTM DNA Polymerase, dNTPs, and optimized buffer, Beijing BioTeke Corporation, P.R. China) and 9.5 μl of sterilized double-distilled water (ddH_2O). 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 50 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.[131]. 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.

Gene loci	Primers	Sequence 5′–3′	References
Internal transcribed spacer region (ITS, including the 5.8S gene)	ITS5	GGA AGT AAA AGT CGT AAC AAG G	[139]
	ITS4	TCC TCC GCT TAT TGA TAT GC	
28S large subunit rDNA (LSU)	LR0R	GTA CCC GCT GAA CTT AAG C	[140]
	LR5	ATC CTG AGG GAA ACT TC	
18S small subunit rDNA (SSU)	NS1	GTA GTC ATA TGC TTG TCT C	[139]
	NS4	CTT CCG TCA ATT CCT TTA AG	
Alternaria major allergen (*Alt-a1*)	Alt-for	ATG CAG TTC ACC ACC ATC GC	[49]
	Alt-rev	ACG AGG GTG AYG TAG GCG TC	
Glyceraldehyde 3-phosphate Dehydrogenase (*GAPDH*)	GDP-1	CAA CGG CTT CGG TCG CAT TG	[141]
	GDP-2	GCC AAG CAG TTG GTT GTG C	
Plasma membrane ATPase (*ATPase*)	ATPDF1	ATC GTC TCC ATG ACC GAG TTC G	[14]
	ATPDR1	TCC GAT GGA GTT CAT GAT AGC C	
The second largest subunit of RNA polymerase II (*RPB2*)	fRPB2-5f	GAY GAY MGW GAT CAY TTY GG CCC	[142]
	fRPB2-7cR	ATR GCT TGY TTR CCC AT	
Translation elongation factor 1-α (*TEF1-α*)	EF1-983F	GCY CCY GGH CAY CGT GAY TTY AT	[143]
	EF1-2218R	ATG ACA CCR ACR GCR ACR GTY TG	
	EF1-728F	CATCGAGAAGTTCGAGAAGG	[144]
	EF1-986R	TACTTGAAGGAACCCTTACC	

(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 = 1.0, scale = 25, providing 95% credibility interval of 110 MYA)[131,148]. 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 relaxed clock (uncorrelated) model was applied with a lognormal distribution of rates for each gene estimated. The best fit of substitution models was selected based on jModeltest2 v.0.1.1[150] for each gene partition, resulting as ITS = GTR+I+G, LSU = GTR+I+G, SSU = TIM2+I+G, *TEF1-α* = SYM+I+G, *RPB2* = TIM2+I+G; Yule processed tree prior with a randomly generated starting tree. The analysis was performed for 100 million generations in BEAST v1.8.4, sampling parameters every 10,000 generations. The effective sample sizes (ESS) were checked by Tracer v1.6[151] and accepted when ESS values were higher than 200. The first 10% trees were discarded as a burn-in phase. The remaining trees were combined in LogCombiner 1.8.0. A maximum clade creditability (MCC) tree was generated by summarized data and estimated in TreeAnnotator v1.8.0. The tree was visualized with FigTree v1.4.[152].

Phylogenetic analyses

The quality of the generated ITS, LSU, SSU, *TEF1-α*, *RPB2*, *GAPDH*, *Alt-a1* and *ATPase* sequences was checked using Bioedit v. 7.1.3.0[138] 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 phylogenic 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 100th 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.

Table 3. The best nucleotide substitution model for each locus based on the Akaike Information Criterion (AIC) generated by MrModeltest v. 2.3.[156].

Phylogenetic analyses	Nucleotide substitution models							
	ITS	LSU	SSU	*GAPDH*	*RPB2*	*TEF1-α*	*Alt-a1*	*ATPase*
A1: *Alternaria* sections	GTR+I+G	GTR+G	TrN+I+G	SYM+I+G	GTR+I+G	TIM1+I+G	GTR+I+G	n/a
A2: *A. alternata*	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	TIM2 +G	GTR+I+G	GTR+I+G	n/a
A3: sect. *Infectoriae*	GTR+I+G	n/a	n/a	GTR+I+G	n/a	n/a	n/a	SYM+G
A4: sect. *Porri*	SYM+I+G	n/a	n/a	TIM2+I+G	GTR+I+G	GTR+G	GTR+I+G	n/a
A5: sect. *Radicina*	GTR+I+G	n/a	n/a	GTR+I+G	TIM2+G	GTR+I+G	n/a	n/a

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 *Schismatomma 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 (BYPP) from MCMC were evaluated with 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, concurring 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 times for class and order status by Liu et al.[129] and Hongsanan et al.[1]. 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 species in sects. *Crivellia*, *Phragmospora*, *Ulocladium*, and *Undifilum*, 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-a1* sequence dataset comprises 189 taxa with *Stemphylium vesicarium* (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-a1*: 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 = 3.337861, AT = 1.081773, CG = 0.849184, CT = 5.615040, GT = 1.000000. 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 *Undifilum*. 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 cumini*

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.*

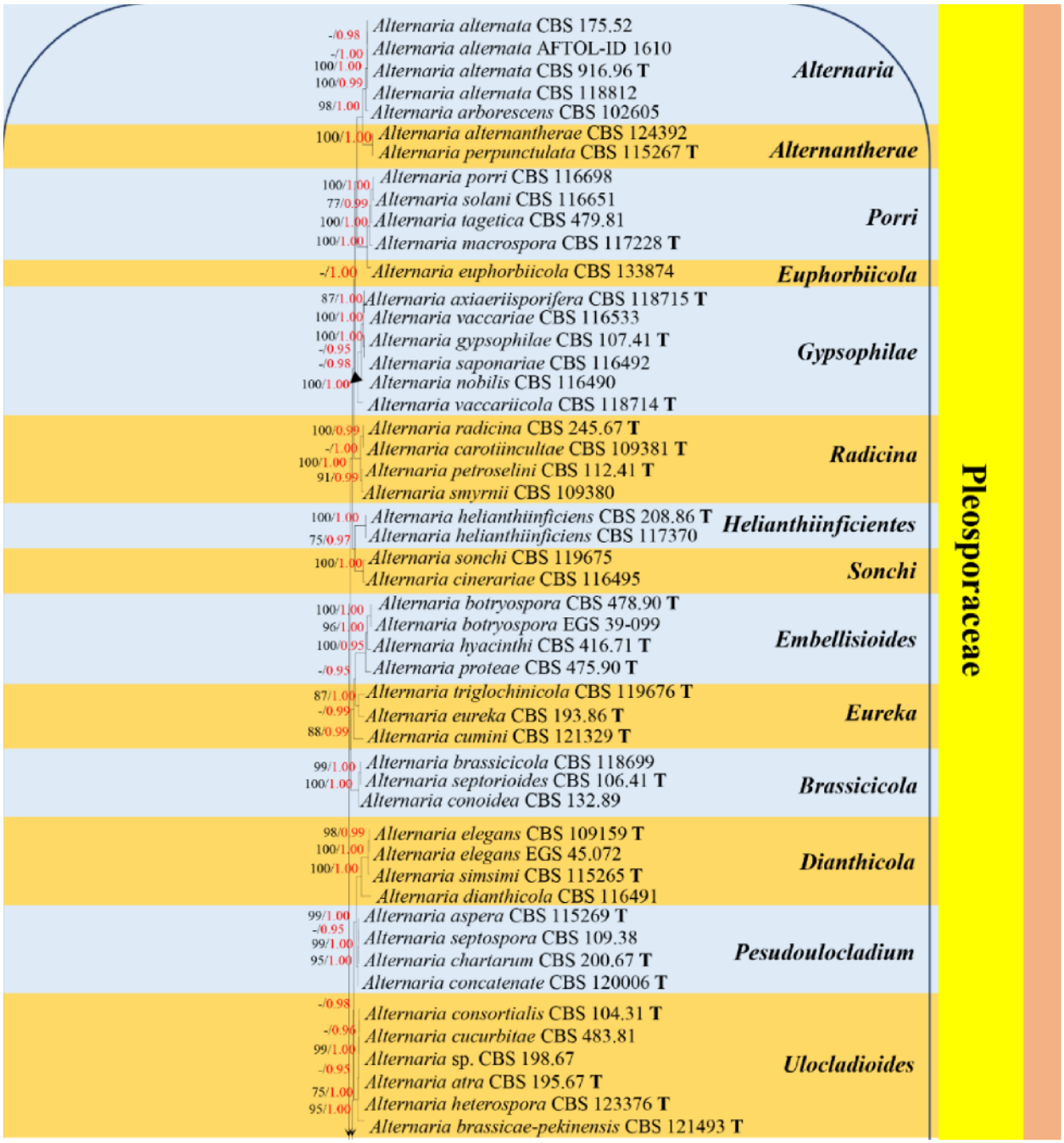

Fig. 1 Phylogenetic construction of Pleosporales using RAxML-based maximum likelihood analysis of a combined ITS, LSU, SSU, *TEF1-α* and *RPB2* DNA sequence dataset. Bootstrap support values for maximum likelihood (ML, black) equal to or greater than 70% and Bayesian posterior probabilities (PP, red) equal to or greater than 0.95 PP are shown above the nodes. The tree is rooted to Arthoniomycetes (*Arthonia dispersa* UPSC2583, *Dendrographa leucophaea* f-minor, *Roccella fuciformis* Tehler 8171 and *Schismatomma decolorans* Ertz 5003). The type strains are indicated by boldface 'T'.

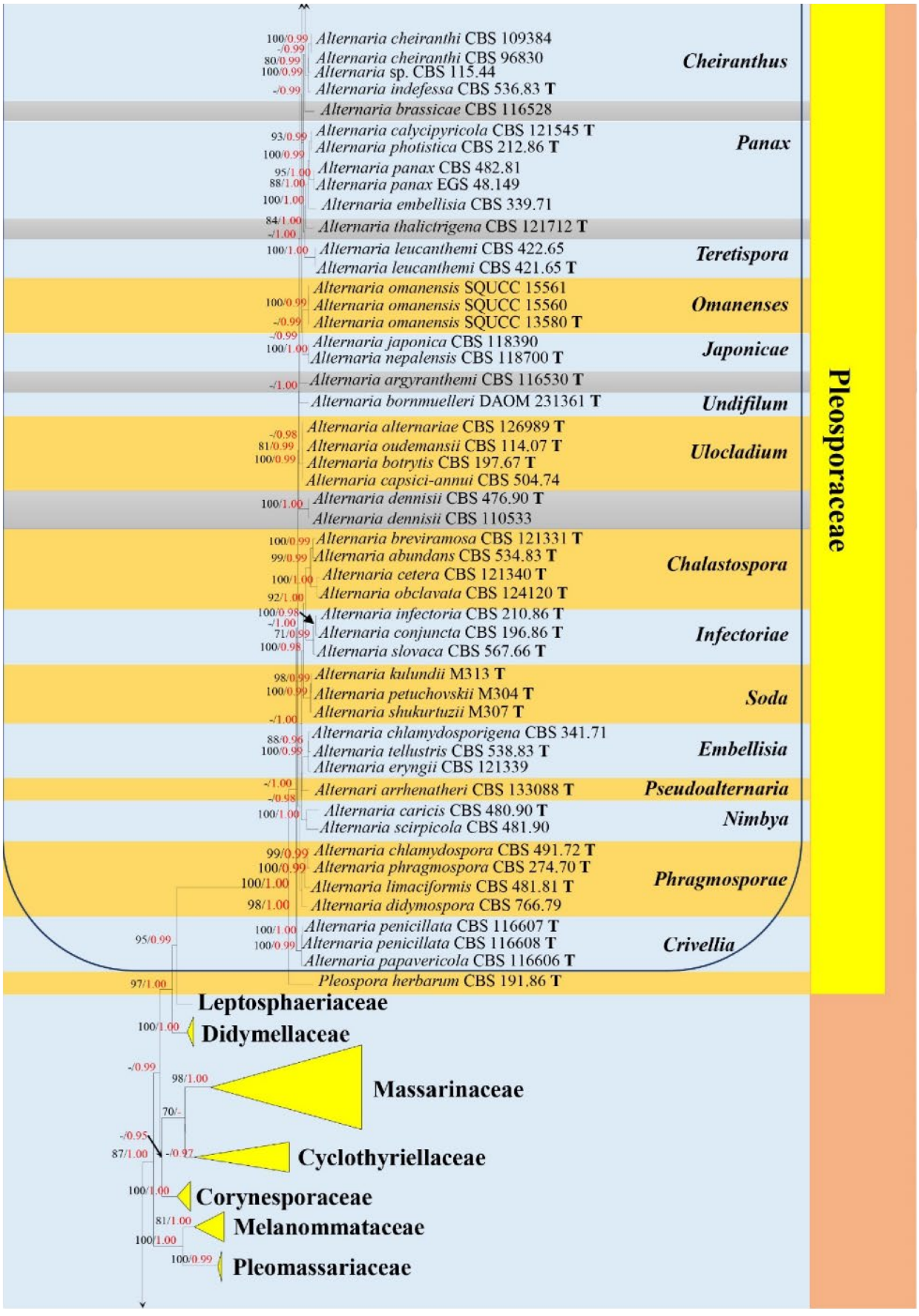

Fig. 1 (continued)

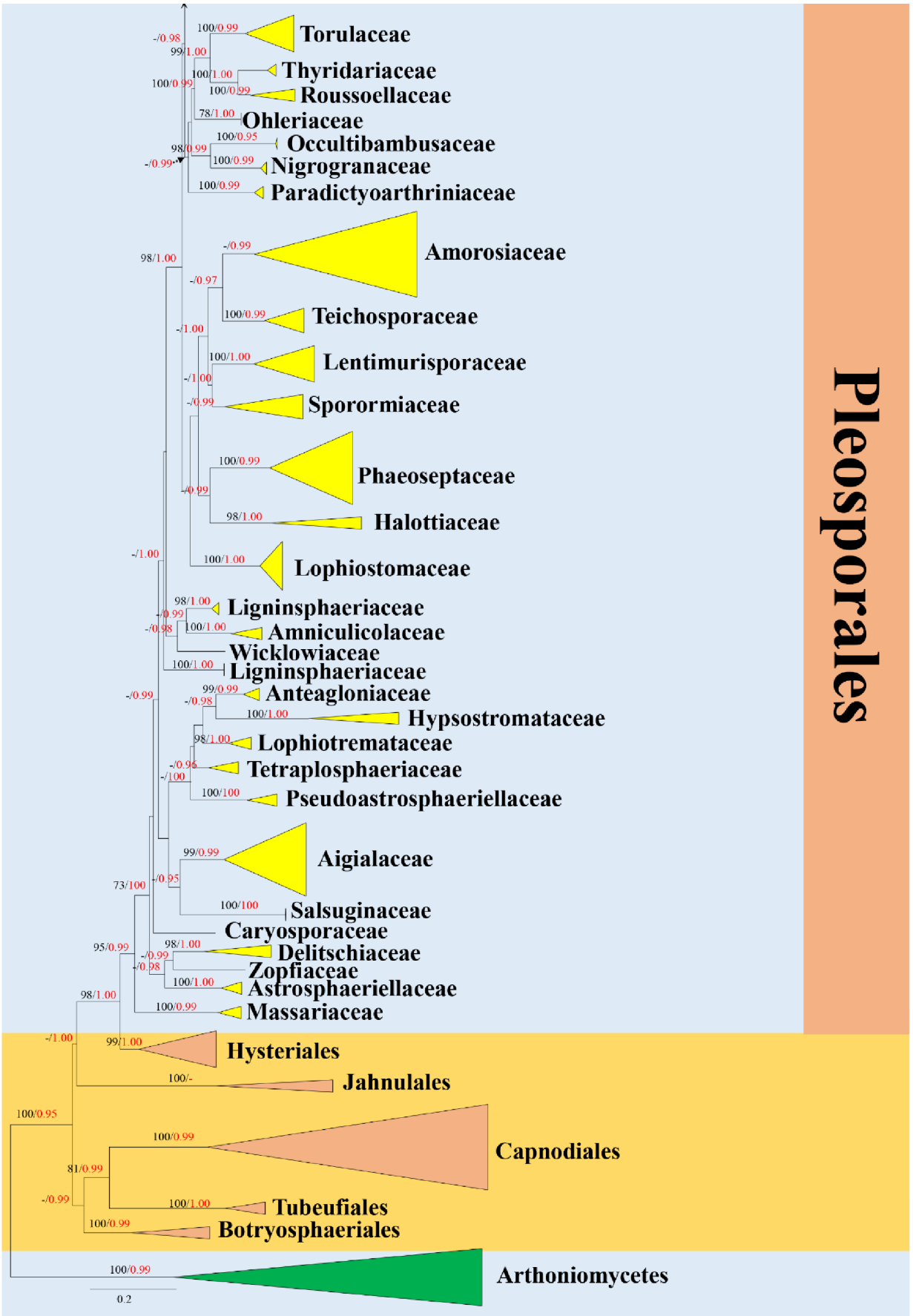

Fig. 1 (continued)

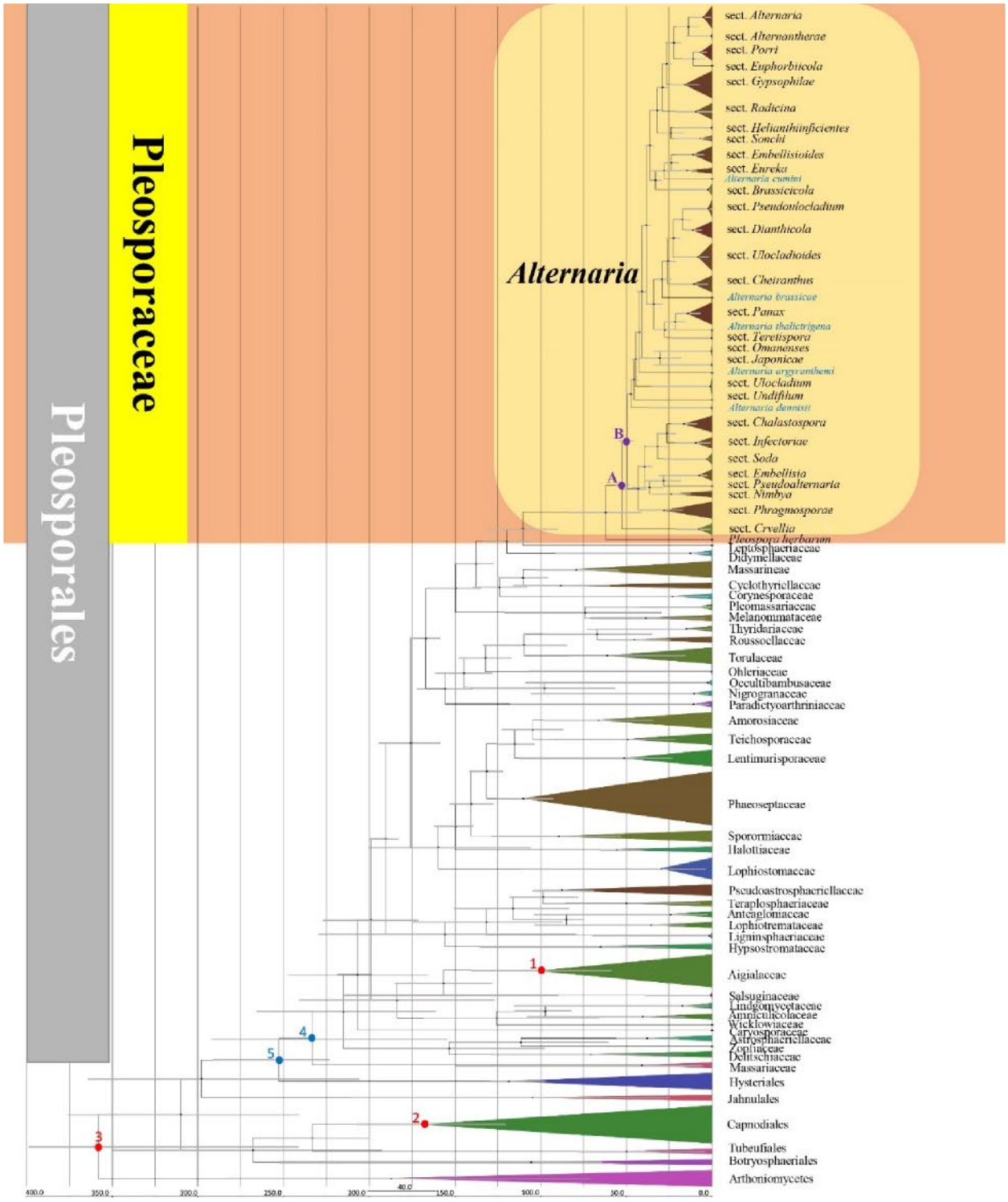

Fig. 2 Maximum clade credibility (MCC) tree with divergence times estimates obtained from BEAST. Numbers in red indicate the fossil (1, 2) and secondary (3) points. Numbers in blue indicate divergence time estimate of Pleosporales (stem age: 5, crown age: 4). Letters in purple indicate divergence time estimate of *Alternaria* (stem age: A, crown age: B). Single lineages of *Alternaria* species are highlighted in blue.

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 *A. 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

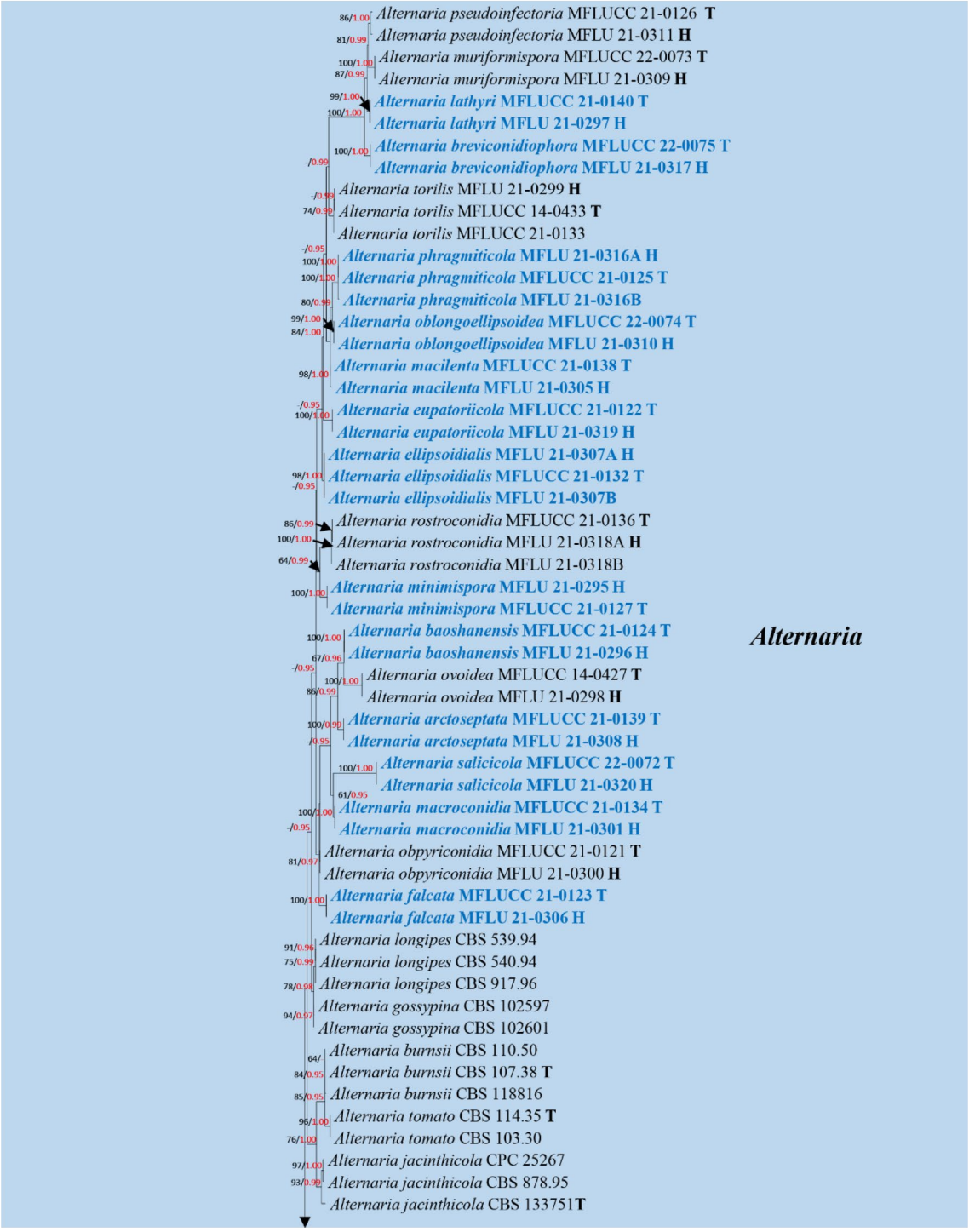

Fig. 3 Phylogenetic construction of genus *Alternaria* using RAxML-based maximum likelihood analysis of a combined ITS, LSU, SSU, *TEF1-α*, *RPB2*, *GAPDH* and *Alt-a1* DNA sequence dataset. Bootstrap support values for maximum likelihood (ML, black) equal to or greater than 70% and Bayesian posterior 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'.

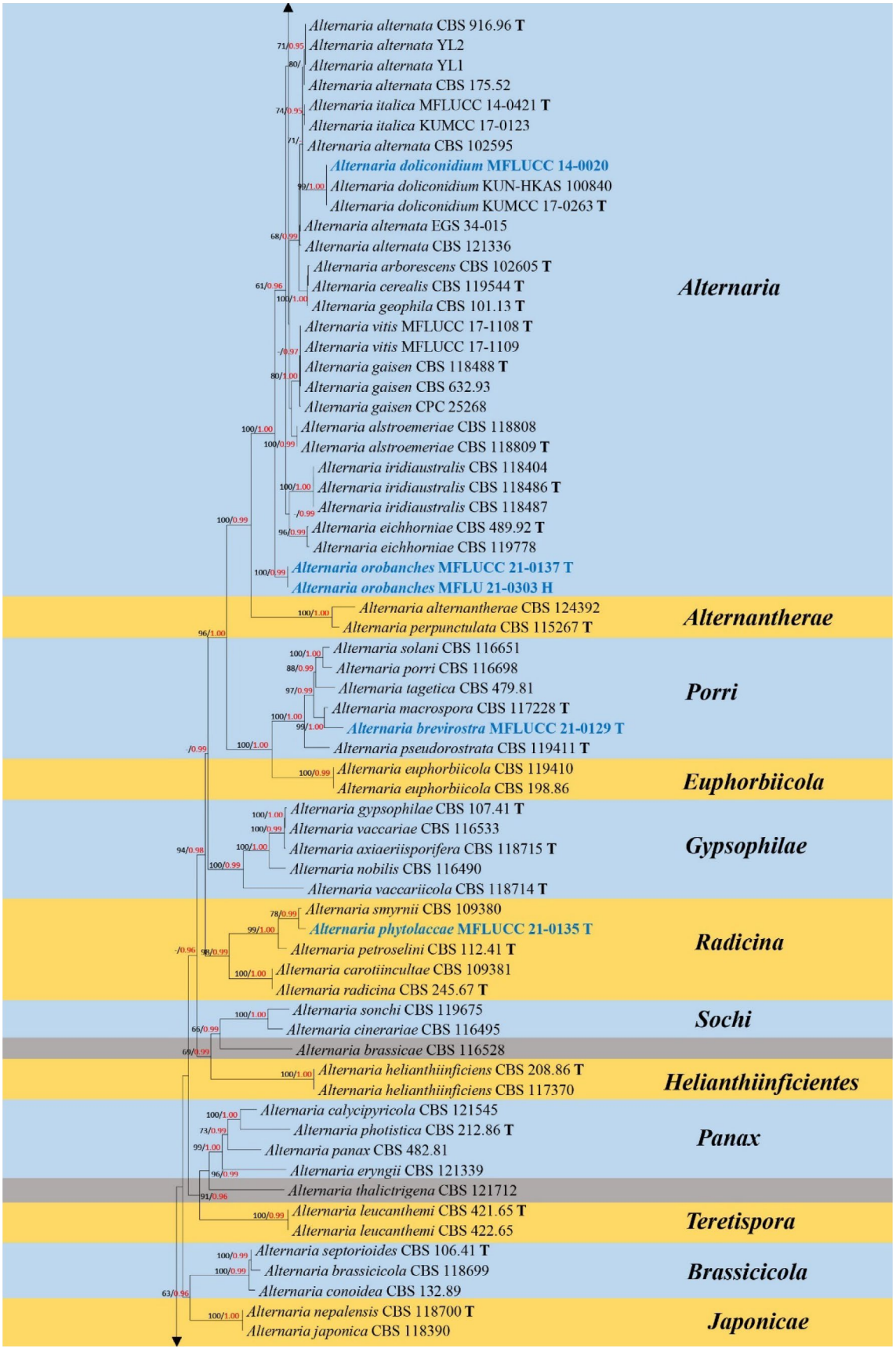

Fig. 3 (continued)

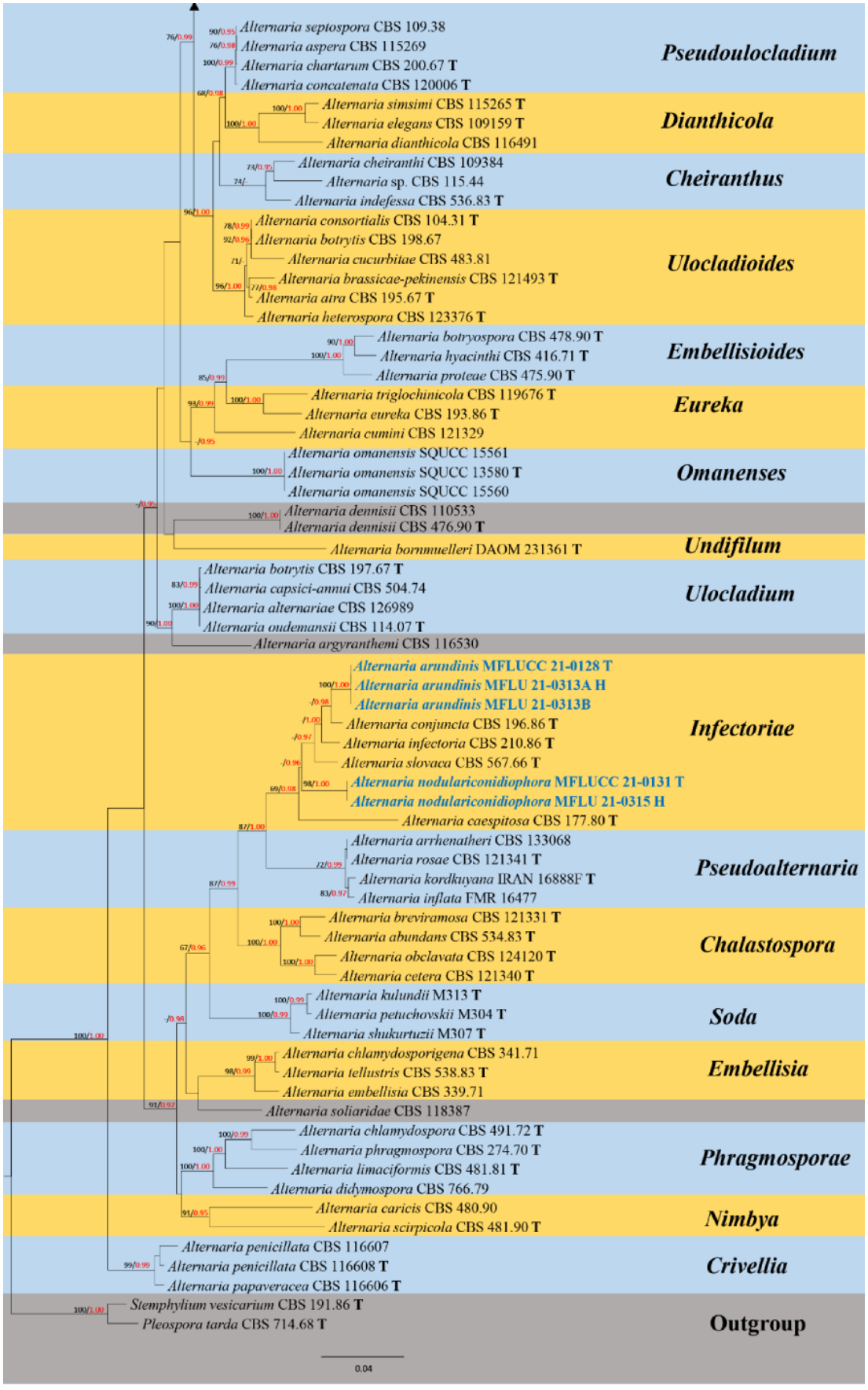

Fig. 3 (continued)

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

Order	Family	Genus	Sections	Divergence times (crown age)	Divergence times (stem age)
Pleosporales				233 (168–301) Mya	252 (184–326) Mya
	Pleosporaceae			110 (79–148) Mya	120 (84–159) Mya
		Alternaria		53 (36–71) Mya	62 (42–85) Mya
			Alternaria sect. *Alternantherae*	0.4 (0–1.5) Mya	14 (6.7–21) Mya
			Alternaria sect. *Alternaria*	5 (1.7–10) Mya	14 (6.7–21) Mya
			Alternaria sect. *Brassicicola*	2.3 (0.5–5.5) Mya	33 (22–45) Mya
			Alternaria sect. *Chalastospora*	16 (8.8–26) Mya	26 (16–38) Mya
			Alternaria sect. *Cheiranthus*	11 (4.23–20) Mya	26 (16–38) Mya
			Alternaria sect. *Crivellia*	7.6 (1.5–19) Mya	53 (36–71) Mya
			Alternaria sect. *Dianthicola*	11 (5.4–18) Mya	17 (10–27) Mya
			Alternaria sect. *Embellisia*	7.4 (2.5–15) Mya	28 (14–43) Mya
			Alternaria sect. *Embellisioides*	11 (5–19) Mya	24 (14–36) Mya
			Alternaria sect. *Eureka*	14 (5.6–24) Mya	28 (18–44) Mya
			Alternaria sect. *Euphorbiicola*	-	11 (5.6–17) Mya
			Alternaria sect. *Gypsophilae*	16 (7.6–26) Mya	27 (18–37) Mya
			Alternaria sect. *Helianthiinficientes*	0.11 (0–0.3) Mya	24 (13–36) Mya
			Alternaria sect. *Infectoriae*	9.5 (4–17) Mya	26 (16–38) Mya
			Alternaria sect. *Japonicae*	–	31 (14–47) Mya
			Alternaria sect. *Nimbya*	24 (11–39) Mya	36 (28–51) Mya
			Alternaria sect. *Omanenses*	–	30 (14–47) Mya
			Alternaria sect. *Panax*	14 (6.8–23) Mya	22 (12–33) Mya
			Alternaria sect. *Phragmosporae*	28 (13–44) Mya	42 (28–58) Mya
			Alternaria sect. *Porri*	6.7 (3–11) Mya	11 (5.6–17) Mya
			Alternaria sect. *Pseudoalternata*	–	28 (14–43) Mya*
			Alternaria sect. *Pseudoulocladium*	2.1 (0.4–5.8) Mya	17 (9.5–27) Mya
			Alternaria sect. *Radicina*	9.3 (3.6–18) Mya	29 (19–40) Mya
			Alternaria sect. *Soda*	3 (0.5–8.4) Mya	32 (26–54) Mya
			Alternaria sect. *Sonchi*	6.8 (2–14) Mya	24 (13–36) Mya
			Alternaria sect. *Teretispora*	0.2 (0–1.03) Mya	27 (17–40) Mya
			Alternaria sect. *Ulocladioides*	8.1 (3–17) Mya	22 (13–32) Mya
			Alternaria sect. *Ulocladium*	0.9 (0.1–2.5) Mya	44 (32–60) Mya
			Alternaria sect. *Undifilum*	–	45 (32–62) Mya

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.[12]. 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. *Pseudoalternaria*. 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[14,15,70].

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

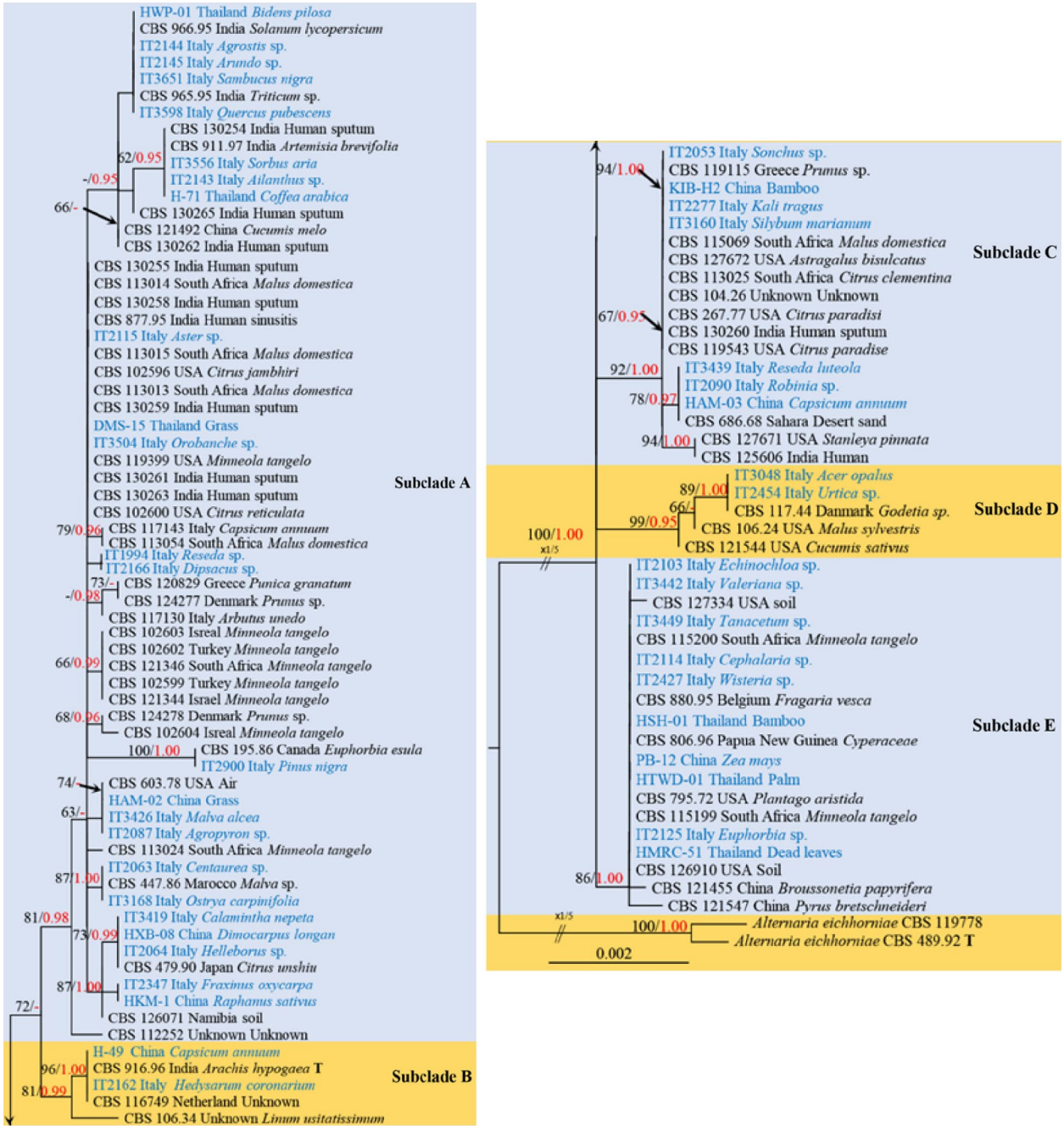

Fig. 4 Phylogenetic construction of *Alternaria alternata* using RAxML-based analysis of a combined ITS, LSU, SSU, *TEF1-α*, *RPB2*, *GAPDH* and *Alt-a1* DNA sequence dataset. Bootstrap support values for maximum likelihood (ML, black) equal to or greater than 60% and Bayesian posterior probabilities (PP, red) equal to or greater than 0.95 are shown above the nodes. The tree is rooted to *Alternaria eichhorniae* (CBS 489.92) and *Alternaria eichhorniae* (CBS 119778). Newly generated strains are in blue, and the type strains are indicated by 'T'.

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-

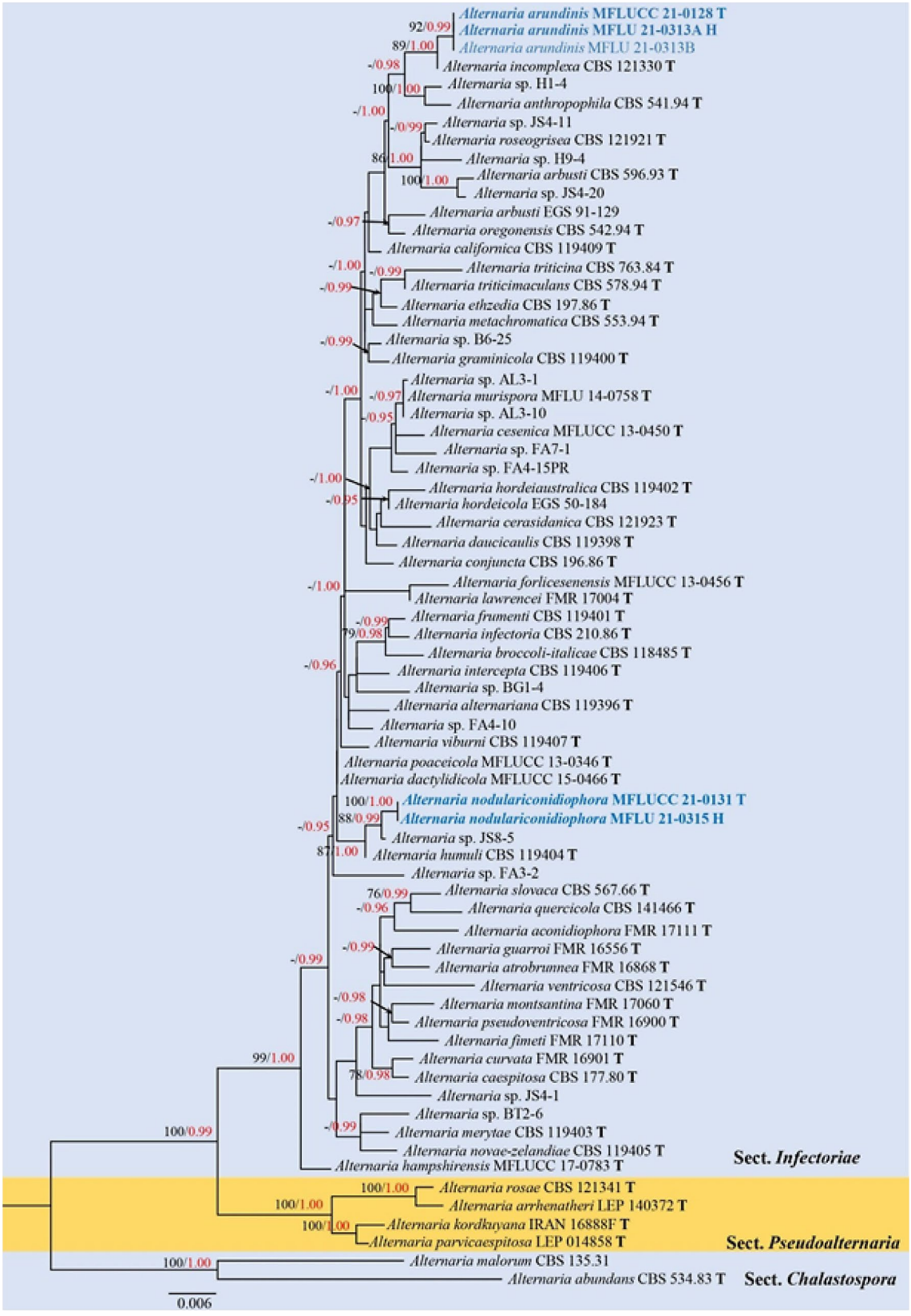

Fig. 5 Phylogenetic construction of *Alternaria* sect. *Infectoriae* using RAxML-based analysis of a combined ITS, *GAPDH* and *ATPase* DNA sequence dataset. Bootstrap support values for maximum likelihood (ML, black) equal to or greater than 70% and Bayesian posterior probabilities (PP, red) equal to 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'.

0129, MFLUCC 21-0130), formed a sister clade with *A. rostellata* (CBS 117366) and clustered with *A. nitrimali* (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

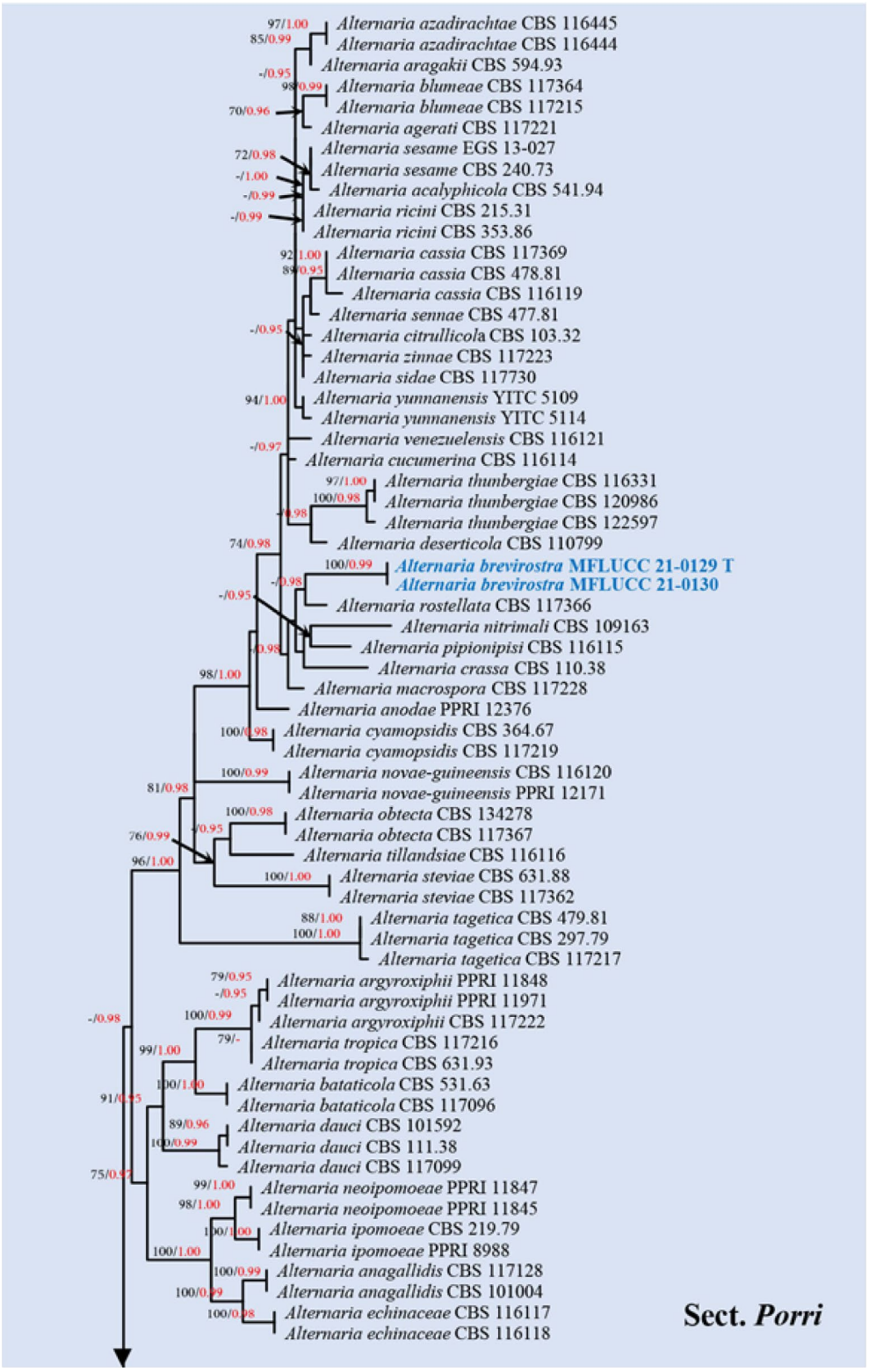

Fig. 6 Phylogenetic construction of *Alternaria* sect. *Porri* using RAxML-based analysis of a combined ITS, *GAPDH*, *TEF1-α*, *RPB2* and *Alt-a1* DNA sequence dataset. Bootstrap support values for maximum likelihood (ML, black) equal to or greater than 70% and Bayesian posterior probabilities (PP, 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'.

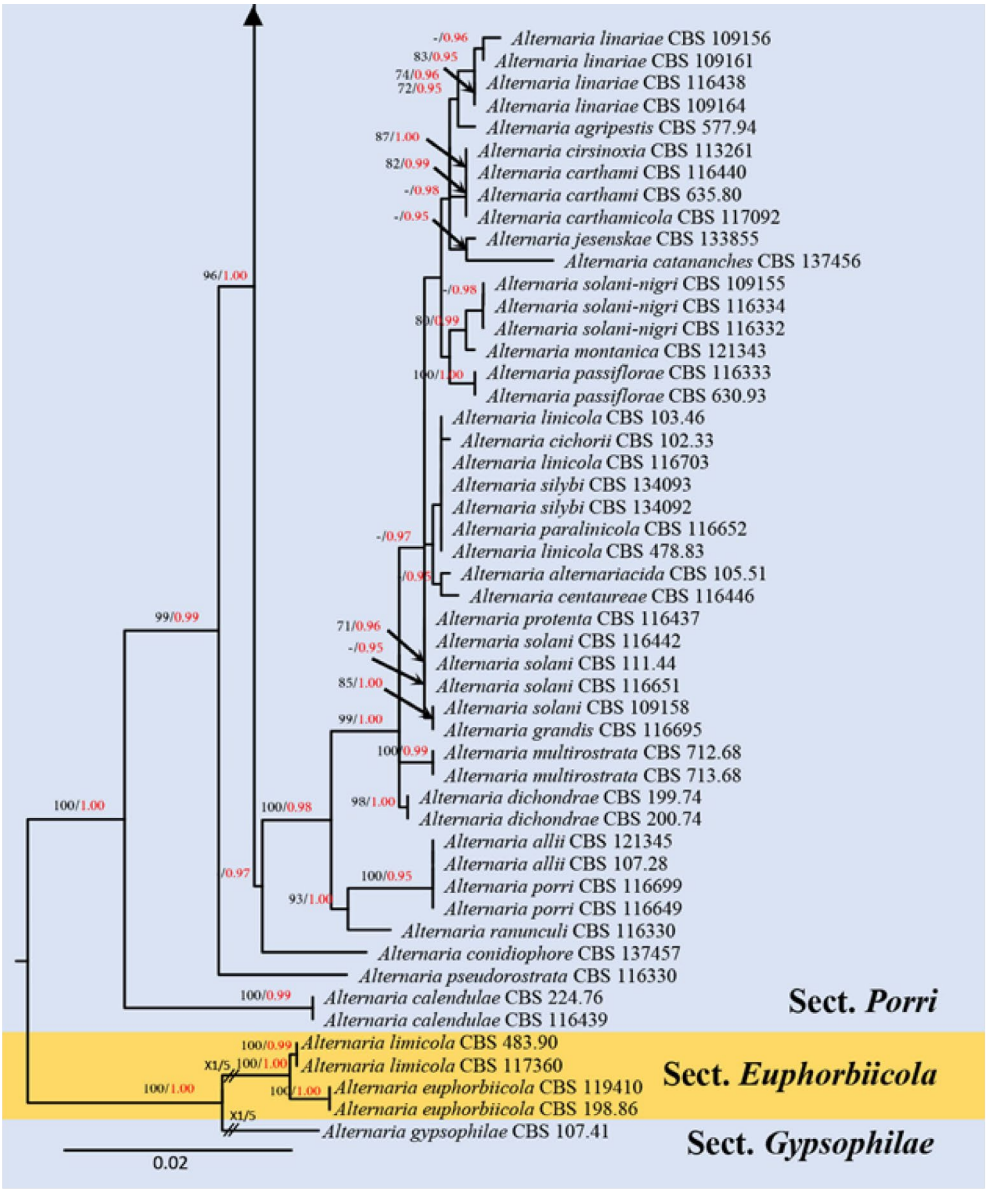

Fig. 6 (continued)

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 phytolaccae*, with other species in sect. *Radicina* and the closely related sect. *Gypsophilae*. 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. helianthiinficiens* (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. phytolaccae* (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

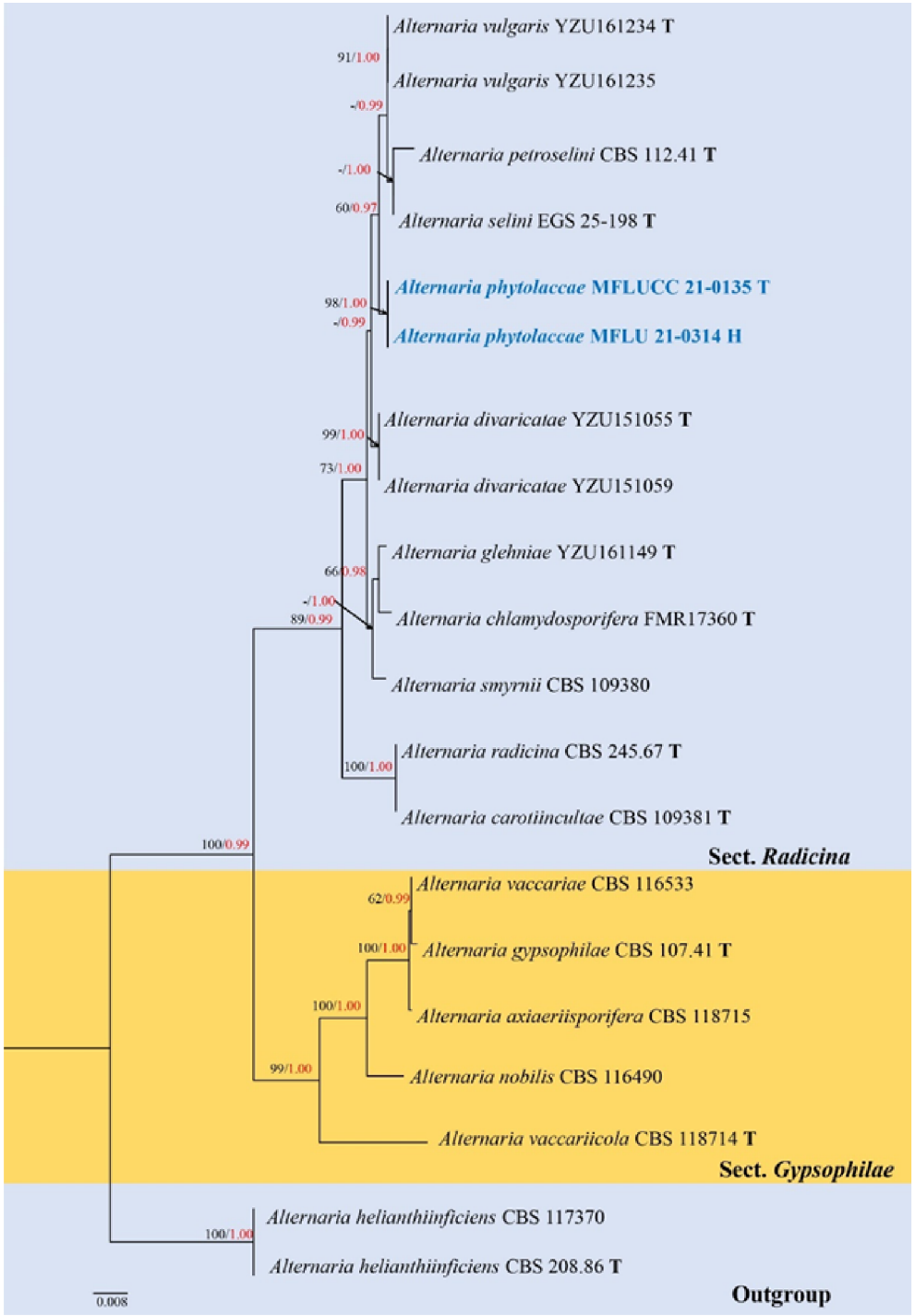

Fig. 7 Phylogenetic construction of *Alternaria* sect. *Radicina* using RAxML-based analysis of a combined ITS, *TEF1-α*, *GAPDH* and *Alt-a1* DNA sequence dataset. Bootstrap support values for maximum likelihood (ML, black) equal to or greater than 60% and Bayesian posterior probabilities (PP, red) equal to or greater than 0.95 PP are shown above the nodes. The tree is rooted to *A. helianthiinficiens* (CBS 208.86 and CBS 117370). Newly generated strains are in blue. The type strains obtained from ex-type culture are indicated by 'T' and the type strains obtained from holotype specimen are indicated by 'H'.

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. ellipsoidialis*, *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.

Fig. 8 Sporulation in *Alternaria* spp. (a) *A. eupatoriicola* (MFLU 21-0319). (b) *A. lathyri* (MFLU 21-0297). (c) *A. oblongoellipsoidea* (MFLU 21-0310). (d) *A. macilenta* (MFLU 21-0305). (e) *A. baoshanensis* (MFLU 21-0296). (f) *A. falcata* (MFLU 21-0306). (g) *A. ellipsoidialis* (MFLU 21-0307). (h) *A. arctoseptata*. (i) *A. salicicola* (MFLU 21-0320). (j) *A. arundinis* (MFLU 21-0313). (k) *A. phytolaccae* (MFLU 21-0314). (l) *A. breviconidiophora* (MFLU 21-0317). (m) *A. phragmiticola* (MFLU 21-0316). (n) *A. minimispora* (MFLU 21-0295). Scale bars: (a)–(n) = 10 μm.

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

Basionym: *Torula alternata* Fr., Syst. Mycol. (Lundae) 3: 500. 1832. (nom. sanct.)

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) × (9–)12–14(–15.5) µm ($\bar{x}$ = 181.4 × 13.2 µm, 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) ×

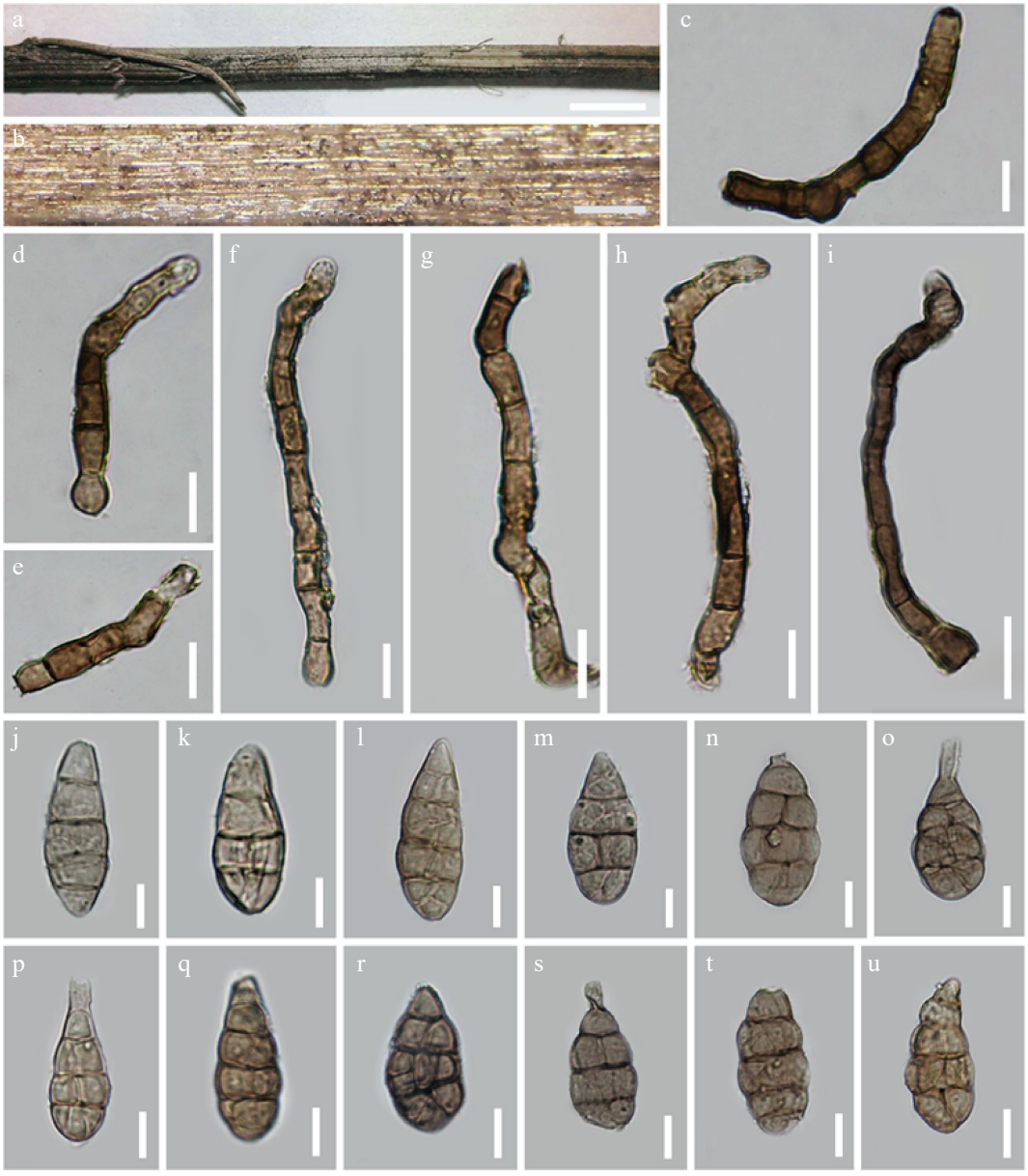

Fig. 9 *Alternaria alternata* (MFLU 21-0302). (a), (b) Colonies on dead branch. (c)–(i) Conidiophores. (j)–(u) Conidia. Scale bars: (a) = 0.1 cm, (b) = 300 µm, (c)–(u) = 20 µm.

(10–)11.5–13(–14) μm ($\bar{x}$ = 14.3 × 12.2 μm, n = 100), mono- to polytretic, integrated, terminal, determinate, percurrent, subhyaline to pale brown, smooth, thin-walled, rounded or doliiform at apex, with 1–3 apical conidiogenous loci. *Conidia* (76–)82.5–91.5(–98) × (22.5–)29–37(–39) μm ($\bar{x}$ = 86.4 × 32.4 μm, n = 100) acrogenous, sometimes catenate, dry, muriform, straight, sometimes curved, ovoid to chiefly obclavate or obpyriform, sometimes formed short, narrow, unbranched beak, grey-brown to brown, 3–4(–8) transverse septa, and 1–2 longitudinal septa, with aseptate 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 ºC, 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 doliiform, aseptate, 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 (MFLU 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-a1* 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, Asteraceae, Betulaceae Brassicaceae, Caprifoliaceae, Fagaceae, Lamiaceae, Malavaceae, Orobanchaceae, Pinaceae, Poaceae, Rubiaceae, Resedaceae, 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 saprobic 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 sinusitis 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 jambhiri* (CBS 102596), *C. reticulata* (CBS 102600) and *Minneola tangolo* (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 annuum* (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, IT 2277, IT 3160, IT 3439, IT 2090 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 5. Additional collections of *Alternaria alternata* collected from Yunnan, China, Italy and Thailand in this study.

Culture collection	Original code	Herbarium no.	Origin	Host and habitat	Collection date	Collector
KUNCC 22-10823	IT2053	HKAS 124866 MFLU 15-2585	Italy, Province of Forlì-Cesena, Premilcuore	Dead stem of *Sonchus* sp. (Asteraceae)	18 August 2014	E. Camporesi
KUNCC 22-10824	IT2063	HKAS 124867	Italy, Province of Forlì-Cesena, Verghereto, Montecoronaro	Dead hanging stem of *Centaurea* sp. (Asteraceae)	20 August 2014	E. Camporesi
KUNCC 22-10825	IT2064	HKAS 124868	Italy, Province of Forlì-Cesena, Fiumicello di Premilcuore	Dead hanging stem of *Helleborus* sp. (Ranunculaceae).	28 August 2014	E. Camporesi
KUNCC 22-10826	IT2087	HKAS 124869	Italy, Province of Forlì-Cesena, Quattro di Forlì	Dead hanging stem of *Agropyron* sp. (Asteraceae)	1 September 2014	E. Camporesi
KUNCC 22-10827	IT2090	HKAS 124870	Italy, Province of Forlì-Cesena, Predappio, Rocca delle Caminate	Dead leaf petiole of *Robinia* sp. (Fabaceae)	4 September 2014	E. Camporesi
KUNCC 22-10828	IT2103	HKAS 124871	Italy, Province of Forlì-Cesena, Meldola	Dead hanging stem of *Echinochloa* sp. (Poaceae)	8 September 2014	E. Camporesi
KUNCC 22-10829	IT2114	HKAS 124872	Italy, Province of Forlì-Cesena, Tessello	Dead hanging stem of *Cephalaria* sp. (Dipsacaseae)	16 September 2014	E. Camporesi
KUNCC 22-10830	IT2115	HKAS 124873	Italy, Province of Forlì-Cesena, Civitella di Romagna	Dead hanging stem of *Aster* sp. (Asteraceae)	19 September 2014	E. Camporesi
KUNCC 22-10831	IT2125	HKAS 124874	Italy, Province of Arezzo, Stia, Montemezzano	Dead hanging stem of *Euphorbia* sp. (Euphorbiaceae)	22 September 2014	E. Camporesi
KUNCC 22-10832	IT2143	HKAS 124875	Italy, Province of Forlì-Cesena, Galeata, San Zeno	Dead hanging leaf petiole of *Ailanthus* sp. (Simaroubaceae)	30 September 2014	E. Camporesi
KUNCC 22-10833	IT2144	HKAS 124876	Italy, Province of Forlì-Cesena, Cabelli di Santa Sofia	Dead hanging stem of *Agrostis* sp. (Poaceae)	2 October 2014	E. Camporesi
KUNCC 22-10834	IT2145	HKAS 124877	Italy, Province of Forlì-Cesena, Monte Mirabello	Dead hanging leaf of *Arundo* sp. (Poaceae)	3 October 2014	E. Camporesi
KUNCC 22-10835	IT2162	HKAS 124878	Italy, Province of Forlì-Cesena, Santa Sofia	Dead hanging stem of *Hedysarum coronarium* L. (Papilionaceae)	7 October 2014	E. Camporesi
KUNCC 22-10836	IT2166	HKAS 124879	Italy, Province of Forlì-Cesena, Meldola, Piandispino	Dead hanging stem of *Dipsacus* sp. (Caprifoliaceae)	7 October 2014	E. Camporesi
KUNCC 22-10837	IT2277	HKAS 124880	Italy, Province of Ravenna, Lido di Dante	Dead hanging stem of *Kali tragus* (L.) Scop. (Amaranthaceae)	2 December 2014	E. Camporesi
KUNCC 22-10838	IT2347	HKAS 124881	Italy, Province of Forlì-Cesena, Collina di Forlì	Several samaras of *Fraxinus oxycarpa* Willd. (Oleaceae)	21 January 2015	E. Camporesi
KUNCC 22-10839	IT2427	MFLU 15-1823	Italy, Province of Forlì-Cesena, Forlì, Via Nenni	Dead hanging stem of *Wisteria* sp. (Caprifoliaceae)	30 March 2015	E. Camporesi
KUNCC 22-10840	IT2454	HKAS 124883	Italy, Province of Forlì-Cesena, Predappio, Rocca delle Caminate	Dead stem of *Urtica* sp. (Urticaceae)	21 April 2015	E. Camporesi
KUNCC 22-10841	IT2900	MFLU 16-1116	Italy, Province of Forlì-Cesena, Santa Sofia, Camposonaldo	Dead needles of *Pinus nigra* J.F. Arnold (Pinaceae)	23 March 2016	E. Camporesi
KUNCC 22-10842	IT3048	MFLU 16-2277	Italy, Province of Forlì-Cesena, Fiumicello di Premilcuore	Dead hanging stem of *Acer opalus* Mill. (Sapindaceae)	27 July 2016	E. Camporesi
KUNCC 22-10843	IT3160	MFLU 16-2883	Italy, Province of Forlì-Cesena, Forlì, Ravaldino in Monte	Dead stem of *Silybum marianum* (L.) Gaertn. (Asteraceae)	15 November 2016	E. Camporesi
KUNCC 22-10844	IT3168	MFLU 16-2904	Italy, Province of Forlì-Cesena, Forlì, Parco Urbano	Dead hanging fruits of *Ostrya carpinifolia* Scop. (Betulaceae)	19 November 2016	E. Camporesi
KUNCC 22-10845	IT3419	HKAS 124888	Italy, Province of Arezzo, Poppi, Quota	Dead hanging stem of *Calamintha nepeta* (Lamiaceae)	25 July 2017	E. Camporesi
KUNCC 22-10846	IT3426	HKAS 124889	Italy, Province of Arezzo, near Croce di Pratomagno	Dead hanging stem of *Malva alcea* L. (Malavaceae)	1 August 2017	E. Camporesi
KUNCC 22-10847	IT3439	HKAS 124890	Italy, Province of Arezzo, Stia, Montemezzano	Dead hanging stem of *Reseda luteola* L. (Resedaceae)	13 August 2017	E. Camporesi
KUNCC 22-10848	IT3442	HKAS 124891	Italy, Province of Arezzo, Montemignaio	Dead hanging stem of *Valeriana* sp. (Caprifoliaceae)	12 August 2017	E. Camporesi
KUNCC 22-10849	IT3449	HKAS 124892	Italy, Province of Forlì-Cesena, Bagno di Romagna, Riofreddo	Dead hanging stem of *Tanacetum* sp. (Asteraceae)	22 August 2017	E. Camporesi
KUNCC 22-1050	IT3504	MFLU 17-1778	Italy, Province of Forlì-Cesena, Bagno di Romagna, Acquapartita	Dead hanging stem of *Orobanche* sp. (Orobanchaceae)	25 September 2017	E. Camporesi
KUNCC 22-10851	IT3556	HKAS 124894	Italy, Province of Forlì-Cesena, Santa Sofia	Dead leaf of *Sorbus aria* Crantz (Rosaceae)	15 November 2017	E. Camporesi
KUNCC 22-10852	IT3598	HKAS 124895	Italy, Province of Ravenna, Faenza, Santa Lucia	Dead leaves of *Quercus pubescens* Willd. (Fagaceae)	13 December 2017	E. Camporesi
KUNCC 22-10853	IT3651	HKAS 124896	Italy, Province of Forlì-Cesena, Meldola	Dead hanging branch of *Sambucus nigra* L. (Adoxaceae)	31 December 2017	E. Camporesi
KUNCC 22-10854	KIB-H2	HKAS 124897	China, Yunnan, Kunming Institute of Botany	Dead fallen leave of bamboo (Poaceae)	26 December 2014	J.F. Li
KUNCC 22-10855	HKM-1	HKAS 124898	China, Yunnan, Kunming, Xundian	Dead stem of *Raphanus sativus* L. (Brassicaceae)	13 March 2015	J.F. Li
KUNCC 22-10856	H-49	HKAS 124899	China, Yunnan, Baoshan	Dead branch of *Capsicum annuum* L. (Solanaceae)	22 October 2015	J.F. Li
KUNCC 22-10857	PB-12	HKAS 124900	China, Yunnan, Pingbian, Dawei Mountain	Dead stem of *Zea mays* L. (Poaceae)	20 September 2017	J.F. Li

(to be continued)

Table 5. (continued)

Culture collection	Original code	Herbarium no.	Origin	Host and habitat	Collection date	Collector
KUNCC 22-10858	HXB-08	HKAS 124901	China, Yunnan, Xishuangbanna	Dead fallen leaves of *Dimocarpus longan* Lour. (Sapindaceae)	8 June 2018,	J.F. Li
KUNCC 22-10859	HAM-02	HKAS 124902	China, Yunnan, Honghe, Amu Mountain	Dead fallen leaves of grass (Poaceae)	15 June 2018	J.F. Li
KUNCC 22-10860	HAM-03	HKAS 124903	China, Yunnan, Honghe, Amu Mountain	Dead aerial stem of *Capsicum annuum* (Solanaceae)	15 June 2018	J.F. Li
KUNCC 22-10861	HSH-01	HKAS 124904	Thailand, Chiang Rai, Muang, Singha Park	Dead culms of bamboo (Poaceae)	23 February 2016	J.F. Li
KUNCC 22-10862	HMRC-51	HKAS 124905	Thailand, Chiang Mai, Mae Taeng, Mushroom Research Center (M.R.C)	Dead fallen leaves of unidentified plant	23 March 2016	J.F. Li
KUNCC 22-10863	DMS-15	HKAS 124906	Thailand, Chiang Rai, Doi Mae Salong	Dead leaves of grass (Poaceae)	24 May 2016	J.F. Li
KUNCC 22-10864	HTWD-01	HKAS 124807	Thailand, Chiang Rai, Mae Fah Luang	Dead leaves of palm (Arecaceae)	25 September 2016	J.F. Li
KUNCC 22-10865	H-71	HKAS 124908	Thailand, Chiang Rai, Doi Chang	Dead leaves of *Coffea arabica* L. (Rubiaceae)	25 July 2018	J.F. Li
KUNCC 22-10866	HWP-01	HKAS 124909	Thailand, Chiang Rai, Wiang Pa Pao	Dead stems of *Bidens pilosa* L. (Asteraceae)	16 October 2018	J.F. Li

aristida (Plantaginaceae) (CBS 795.72) in USA, two strains isolated from *Minneola tangelo* in South Africa (CBS 115200, CBS 115199), an isolate from *Fragaria vesca* in Belgium (CBS 880.95), an isolate from Cyperaceae in Papua New Guinea (CBS 806.96) and two strains isolated from *Broussonetia papyrifera* (CBS 121455) and *Pyrus bretschneideri* (CBS 121547).

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

Index Fungorum number: IF 558434; *Facesoffungi number*: FoF12652; Fig. 10

Etymology: Referring to the constricted septate conidia.

Holotype: MFLU 21-0308

Saprobic on dead standing stem of *Lathyrus* sp. (Fabaceae). **Sexual morph** Undetermined. **Asexual morph** *Mycelium* superficial on the substrate, composed of dark brown hyphae. *Conidiophores* 50–100 × 8–12 μm ($\bar{x}$ = 82 × 9 μm, n = 30), macronematous, straight or flexuous, cylindrical, pale brown to light brown, septate, smooth, thick-walled, arising from a stomatic base, sometimes with swollen knots. *Conidiogenous cells* 11–12 × 10–14 μm ($\bar{x}$ = 11.5 × 12 μm, n = 20), mono- to polytretic, integrated, terminal, determinate or percurrent, cylindrical, subhyaline to pale yellowish, doliiform at apex, with 1–2 conidiogenous loci, smooth, thin-walled. *Conidia* 15–75 × 10–35 μm ($\bar{x}$ = 60 × 25 μm, n = 30) acrogenous, solitary or borne in chain with at least 2–3 conidia, dry, simple, straight or curved, subglobose to ovoid when immature, becoming ellipsoidal to obpyriform or obclavate when mature, with short, narrow, unbranched, aseptate apical beak, occasionally lacking beak, initially yellowish-brown or olivaceous brown, laterally brown to dark brown, sectored, 2–3(–6) transverse septa, with 1–2 longitudinal or oblique septa in some transverse divisions, constricted at some transverse septa, smooth or verrucose, thick-walled, sometimes formed apically, or laterally on secondary conidiophores with 1 conidiogenous locus. *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 within 7 d at 25 °C, mycelium superficial, effuse, radially striate, with irregular edge, white to brown 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 °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, Fiumana, 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. lathyri*. *Alternaria arctoseptata* can be distinguished from *A. lathyri* in 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 stomatic base, which are darker in *A. lathyri*. 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. lathyri*. *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 monotretic, 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[68]. 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

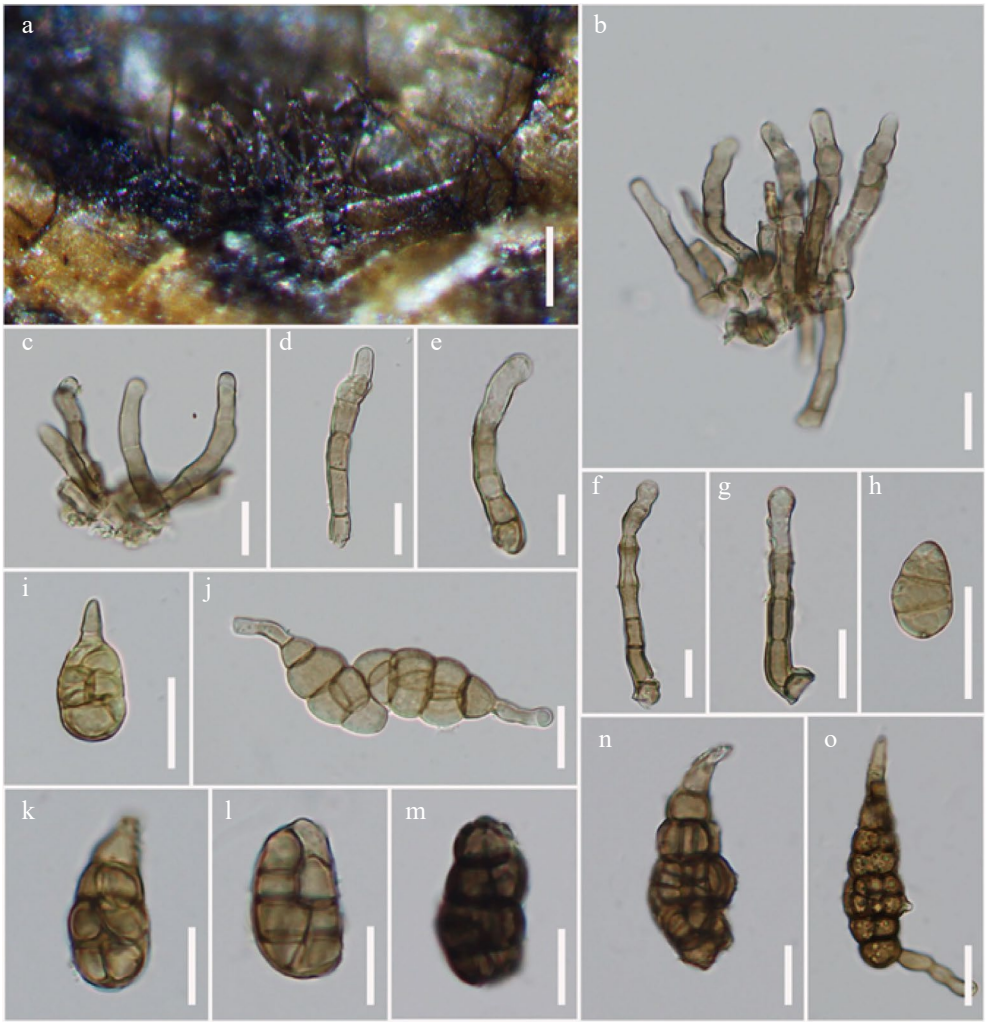

Fig. 10 *Alternaria arctoseptata* (MFLU 21-0308, holotype). (a) Colonies on dead stem of *Lathyrus* sp. (Fabaceae). (b)–(g) Conidiophores bearing conidiogenous cells. (h), (i) Immature conidia. (j), (o) Conidia formed secondary conidiophores. (k)–(n) Mature conidia. Scale bars: (a) = 200 μm, (b)–(o) = 20 μm.

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 × 14 μm, 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 × 7.5 μm, n = 20), mono- to polytretic, integrated, terminal, determinate or percurrent, cylindrical, subhyaline to light brown, doliiform 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 × 18 μm, 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 °C, 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 °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 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

Fig. 11 *Alternaria baoshanensis* (MFLU 21-0296, holotype). (a) Colonies on dead rattan of *Curcubita moschata*. (b)–(e) Conidiophores with a distinct conidiogenous locus. (f)–(l) Variation in shape of conidia. Scale bars: (a) = 200 μm, (b)–(e) = 30 μm, (f)–(l) = 20 μm.

versicolorous conidiophores[68]. Multi-locus phylogeny demonstrated that two strains of *A. baoshanensis* (MFLUCC 21-0124, MFLU 21-0296) form a robust clade (100% ML, 1.00 PP), sister to *A. ovoidea* with 67% ML, 0.96 PP support (Fig. 3). *Alternaria baoshanensis* differs from *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 *A. ovoidea* has conidiogenous loci cicatrized on conidial secession[68]. Furthermore, *A. baoshanensis* has slightly smaller conidia (25–60 × 12–22 μm *vs*. 48–65 × 15.5–30 μm)[68]. Conidia of *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 *A. ovoidea* are solitary, ovoid, orangish brown to copper brown, with 1–3 transverse septa, and 1 longitudinal septum in transverse divisions[68].

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

Index Fungorum number: IF 558436; *Facesoffungi number*: FoF 12654; Fig. 12

Etymology: Named after its short conidiophores and small conidial structures.

Holotype: MFLU 21-0317

Saprobic on dead hanging branches of *Digitalis* sp. (Scrophulariaceae). **Sexual morph** Undetermined. **Asexual morph** *Mycelium* superficial on the substrate, composed of brown to dark brown hyphae. *Conidiophores* 25–88 × 6–10 μm ($\bar{x}$ = 45 × 9 μm, n = 40), macronematous, straight or flexuous, cylindrical, dark brown, smooth, thick-walled, septate, unbranched, arising from stromatic base. *Conidiogenous cells* 8–11 × 8–9 μm ($\bar{x}$ = 9.5 × 8 μm, n = 20), mono- to polytretic, integrated, terminal, determinate or percurrent, cylindrical, paler light brown, apically doliiform, with one or a few conidiogenous loci. *Conidia* 8.6–12 × 7–10 μm ($\bar{x}$ = 10 × 8 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. *Conidial secession* schizolytic.

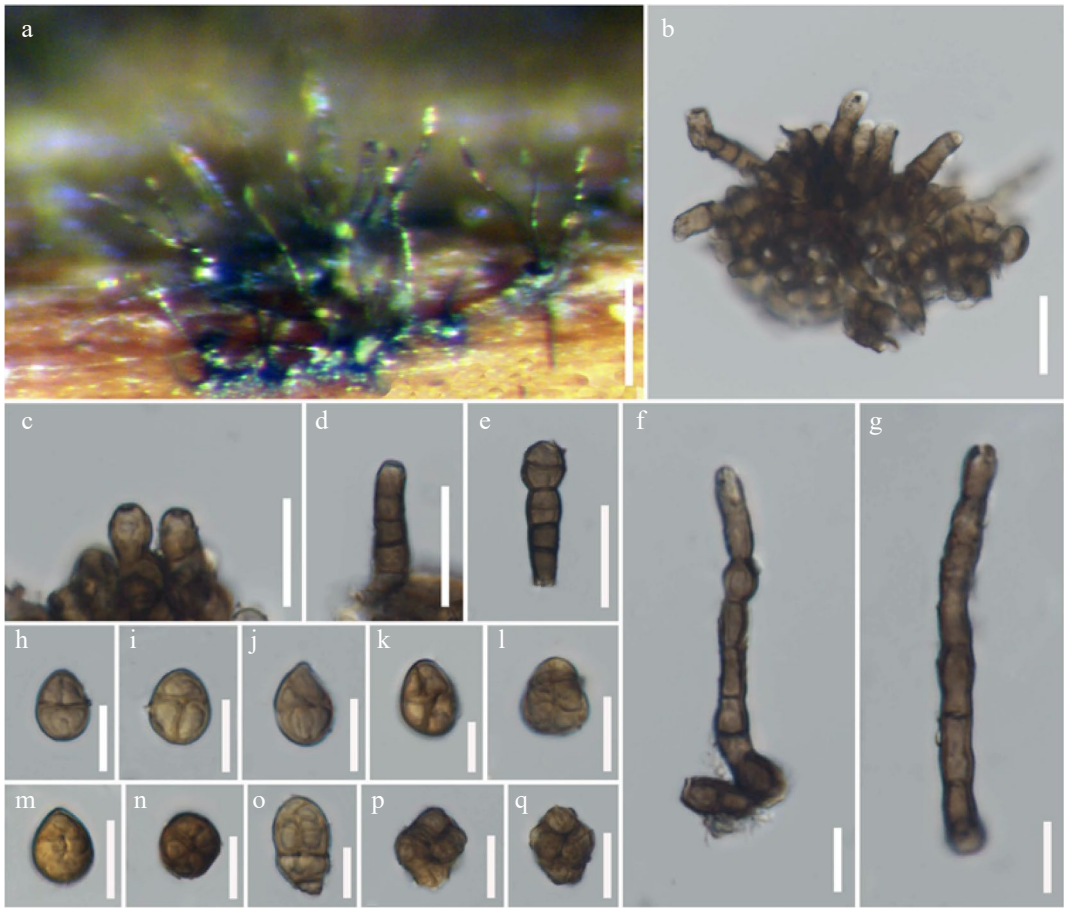

Fig. 12 *Alternaria breviconidiophora* (MFLU 21-0317, holotype). (a) Colonies on dead branch. (b) Conidiophores arising on stomatic base. (c)–(g) Conidiophores. (h)–(q) Conidia. Scale bars: (a) = 50 μm, (b)–(g) = 20 μm, (h)–(q) = 10 μm.

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 25ºC, 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 ($\bar{x}$= 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 11/575 bp (1.9% difference, no gap), differs from *A. muriformispora* 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.

Alternaria doliconidium J.F. Li, Camporesi & K.D. Hyde, in Wanasinghe et al., Fungal Diversity: 10.1007/s13225-018-0395-7, (2018)[147]

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 ($\bar{x}$ = 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 ($\bar{x}$ = 9.6 × 10.2 μm, n = 100), mono- to polytretic, sympodial, integrated, terminal,

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.

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 × 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.

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 °C, mycelium superficial, effuse, radially striate, with irregular edge, grey to light brown hyphae. Conidia sporulated on OA within 30 d, phragmosporous to muriform, 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.[66] 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 doliconidium* 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* (MFLUCC 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. italica* (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. italica*, 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. italica* with *A. alternata* is unresolved in this study, pending further study.

Alternaria ellipsoidialis 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

Saprobic 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 ($\bar{x}$ = 145 × 6.5 μm, n = 30), macronematous, solitary, straight or flexuous, cylindrical, light brown to brown, septate, smooth or verrucose, thick-walled, geniculate near conidiogenous loci. *Conidiogenous cells* 6–9 × 5–7 μm ($\bar{x}$ = 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 ($\bar{x}$ = 60 × 28 μm, n = 30) acrogenous, solitary or borne in chains with at least 2 conidia, straight, curved, ellipsoidal to ovoid, or obpyriform, with short to long, aseptate, unbranched apical beak, sometimes lacking beak, pale to yellowish-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 °C, 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 °C, 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, ellipsoidal to ovoid, or obpyriform, 60 × 30 μm (Fig. 8g).

Material examined – Italy, Province of Arezzo, 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 ellipsoidialis* resembles *A. falcata* due to its ellipsoidal conidia with short beak and curved conidiophores. However, *A. ellipsoidialis* differs from *A. falcata* in having solitary conidiophores with several geniculate conidiogenous loci proliferations at apex, which is rather polytretic than *A. falcata*. In multi-locus phylogenetic analyses (Fig. 3), *A. ellipsoidialis* formed an independent subclade closely related with *A. eupatoriicola* and distant from *A. falcata*. *Alternaria ellipsoidialis* 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. ellipsoidialis*. A *RPB2* nucleotide base comparison showed that *A. ellipsoidialis* differs from *A. eupatoriicola* in 9/550 bp (1.6% difference, no gap). In *GAPDH*, *A. ellipsoidialis* differs from *A. eupatoriicola* in 13/520 bp (2.5% difference, no gap), and in *Alt-a1* the species

Table 6. Nucleotide base comparison of *Alternaria doliconidium* (MFLUCC 14-0020) with closely related taxa.

Species name	Strain no.	Nucleotide difference of gene sequences (no gaps)				
A. doliconidium	MFLUCC 14-0020	ITS	*TEF1-α*	*RBP2*	*GAPDH*	*Alt-a1*
A. alternata	CBS 102595	8/520 bp (1.5%)	14/256 bp (4.7%)	30/875 bp (3.4%)	16/582 bp (2.7%)	12/476 bp (2.5%)
A. alternata	CBS 916.96	8/520 bp (1.5%)	14/256 bp (4.7%)	28/875 bp (3.2%)	18/582 bp (3.1%)	12/476 bp (2.5%)
A. alternata	CBS 175.52	10/520 bp (1.9%)	16/256 bp (6.3%)	30/875 bp (3.4%)	17/582 bp (2.9%)	12/476 bp (2.5%)
A. alternata	YL1	9/520 bp (1.7%)	14/256 bp (4.7%)	30/875 bp (3.4%)	16/582 bp (2.7%)	12/476 bp (2.5%)
A. alternata	YL2	9/520 bp (1.7%)	14/256 bp (4.7%)	30/875 bp (3.4%)	17/582 bp (2.9%)	12/476 bp (2.5%)
A. doliconidium	HKAS 100840	1/520 bp, (0.2%)	0%	N/A	N/A	N/A
A. doliconidium	MFLUCC 17-0263	1/520 bp, (0.2%)	0%	N/A	N/A	N/A
A. italica	MFLUCC 14-0231	6/520 bp, (1.2%)	11/256 bp (4.3%)	25/875 bp, (2.9%)	N/A	N/A
A. italica	KUMCC 17-0123	7/520 bp, (1.3%)	N/A	N/A	N/A	N/A

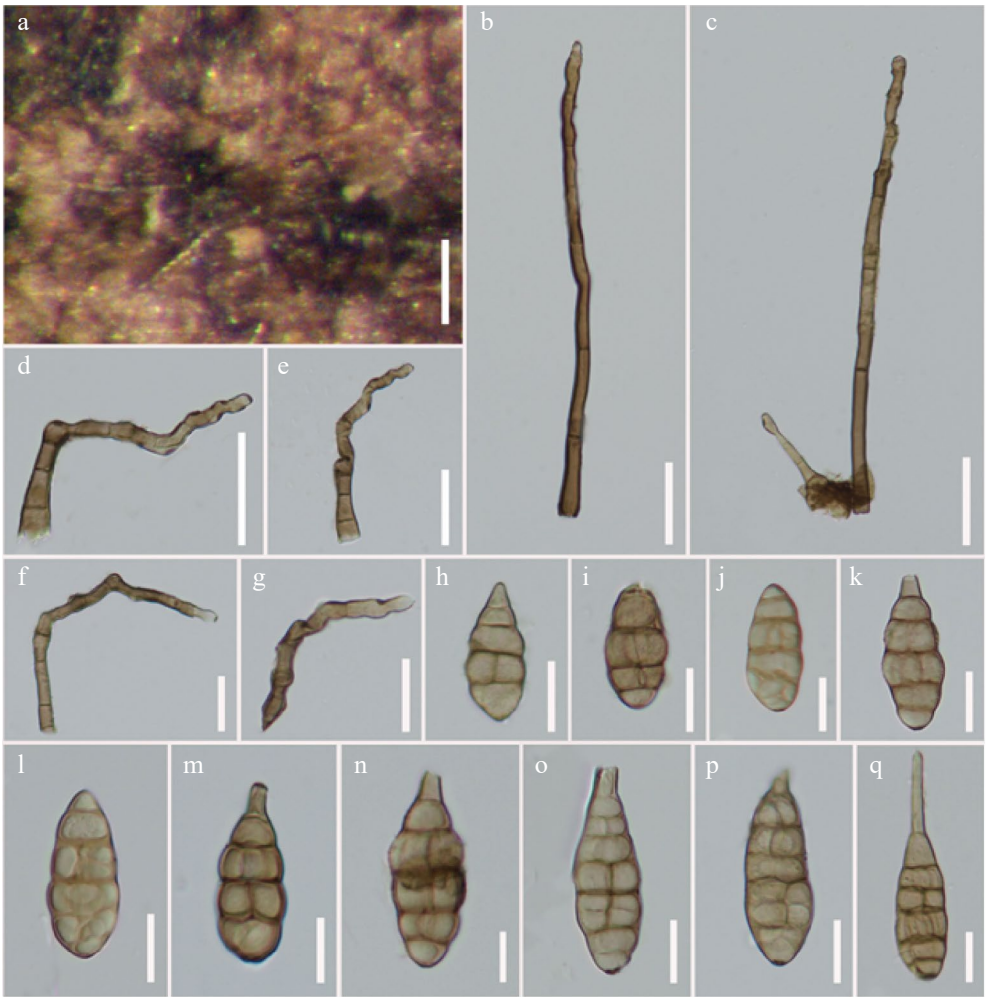

Fig. 14 *Alternaria ellipsoidialis* (MFLU 21-0307, holotype). (a) Colonies on dead hulls of *Brassica* sp. (b)–(g) Conidiophores bearing conidiogenous cells with a few apical conidiogenous loci. (h)–(q) Conidia. Scale bars: (a) = 300 μm, (b)–(g) = 30 μm, (h)–(q) = 20 μm.

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 ($\bar{x}$ = 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 ($\bar{x}$ = 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 ($\bar{x}$ = 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 °C, 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 °C, 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. 15 *Alternaria eupatoriicola* (MFLU 21-0319, holotype). (a) Colonies on dead hanging stem of *Eupatorium cannabinum*. (b)–(f) Conidiophores bearing conidiogenous cells. (g)–(q) Conidia. Scale bars: (a) = 300 μm, (b)–(m) = 20 μm.

Alternaria. The species is basal to *A. pseudoinfectoria*, *A. muriformispora*, *A. lathyri, A. breviconidiophora, 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 ($\bar{x}$ = 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 ($\bar{x}$ = 10.5 × 4.5 μm, n = 20), mono- to polytretic, integrated, terminal, determinate or percurrent, cylindrical, subhyaline, apically doliiform to coronal, with 1–2 conidiogenous loci, smooth, thick-walled. *Conidia* 20–50 × 12–23 μm ($\bar{x}$ = 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, aseptate, 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 °C, 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 °C, 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

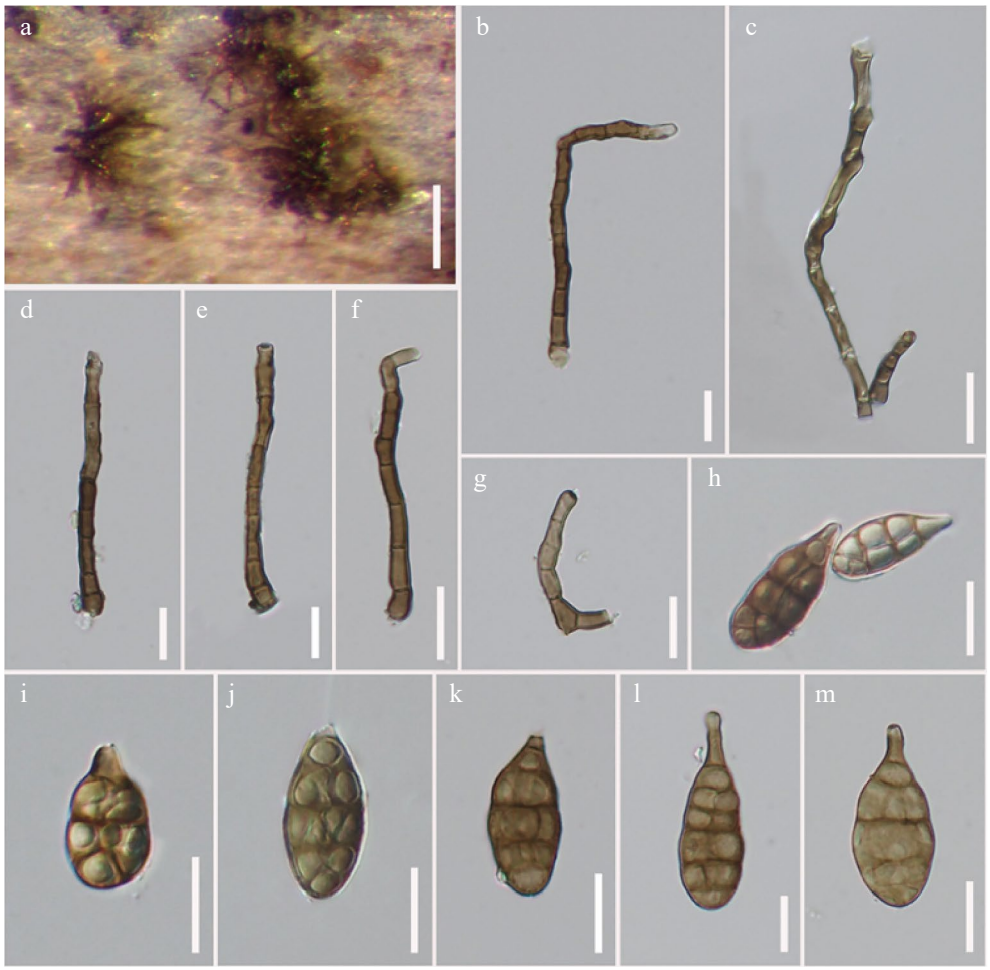

Fig. 16 *Alternaria falcata* (MFLU 21-0306, holotype). (a) Colonies on dead hanging stem of *Atriplex* sp. (b)–(g) Conidiophores bearing conidiogenous cells. (h)–(m) Conidia. Scale bars: (a) = 150 μm, (b)–(m) = 20 μm.

μm *vs*. 60 × 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 × 15 μm *vs*. 38 × 18 μm) and longer (96 × 7 μm *vs*. 48 × 14 μm) solitary concolorous conidiophores, while the species differs from *A. ovoidea* in having smaller (40 μm × 15 μm *vs*. 55 × 27 μm) and paler brown conidia, with a short beak, and shorter (96 × 7 μm *vs*. 280 × 8 μm), curved conidiophores[68]. 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. oviodea* 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.

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 × 11–15 μm ($\bar{x}$ = 115 × 14 μm, n = 20), macronematous, mononematous, straight or flexuous, cylindrical, dark brown to black, smooth, septate, unbranched, thick-walled. *Conidiogenous cells* 13–15 × 8–10 μm ($\bar{x}$ = 12.5 μm × 9 μm, n = 20), mono- to polytretic, integrated, terminal, determinate or percurrent, paler or light brown, smooth, thin-walled, apically rounded to doliiform, with 2–4 conidiogenous loci. *Conidia* 40–65 × 18–31 μm ($\bar{x}$ = 55 × 25 μm, n = 20) acrogenous, borne in chain with at least 2 conidia, straight or curved, ovoid to obpyriform, beakless, 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

Fig. 17 *Alternaria lathyri* (MFLU 21-0297, holotype). (a) Colonies on dead stem dead aerial stem of *Lathyrus* sp. (b) Conidiophores and conidia. (c)–(h) Conidiophores bearing conidiogenous cells. (i)–(n) Conidia. (o) Germinated conidium. Scale bars: (a) = 200 μm, (b)–(o) = 20 μm.

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.

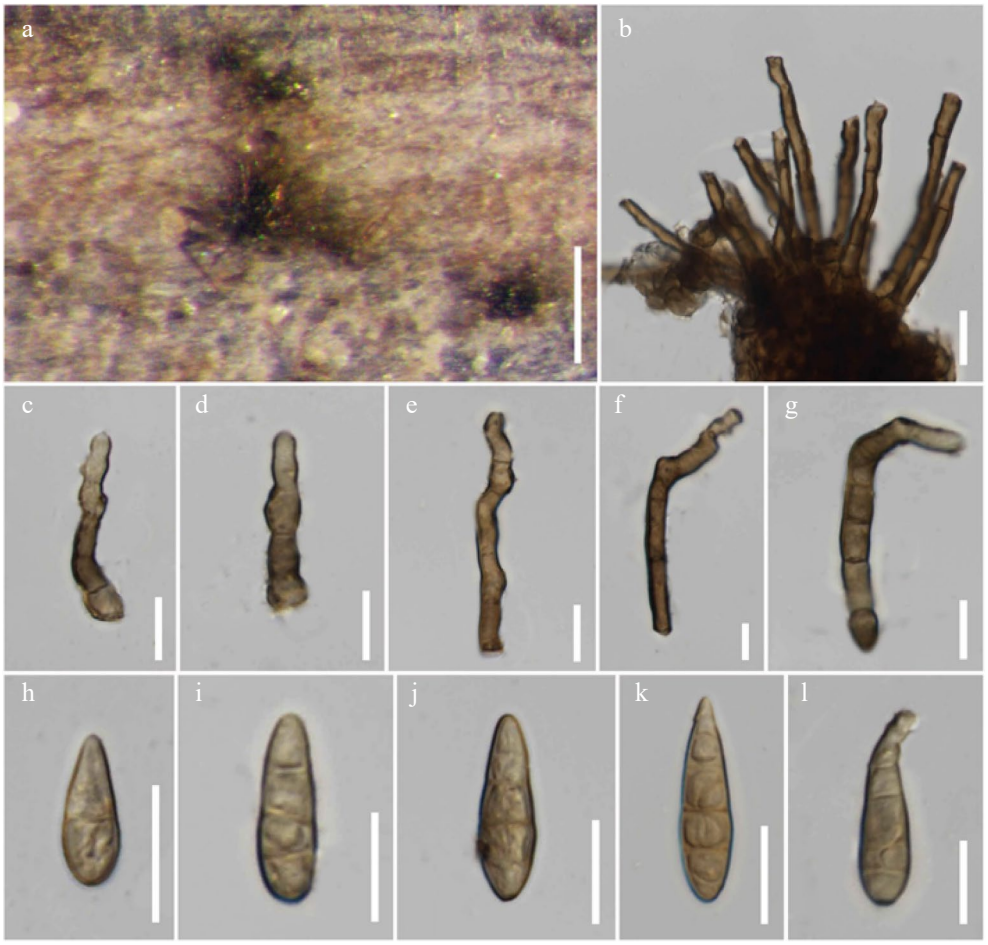

Fig. 18 *Alternaria macilenta* (MFLU 21-0305, holotype). (a) Colonies on dead stem of *Scabiosa* sp. (b)–(g) Conidiophores. (h)–(l) Conidia. Scale bars: (a) = 150 μm, (b)–(l) = 20 μm.

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 ($\bar{x}$ = 85 × 11 μm, n = 30), macronematous, brown, straight or flexuous, cylindrical, septate, unbranched, smooth, thick-walled, aggregated, arising from a stomatic base. *Conidiogenous cells* 20–25 × 8–10 μm ($\bar{x}$ = 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 ($\bar{x}$ = 35 × 9.5 μm, n = 30) acrogenous, solitary or borne in chains with at least 2 conidia, straight, sometimes curved at the apex, subcylindrical to obclavate, beakless, pale brown to light greyish brown, 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 striated, with irregular edge, pale white to white 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 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 Forlì-Cesena, Dovadola, on dead standing stem of *Scabiosa* sp. (Caprifoliaceae), 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. 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.

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 ($\bar{x}$ = 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 ($\bar{x}$ = 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 ($\bar{x}$ = 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 °C, 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

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 conidiogenous 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 Forlì-Cesena, Santa Sofia, Collina di Pondo, on dead aerial branches of *Spartium 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 monotretic conidiogenous 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* (MFLUCC 22-0072, MFLU 21-0320) with 61% ML, 0.95 PP support (Fig. 3). *Alternaria macroconidia* differs *A. salicicola* (MFLUCC 22-0072, MFLU 21-0320) in having larger (75.6 × 27.7 μm *vs*. 45 × 32 μm), olivaceous brown to golden brown or brown conidia, with 3–5 transverse disto- or eusepta, and one longitudinal or oblique or Y-shaped septum in some transverse division. While *A. salicicola* (MFLUCC 22-0072, MFLU 21-0320) has subglobose to obclavate or obpyriform, light yellowish-brown to light brown conidia, with a longer beak, sectored, with several transverse and longitudinal distosepta. In *GAPDH*, *A. macroconidia* differs from *A. salicicola* in 23/569 bp (4% difference, no gap). In *Alt-a1*, *A. macroconidia* differs from *A. salicicola* in 12/520 bp (2.3% difference, no gap). Based on distinct morphological characteristics and phylogenetic support, *A. macroconidia* is introduced as a new species in this study.

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

Index Fungorum number: IF 558443; *Facesoffungi number*: FoF 12661; Fig. 20

Etymology: Named after its tiny conidia.

Holotype: MFLU 21-0295

Saprobic on rotten peel of *Citrullus 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 ($\bar{x}$ = 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 ($\bar{x}$ = 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 conidiogenous loci. *Conidia* 13–25 × 8–11 μm ($\bar{x}$ = 20 × 9.5 μm, n = 30) acrogenous, borne in chain with 2–3 conidia, straight, curved, subglobose to ovoid, sometimes obpyriform or obturbinate, 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 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 rotten peel of *Citrullus 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 conidiogenous 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*[68]. 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 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 ($\bar{x}$ = 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 ($\bar{x}$ = 4.5 × 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 conidiogenous loci. *Conidia* 35–60 × 18–25 μm ($\bar{x}$ = 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, septate beak, pale brown to brown, sectored, 4–7

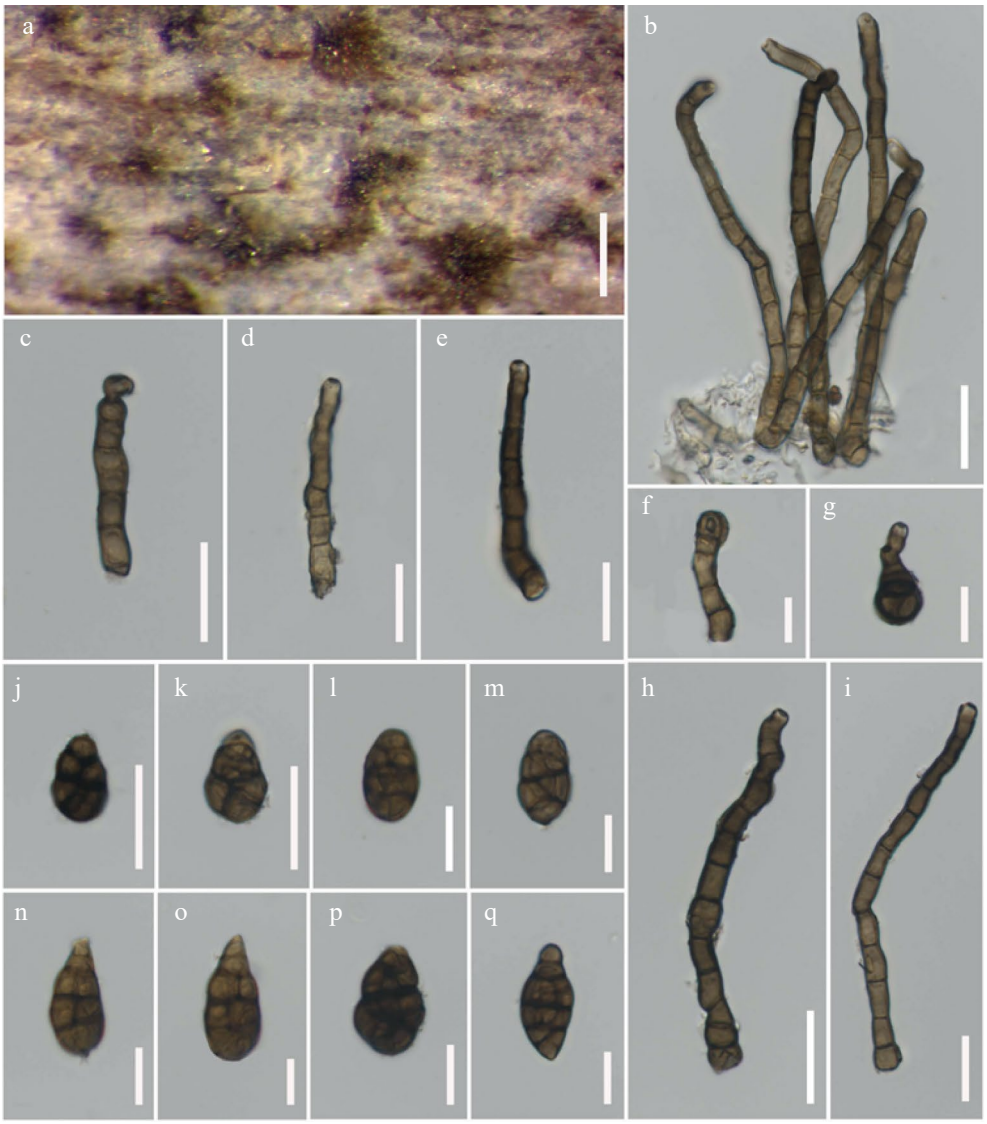

Fig. 20 *Alternaria minimispora* (MFLU 21-0295, holotype). (a) Colonies on rotten peel of *Citrullus lanatus*. (b)–(e), (h), (i) Conidiophores bearing conidiogenous cells. (f) Conidiogenous cells. (g) Secondary conidiophores arising from conidia. (j)–(q) Conidia. Scale bars: (a) = 300 μm, (b)–(e), (h), (i) = 30 μm, (f), (g), (j)–(q) = 10 μm.

transverse eusepta, with 1–2 longitudinal, or oblique or Y-shaped septa in transverse divisions, smooth to minutely 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 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

Fig. 21 *Alternaria oblongoellipsoidea* (MFLU 21-0310, holotype). (a) Colonies on dead stem of *Cichorium intybus*. (b)–(h) Conidiophores bearing conidiogenous cells. (i)–(l) Conidia. (m) Germinated conidium. Scale bars: (a) = 300 μm, (b)–(m) = 20 μm.

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 ($\bar{x}$ = 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 ($\bar{x}$ = 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 ($\bar{x}$ = 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 °C, mycelium superficial, effuse, radially striate, 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 °C, 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 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 stomatic 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

Fig. 22 *Alternaria orobanches* (MFLU 21-0303, holotype). (a) Colonies on dead stem of *Orobanche* sp. (b)–(g) Conidiophores bearing conidiogenous cells. (h) Conidiophores bearing conidiogenous cells with attached conidia. (i)–(q) Conidia. (r) Germinated conidium. Scale bars: (a) = 100 μm, (b)–(r) = 20 μm.

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 ($\bar{x}$ = 90 × 6.5 μm, n = 30), macronematous, straight or flexuous, cylindrical, dark brown, septate, smooth, thick-walled. *Conidiogenous cells* 6–8 × 8–10 μm ($\bar{x}$ = 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 ($\bar{x}$ = 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 °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, 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-

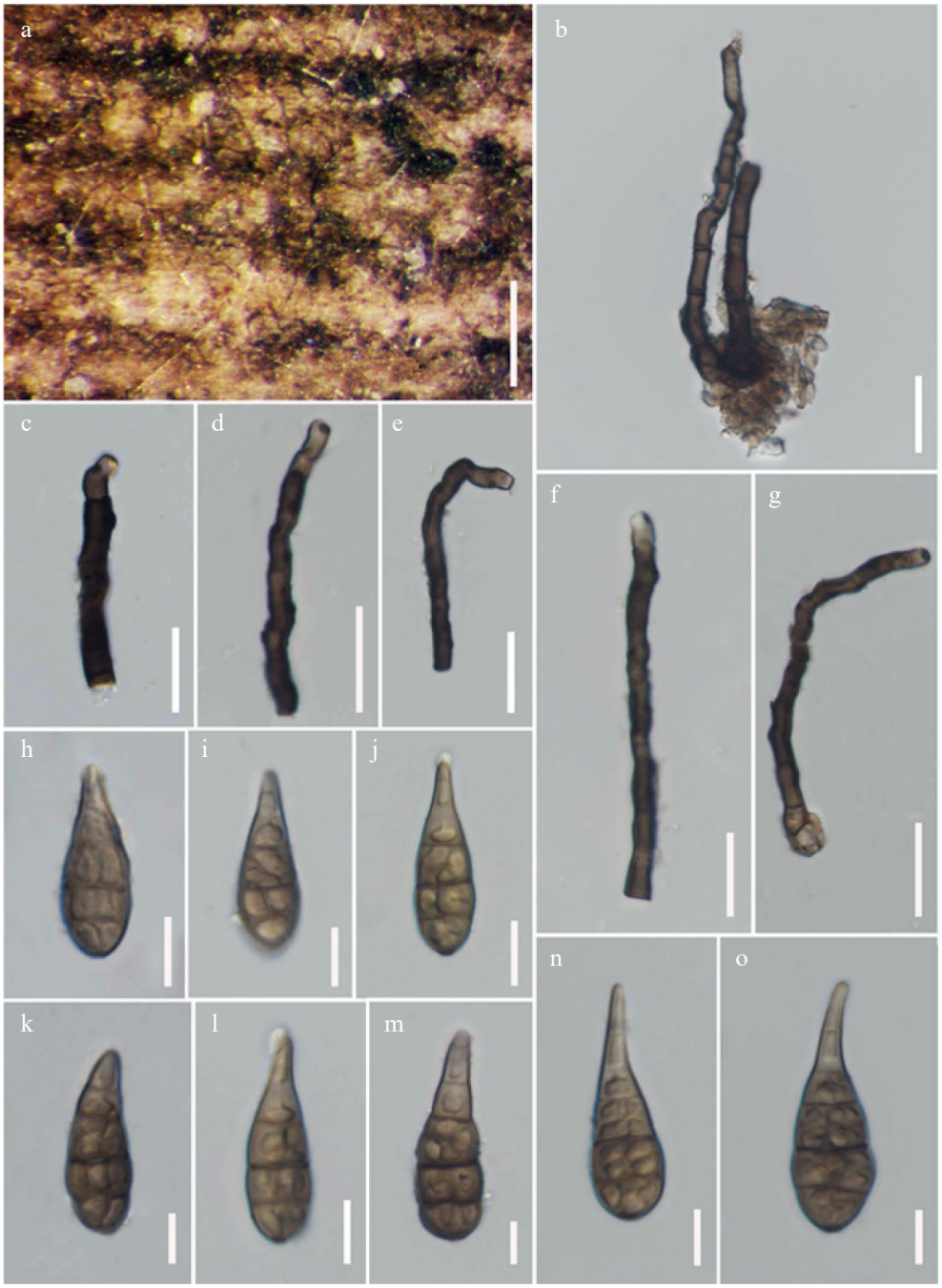

Fig. 23 *Alternaria phragmiticola* (MFLU 21-0316, holotype). (a) Colonies on dead stem *Phragmites* sp. (b)–(g) Conidiophores bearing conidiogenous cells. (h)–(o) Conidia. Scale bars: (a) = 200 μm, (b)–(o) = 20 μm.

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

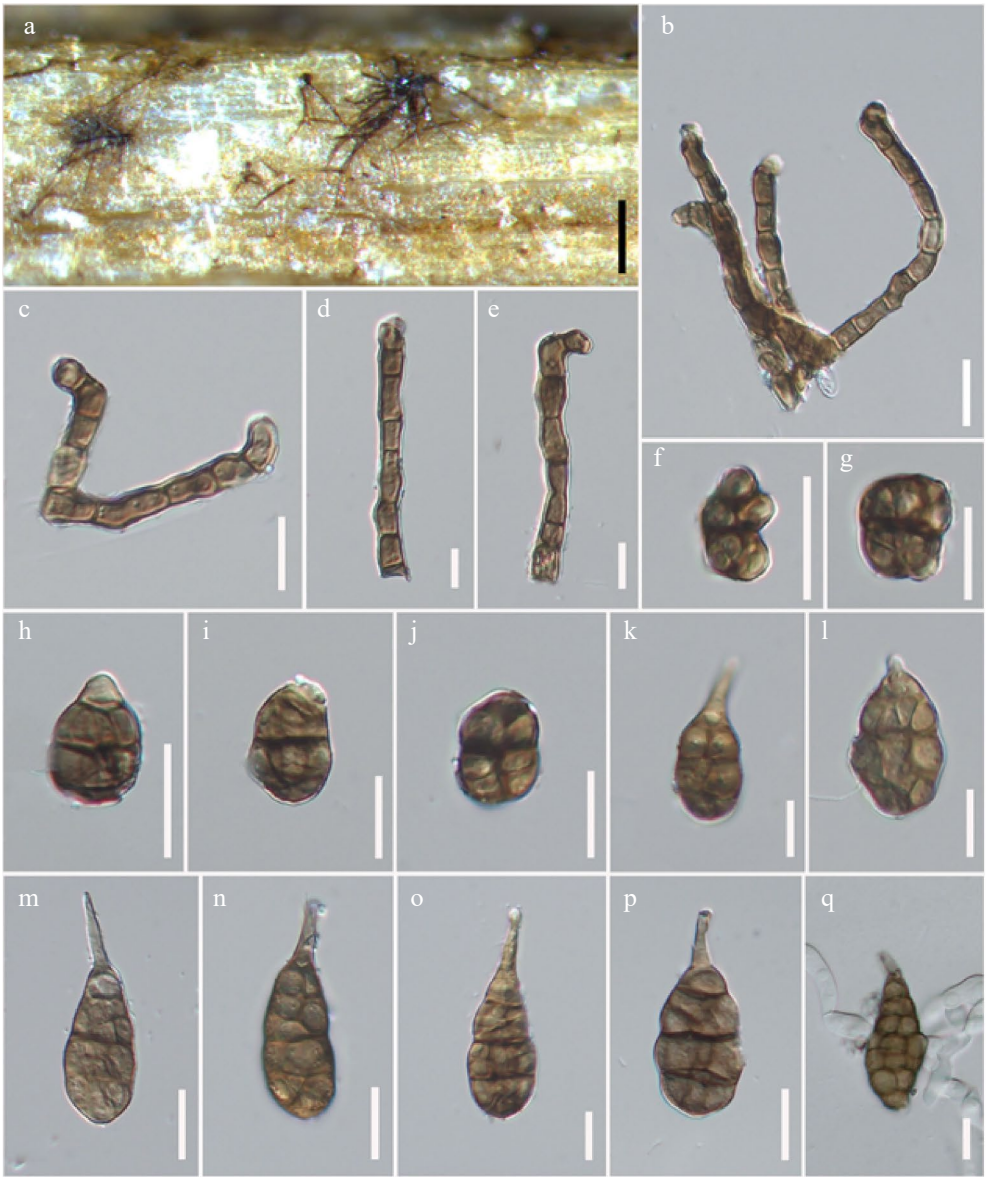

Fig. 24 *Alternaria salicicola* (MFLU 21-0320, holotype). (a) Colonies on dead twig of *Salix alba*. (b)–(e) Conidiophores bearing conidiogenous cells. (f)–(p) Conidia. (q) Germinated conidium. Scale bars: (a) = 150 μm, (b)–(q) = 20 μm.

host substrate, with dark hyphae. *Conidiophores* 110–150 × 10–15 μm ($\bar{x}$ = 135 × 13 μm, 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 × 8–10(–14) μm ($\bar{x}$ = 12.3 × 8.5 μm, 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 × 12–38 μm ($\bar{x}$ = 45 × 32 μm, 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 °C, 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 °C, 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 d, borne in chains with at least 2 conidia, brown to dark brown, with secondary conidiophores, acicular to doliiform, 45 × 30 μm (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*.

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. *Infectoriae* 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 novae-zelandins 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 ($\bar{x}$ = 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 ($\bar{x}$ = 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 ($\bar{x}$ = 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 °C, mycelium superficial, effuse, radially striate, with irregular

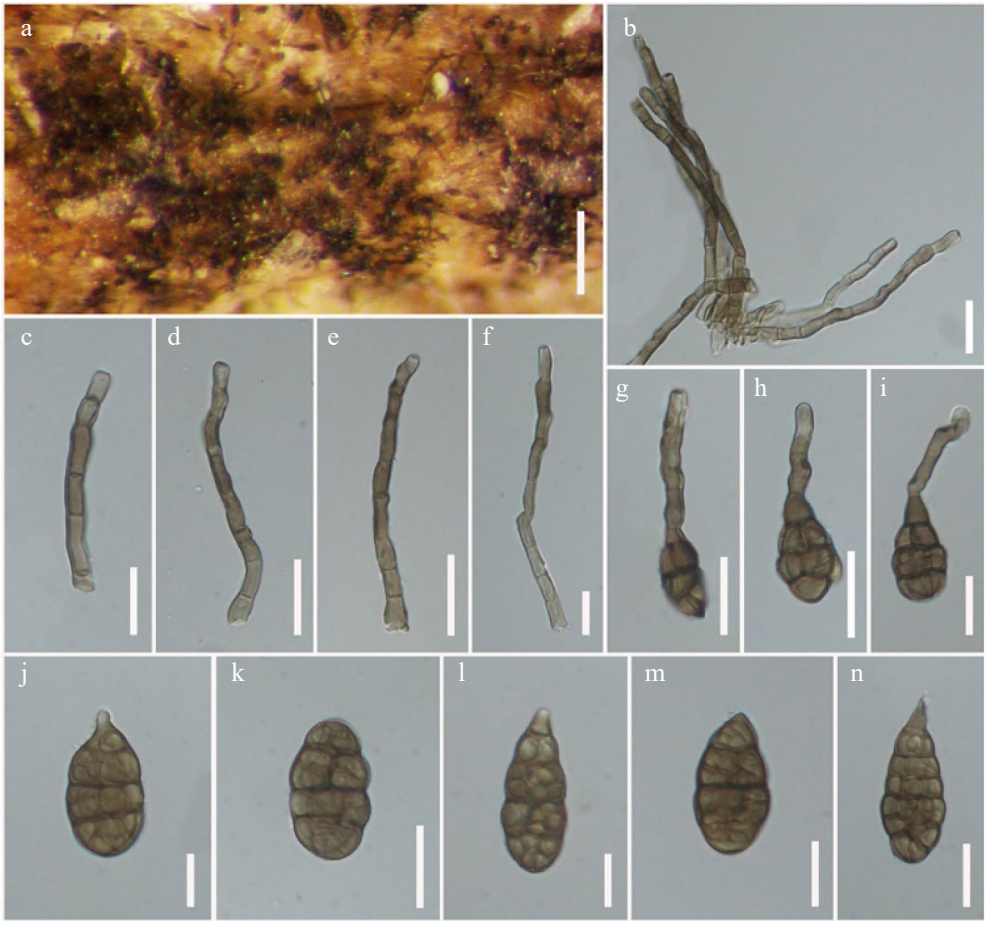

Fig. 25 *Alternaria arundinis* (MFLU 21-0313, holotype). (a) Colonies on dead stem of *Arundo donax*. (b)–(f) Conidiophores bearing conidiogenous cells. (g)–(i) Conidia formed secondary conidiophores. (j)–(n) Conidia. Scale bars: (a) = 150 µm, (b)–(n) = 20 µm.

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 ºC, mycelium superficial, effuse, partly immersed on the media, radially striate, with irregular edge, composed of septate, branched, smooth, thin-walled, 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, with long secondary conidiophores, ellipsoidal to ovoid, or obclavate, 40 × 20 µm (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 µm *vs*. 100 × 4 µm) and slightly larger conidia (38 × 20 µm *vs*. 18–25 × 5–8 µm), which formed secondary conidiophores with several conidiogenous loci, while the conidia can raise up to 30–40 × 8–13 µm, 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 µm *vs*. 26–120 × 4–7 µm) 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 µm *vs*. 11–63 × 6–11 µm), and more longitudinal or oblique euseptate (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.

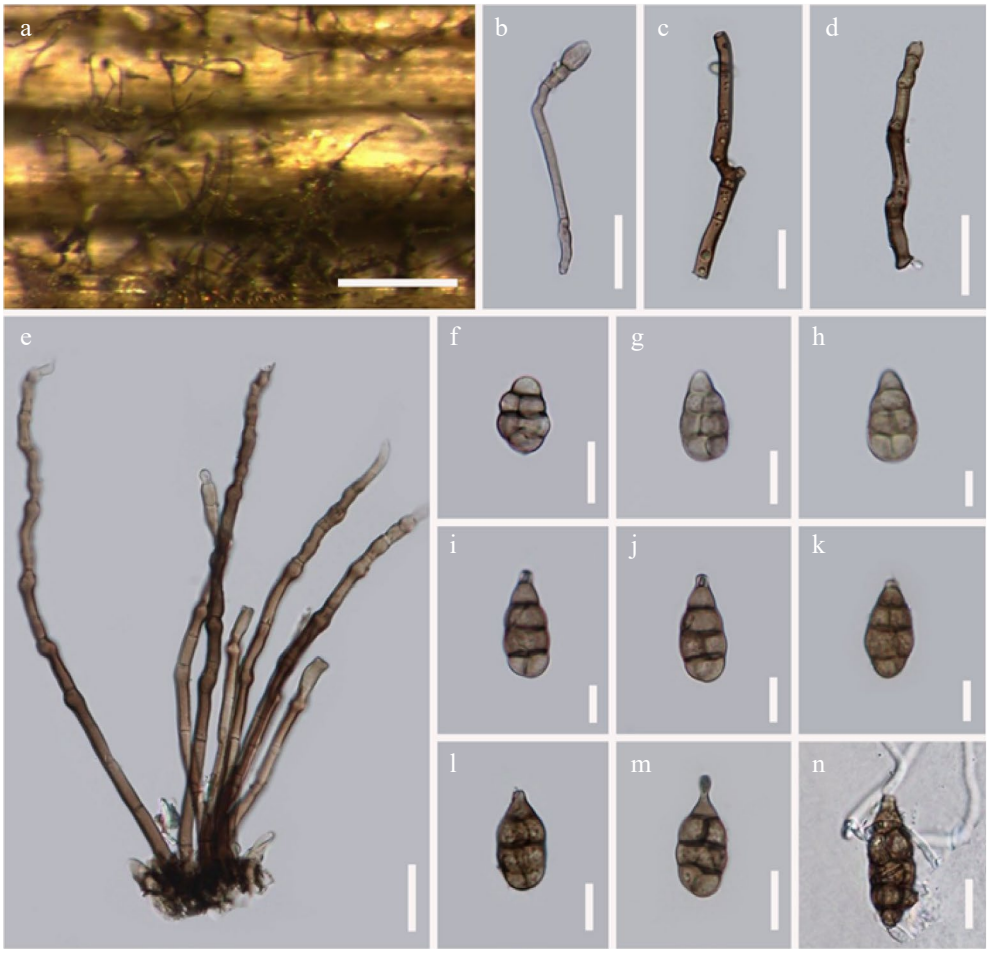

Fig. 26 *Alternaria nodulariconidiophora* (MFLU 21-0315, holotype). (a) Colonies on dead stem of *Heracleum sphondylium*. (b)–(e) Geniculate conidiophores bearing conidiogenous cells. (f)–(m) Conidia. (n) Germinated conidium. Scale bars: (a) = 100 µm, (b)–(n) = 20 µm.

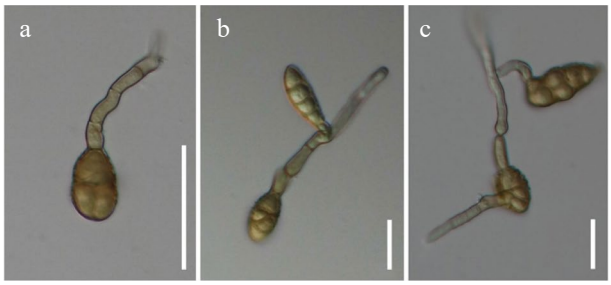

Fig. 27 *Alternaria nodulariconidiophora* (MFLUCC 21-0131) sporulated on PDA. (a) Conidium formed a geniculate secondary conidiophore. (b), (c) Secondary conidiophores bearing conidia with three-dimensional branching patterns. Scale bars: (a)–(c) = 30 μm.

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 ($\bar{x}$ = 175.2 × 18 μm, n = 30), macronematous, aggregated on a stomatic base, straight or flexuous, nodular, cylindrical, light brown to brown, septate, smooth and thick-walled. *Conidiogenous cells* (5.5–)7–9 × 8.6–10 μm ($\bar{x}$ = 8.6 × 9.5 μm, n = 20), holo- to polytretic, integrated, terminal, determinate or percurrent, cylindrical, subhyaline to pale brown, smooth, thin-walled, apically doliiform, with 1–2 conidiogenous loci on bulge. *Conidia* (36–)45–54 × 19–37 μm ($\bar{x}$ = 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 verucose, 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 °C, 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 transverse eusepta, 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, Piandispino, 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 nodularconidiophora* 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 nodularconidiophora* is characterized by subglobose to ovoid, or obturbinate to obpyriform conidia, with a rostrate apex, geniculate conidiophores with swollen knots, arising from a stomatic 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[165]. A ITS nucleotide pairwise comparison showed that *A. nodularconidiophora* 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% diference, no gap) and also differs from *A. humuli* in 11/900 bp (1.5% difference, no gap) in *ATPase* nucleotide pairwise comparison.

Section *Porri* D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 541. 2013.

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. (Plantagineae). **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 ($\bar{x}$ = 68 × 13 μm, n = 30), macronematous, aggregated at the base, flexuous, cylindrical, pale yellowish-brown to light brown, septate, unbranched, smooth, thick-walled. *Conidiogenous cells* 5–6 × 7–7.5 μm ($\bar{x}$ = 5.5 × 7.2 μm, n = 20), polytretic, integrated, terminal, determinate or percurrent, spathulate or dolabriform, subhyaline to pale brown, smooth, thin-walled. *Conidia* 75–84 × 15–20 μm ($\bar{x}$ = 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 °C, mycelium superficial, effuse, radially striate, with irregular edge, brown to dark brown hyphae; conidia not sporulated *in vitro* within 60 d. Colonies growing on PCA, pale white to white, 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, 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. (Plantagineae), 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-

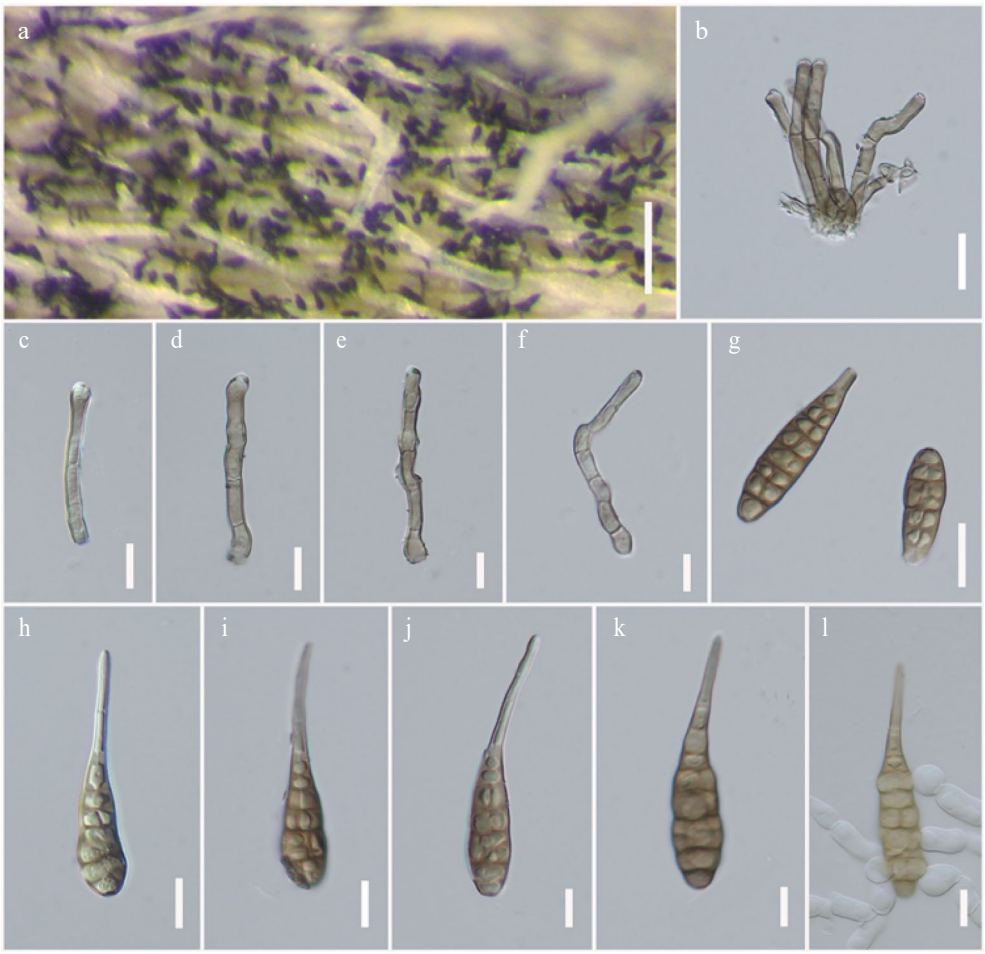

Fig. 28 *Alternaria brevirostra* (MFLU 21-0312, holotype). (a) Colonies on dead stem of *Plantago* sp. (b)–(f) Conidiophores bearing conidiogenous cells. (g)–(k) Conidia. (l) Germinated conidium. Scale bars: (a) = 100 μm, (b)–(l) = 20 μm.

0304), living culture = MFLUCC 21-0130.

Notes – *Alternaria brevirostra* corresponds to species in sect. *Porri via* being borne in chains, long and filamentous rostrate, multiple transverse and longitudinal septa conidia[11]. In phylogenetic analyses, *A. brevirostra* formed a sister clade with *A. rostellata* (CBS 117366) with significant support in BI analysis (0.98 PP; Fig. 6) and clustered with *A. nitrimali* (CBS 109163), *A. pipionipisi* (CBS 116115), *A. crassa* (CBS 110.38) and *A. macrospora* (CBS 117128). *Alternaria brevirostra* can be distinguished from *A. rostellata* in having shorter conidiophores (55–72 × 10–15 μm *vs.* 150–200 × 6.5 μm) and conidiophores were aggregated at the base with polytretic, integrated, terminal, determinate or percurrent conidiogenous cells, whereas *A. rostellata* has simple or branched conidiophores with a single dark conidium terminating each conidiophore[164]. Conidia of *A. rostellata* were slightly shorter (50–80 × 20–30 μm) and solitary, ellipsoidal to broadly ovoid, dilute tawny brown to dark brown in age, smooth to moderately punctate-rough, with 7–9 transverse septa and 1–3 longitudinal septa, with subhyaline, narrow beak at the apex, occasionally a filamentous beak enlarged terminally into a second conidiophore[164]. While conidia of *A. brevirostra* were subcylindrical to obclavate, light yellowish-brown to brown, with 5–7 transverse distosepta, with 1–2 longitudinal or oblique septa in some transverse divisions, smooth, thin-walled, with slightly long, narrow, colorless, acicular, aseptate rostrum.

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), and differed from *A. macrospora* (CBS 117228) by 11/539 bp (2% difference, no gap).

Section *Radicina* D.P. Lawr., Gannibal, Peever & B.M. Pryor, Mycologia 105: 541. 2013.

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 ($\bar{x}$ = 174 × 9 µm, n = 30), macronematous, 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 ($\bar{x}$ = 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.

μm, n = 20), polytretic, integrated, terminal, determinate or percurrent, dolabriform to spathulate, subhyaline, smooth, thin-walled, apically doliiform, with 2–3 conidiogenous loci on side of cell. *Conidia* 30–65 × 20–30 μm ($\bar{x}$ = 45 × 24 μm, n = 30) acrogenous, solitary or borne in chain with 2 conidia, clustered or clumps, curved, ellipsoidal 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 cells. Colonies growing on PDA, cottony, brown to dark brown, reaching 5 cm in 7 d at 25 °C, 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 °C, 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, obturbinate to obpyriform, 37 × 20 μm (Fig. 8k).

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

Notes – *Alternaria phytolaccae* 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. phytolaccae* 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. phytolaccae* differs from *A. petroselini* in 8/520 bp (1.5% difference, no gap), differs from *A. selini* in 8/520 bp (1.5% differencee, no gap) and differs from *A. vulgaris* 9/520 bp (1.7% difference, no gap). In *GAPDH*, *A. phytolaccae* 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[11–15,18,19,22,38,70]. 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, doliiform 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, *TEF1-α*, *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 muriform 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, aseptate 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 *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) (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 speciose genera, a phenomenon already reported for Pestalotiopsis-like species[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*, *Gypsophilae* and *Ulocladium*, while dictyospores and phragmospores can be found in sects. *Infectoriae* and *Phragmosporae*[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[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 subclades. Species in the sects. *Porri* and *Euphorbiicola* are also dispersed in one subclade while taxa in the sects. *Embellisa* 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.[12] 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[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.[14,15], while the *Alt-a1* locus is not reliable to amplify some species within this section[11,14,70]. However, the *cmdA* locus has seldom been used for the phylogeny of most *Alternaria* sections and species[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[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. nodularconidiophora* (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. nodularconidiophora* 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.[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[11,14,22]. 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.[4], Marin-Felix et al.[70] and Tao et al.[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, a new species *A. phytolaccae* (MFLUCC 21-0135 and MFLU 21-0314) is justified and correspond to the morphological and phylogenetic features in sect. *Radicina* in Woudenberg et al.[11] and Lawrence et al.[15]. There is a lack of taxonomic data for this section and further investigations need to be explored on fresh samples.

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[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 multi-locus analyses mainly with combined LSU, SSU and *TEF1-α* regions[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. *Crivellia* in Late Paleocene to early Eocene. Although this divergence time estimate corresponds to those reported by Kalgutkar & Sigler[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. *Crivellia*, *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[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. Secttion *Porri* and sect. *Euphorbiicola* diverged from a clade with a divergence time at 10 (5.6–17.4) Mya. Species in sect. *Euphorbiicola* 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). Secttion *Eureka* and sect. *Embellisioides* 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[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. *Pseudoalternaria* 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. *Pseudoalternaria* may not be as reliable. Species in sect. *Crivellia* are characterized by cylindrical, straight to curved to inequilateral, with transverse eusepta, rarely constricted at septa[11], and they are morphologically distinct from species in other *Alternaria* sections, while sect. *Crivellia* 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.[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[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*.

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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.

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