

Genera of phytopathogenic fungi: GOPHY 4

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Abstract: This paper is the fourth contribution in the Genera of Phytopathogenic Fungi (GOPHY) series. The series provides morphological descriptions and information about the pathology, distribution, hosts and disease symptoms, as well as DNA barcodes for the taxa covered. Moreover, 12 whole-genome sequences for the type or new species in the treated genera are provided. The fourth paper in the GOPHY series covers 19 genera of phytopathogenic fungi and their relatives, including *Ascochyta*, *Cadophora*, *Celoporthe*, *Cercospora*, *Coleophoma*, *Cytospora*, *Dendrostoma*, *Didymella*, *Endothia*, *Heterophaeomoniella*, *Leptosphaerulina*, *Melampsora*, *Nigrospora*, *Pezicula*, *Phaeomoniella*, *Pseudocercospora*, *Pteridopassalora*, *Zymoseptoria*, and one genus of oomycetes, *Phytophthora*. This study includes two new genera, 30 new species, five new combinations, and 43 typifications of older names.

Key words: DNA barcodes, Fungal systematics, New taxa, Typifications.

Taxonomic novelties: New genera: *Heterophaeomoniella* L. Mostert, C.F.J. Spies, Halleen & Gramaje, *Pteridopassalora* C. Nakash. & Crous; **New species:** *Ascochyta flava* Qian Chen & L. Cai, *Cadophora domestica* L. Mostert, R. van der Merwe, Halleen & Gramaje, *Cadophora rotunda* L. Mostert, R. van der Merwe, Halleen & Gramaje, *Cadophora vinacea* J.R. Úrbez-Torres, D.T. O’Gorman & Gramaje, *Cadophora vivarii* L. Mostert, Havenga, Halleen & Gramaje, *Celoporthe foliorum* H. Suzuki, Marinc. & M.J. Wingf., *Cercospora alyssopsidis* M. Bakhshi, Zare & Crous, *Dendrostoma elaeocarpi* C.M. Tian & Q. Yang, *Didymella chlamydospora* Qian Chen & L. Cai, *Didymella gei* Qian Chen & L. Cai, *Didymella ligulariae* Qian Chen & L. Cai, *Didymella qilianensis* Qian Chen & L. Cai, *Didymella uniseptata* Qian Chen & L. Cai, *Endothia cerciana* W. Wang. & S.F. Chen, *Leptosphaerulina miscanthi* Qian Chen & L. Cai, *Nigrospora covidalis* M. Raza, Qian Chen & L. Cai, *Nigrospora globospora* M. Raza, Qian Chen & L. Cai, *Nigrospora philosophiae-doctoris* M. Raza, Qian Chen & L. Cai, *Phytophthora transitoria* I. Milenković, T. Májek & T. Jung, *Phytophthora panamensis* T. Jung, Y. Balci, K. Broders & I. Milenković, *Phytophthora variabilis* T. Jung, M. Horta Jung & I. Milenković, *Pseudocercospora delonicicola* C. Nakash., L. Suhaizan & I. Nurul Fazihah, *Pseudocercospora farfugii* C. Nakash., I. Araki, & Ai Ito, *Pseudocercospora hardenbergiae* Crous & C. Nakash., *Pseudocercospora kenyirana* C. Nakash., L. Suhaizan & I. Nurul Fazihah, *Pseudocercospora perrottetiae* Crous, C. Nakash. & C.Y. Chen, *Pseudocercospora platycericicola* C. Nakash., Y. Hatt, L. Suhaizan & I. Nurul Fazihah, *Pseudocercospora stemonicola* C. Nakash., Y. Hatt., L. Suhaizan & I. Nurul Fazihah, *Pseudocercospora terengganuensis* C. Nakash., Y. Hatt., L. Suhaizan & I. Nurul Fazihah, *Pseudocercospora xenopuniciae* Crous & C. Nakash.; **New combinations:** *Heterophaeomoniella pinifoliorum* (Hyang B. Lee *et al.*) L. Mostert, C.F.J. Spies, Halleen & Gramaje, *Pseudocercospora pruni-grayanae* (Sawada) C. Nakash. & Motohashi., *Pseudocercospora togashiana* (K. Ito & Tak. Kobay.) C. Nakash. & Tak. Kobay., *Pteridopassalora nephrolepidicola* (Crous & R.G. Shivas) C. Nakash. & Crous, *Pteridopassalora lygodii* (Goh & W.H. Hsieh) C. Nakash. & Crous; **Typification: Epitypification:** *Botrytis infestans* Mont., *Cercospora abeliae* Katsuki, *Cercospora ceratoniae* Pat. & Trab., *Cercospora cladradistidis* Jacz., *Cercospora cryptomeriicola* Sawada, *Cercospora dalbergiae* S.H. Sun, *Cercospora ebulicola* W. Yamam., *Cercospora formosana* W. Yamam., *Cercospora fukuii* W. Yamam., *Cercospora glochidionis* Sawada, *Cercospora ixorana* J.M. Yen & Lim, *Cercospora liquidambaricola* J.M. Yen, *Cercospora pancratii* Ellis & Everh., *Cercospora pini-densiflorae* Hori & Nambu, *Cercospora profusa* Syd. & P. Syd., *Cercospora pyracanthae* Katsuki, *Cercospora horiana* Togashi & Katsuki, *Cercospora tabernaemontanae* Syd. & P. Syd., *Cercospora trinidadensis* F. Stevens & Solheim, *Melampsora laricis-urbaniana* Tak. Matsumoto, *Melampsora salicis-cupularis* Wang, *Phaeoisariopsis pruni-grayanae* Sawada, *Pseudocercospora angiopteridis* Goh & W.H. Hsieh, *Pseudocercospora basitruncata* Crous, *Pseudocercospora boehmeriigena* U. Braun, *Pseudocercospora coprosmae* U. Braun & C.F. Hill, *Pseudocercospora cratevicola* C. Nakash. & U. Braun, *Pseudocercospora cymbidicola* U. Braun & C.F. Hill, *Pseudocercospora dodonaeae* Boesew., *Pseudocercospora euphorbiacearum* U. Braun, *Pseudocercospora lygodii* Goh & W.H. Hsieh, *Pseudocercospora metrosideri* U. Braun, *Pseudocercospora paraexosporioides* C. Nakash. & U. Braun, *Pseudocercospora symploci* Katsuki & Tak. Kobay. ex U. Braun & Crous, *Septogloeum punctatum* Wakef.; **Neotypification:** *Cercospora aleuritis* I. Miyake; **Lectotypification:** *Cercospora dalbergiae* S.H. Sun, *Cercospora formosana* W. Yamam., *Cercospora fukuii* W. Yamam., *Cercospora glochidionis* Sawada, *Cercospora profusa* Syd. & P. Syd., *Melampsora laricis-urbaniana* Tak. Matsumoto, *Phaeoisariopsis pruni-grayanae* Sawada, *Pseudocercospora symploci* Katsuki & Tak. Kobay. ex U. Braun & Crous.

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INTRODUCTION

Genera of Phytopathogenic Fungi (GOPHY) is a series of publications introduced in 2017, which aims to provide a comprehensive framework for the taxonomy of major phytopathogenic fungal genera. The papers focus on the genera that are related to plant diseases, although it must be acknowledged that pathogenicity of some species has not been verified through Koch's postulates. The most important purpose of the series is to resolve generic and species boundaries of the fungi studied, because many taxa represent species complexes, or are accommodated in poly- and paraphyletic genera (Crous *et al.* 2015b, 2021). This series links to a larger initiative known as the "The Genera of Fungi Project" (www.Mycobank.org, Crous *et al.* 2014a, 2015a, Giraldo *et al.* 2017), which aims to revise the generic names of all currently accepted fungal genera (Kirk *et al.* 2013). Since many genera and species were described before the molecular era, type materials for many of these taxa have not been designated or are missing, and consequently lack DNA barcodes (Schoch *et al.* 2012). Another aim of this project is to validate the application of names by deriving DNA barcodes of type species of genera and type specimens of species (Crous *et al.* 2021). If type material has not been indicated or preserved, then either type species need to be recollected, or epitypes/neotypes designated and registered in MycoBank (Robert *et al.* 2013). The final objective is to have a single scientific name for each fungal taxon (Wingfield *et al.* 2012, Crous *et al.* 2015b, 2021).

Morphological descriptions and information about the pathology, distribution, hosts and disease symptoms, DNA barcodes, whole-genome sequences for the type species or a new species are provided for selected taxa. The whole-genome sequence provides the most fundamental and complete genetic background of each fungus (Chio & Kim 2017), which can resolve issues pertaining to taxonomy, biology, lifestyles, adaptability to stress and host specificity (Haridas *et al.* 2020).

Three issues of GOPHY have been published to date, in which 62 genera were treated, including the introduction of five new genera, 88 new species, 38 new combinations, four new names and 13 typifications of older names (Marin-Felix *et al.* 2017, 2019a, b). In this fourth contribution, a further 19 genera are treated, resulting in the clarification of their taxonomy and phylogenetic relationships, and the introduction of two new genera, 30 new species, five new combinations and 43 typifications of older names. In addition, 12 whole genomes are newly sequenced, assembled and annotated, and five genome sequences are cited from literature.

Mycologists who wish to contribute to future issues of the GOPHY series are encouraged to contact Pedro Crous (p.crous@wi.knaw.nl) before submission, to ensure there is no overlap with activities arising from other research groups. Preference will be given to genera that include novel species, combinations or typifications. Contributions of the treated genera published in each issue of the series, will be placed on www.plantpathogen.org.

MATERIAL AND METHODS

Isolates and morphological analysis

Descriptions of the new taxa and typifications are based on cultures obtained from the following biobanks: Bioresource Collection and Research Center, Food Industry Research and Development Institute, Hsinchu, Taiwan (BCRC); Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands (CBS); working collection of P.W. Crous (CPC), housed at the Westerdijk Fungal Biodiversity Institute (WI); China Forestry Culture Collection Center, Beijing, China (CFCC); Chinese General Microbiological Culture Collection Center, Beijing, China (CGMCC); Culture Collection of the Forestry and Agricultural Biotechnology Institute (FABI), Pretoria, South Africa (CMW); Coleção Octávio de Almeida Drumond, Universidade Federal de Viçosa, Brazil (COAD); Collections at China Eucalypt Research Centre, Chinese Academy of Forestry, Zhanjiang, Guangdong, China (CSF); Lei Cai's personal collection, housed at the Chinese Academy of Sciences (CAS), China (LC); Culture collection of Mendel University in Brno, Czech Republic (CZ and PA); Mycological Herbarium of the Institute of Microbiology, Chinese Academy of Sciences, China (HMAS); Iranian Fungal Culture Collection, Iranian Research Institute of Plant Protection, Tehran, Iran (IRAN), the Genebank Project, NARO, Tsukuba, Ibaraki, Japan (MAFF); Culture Collection, Laboratory of Plant Pathology, Mie University, Tsu, Mie Prefecture, Japan (MUCC); NBRC Culture Collection, Biological Resource Center, National Institute of Technology and Evaluation, Chiba, Japan (NBRC); herbarium, Department of National Chung Hsing University, Taichung, Taiwan (NCHUPP); Pacific Agri-Food Research Centre Fungal Collection, Summerland, BC, Canada (PARC); Culture collection of the South African National Collection of Fungi (NCF), Roodeplaat, Pretoria, South Africa (PPRI), and the Mycological Herbarium of the Graduate School of Life and Environmental Sciences, University of Tsukuba, Tsukuba, Japan (TSH). For fresh collections, we followed the procedures previously described in Crous *et al.* (1991). Colonies were transferred to different media, *i.e.* carrot agar (CA), cornmeal agar (CMA), malt extract agar (MEA), potato dextrose agar (PDA), synthetic nutrient-poor agar (SNA), oatmeal agar (OA), V8-juice agar (V8A), water agar (WA) (Crous *et al.* 2019c), pine needle agar (PNA; Smith *et al.* 1996), and incubated under different conditions to induce sporulation. Requirements of media and conditions of incubation are specified for each genus. Reference strains and specimens are maintained at CBS, CPC, CGMCC, HMAS, LC and PARC.

Vegetative and reproductive structures were mounted in 100 % lactic acid or Shear's solution either directly from specimens or from colonies sporulating on CMA, MEA, OA, PCA, PDA, PNA, SNA or WA. For cultural characterisation, isolates were grown and incubated on different culture media and temperatures as indicated for each genus. Colour notations were rated according to the colour charts of Rayner (1970). For some taxa, the NaOH spot test was carried out on MEA cultures to detect the production of metabolite E (Boerema *et al.* 2004). Taxonomic novelties were deposited in MycoBank (www.Mycobank.org; Crous *et al.* 2004).

DNA isolation, amplification and analyses

Fungal DNA was extracted and purified directly from the colonies or host material as specified for each genus. Primers and protocols for the amplification and sequencing of gene loci, and software used for phylogenetic analyses can be found in the bibliography related to the phylogeny presented for each respective genus. Phylogenetic analyses consisted of Maximum-Likelihood (ML), Bayesian Inference (BI) and Maximum Parsimony (MP). The ML and the BI were carried out using methods described by Hernández-Restrepo *et al.* (2016), and the MP using those described by Crous *et al.* (2006c). Sequence data generated in this study were deposited in GenBank and the alignments and trees in TreeBASE (<http://www.treebase.org>).

Genome sequencing, assembly and annotation

Five to eight 5-mm-diam discs from the edges of 7-d-old PDA cultures were inoculated in 100 mL autoclaved potato dextrose broth (PDB) for each isolate. The flasks were shaken at 150 rpm for 3–7 d at 25 °C. Mycelia were collected and dried on sterilised filter paper, and then lyophilised. Twelve samples were sent to Annoroad Gene Technology Company Limited (Beijing, China) for genomic DNA extraction and Illumina sequencing on a Novaseq 6000.

Paired reads of 150 bp were assembled using SPAdes v. 3.12.0 (Bankevich *et al.* 2012). The quality of genome assembly was assessed using QUAST v. 5.0.2 (Gurevich *et al.* 2013). Protein-coding gene predictions were performed using Funannotate v. 1.7.0 (Love *et al.* 2019). The inferred proteins were functionally annotated using EggNOG-mapper v. 2.0.0 (Huerta-Cepas *et al.* 2017) with diamond as the mapping mode and the eukaryotic taxonomic scope.

RESULTS

Ascochyta Lib., *emend.* Qian Chen & L. Cai, Stud. Mycol. 82: 185. 2015. Fig. 1.

Classification: Dothideomycetes, Pleosporomycetidae, Pleosporales, Didymellaceae.

Type species: *Ascochyta pisi* Lib. Isotype: BR 5020059493320. Epitype and ex-epitype strain: HMAS 246705, CBS 122785 = PD 78/517.

DNA barcodes (genus): LSU, ITS.

DNA barcodes (species): *rpb2*, *tub2*. Table 1. Fig. 2.

Ascomata pseudothecial, immersed or erumpent, subglobose to flattened, or irregular, solitary or confluent, ostiolate, sometimes developing an elongated neck. *Asci* (sub-)cylindrical to (sub-)clavate, or saccate, sometimes slightly curved, 8-spored, bitunicate, sometimes short-stipitate. *Pseudoparaphyses* filamentous, hyaline, thin-walled, septate, conspicuous in immature fructifications, and disappear at maturity. *Ascospores* ovoid to ellipsoidal, slightly biconic, hyaline to yellowish into the ascus, may become brown when released, smooth, 1-septate, sometimes 3-septate, symmetrical or asymmetrical, constricted at the septum,

uniseriate or biseriate; muriform, 4–6-transversely septate, with one vertical septum, slightly constricted at the septa, hyaline to pale yellow, becoming brown to dark brown at maturity, surrounded by a thick mucilaginous sheath. *Conidiomata* pycnidial, subglobose or ampulliform to mammiform, sometimes irregularly shaped, superficial on or immersed into the agar, solitary or confluent, ostiolate or poroid opening formed at the end of the growing process; *conidiomatal wall* pseudoparenchymatous, multi-layered. *Conidiogenous cells* annellidic or phialidic, hyaline, smooth, variable in shape, *i.e.* globose to subglobose, cylindrical, flask-shaped, obpyriform, lageniform, ampulliform to doliform. *Conidia* hyaline or sometimes slightly coloured (yellow to pale brown), smooth- and thin-walled, aseptate or septate, mostly uniseptate, sometimes 2–3-septate, variable in shape, *i.e.* ovoid, oblong, (sub-)cylindrical, ellipsoidal, cymbiform, bacilliform, fusiform, allantoid, straight or slightly curved, eguttulate or guttulate (Boerema & Bollen 1975, Boerema *et al.* 2004, Chen *et al.* 2015b, 2017). *Chlamydospores* may occur in old cultures (Jellis & Punithalingam 1991, Trapero-Casas & Kaiser 1992, Kaiser *et al.* 1997, Chilvers *et al.* 2009).

Cultural characteristics: Colonies on OA white or slightly grey, pale olivaceous to olivaceous black, yellowish brown to dark brown, or dull green, becoming pale luteous-citrine, buff towards the periphery, aerial mycelium floccose, flat or with scant aerial mycelium, sometimes hazel with honey sterile zones, or with darker concentric zones due to pycnidia, margin regular or irregular.

Optimal media and cultivation conditions: OA or sterile pine needles placed on OA under nuv-light (12 h light, 12 h dark) to promote sporulation at 25 °C.

Distribution: Worldwide.

Hosts: Occurring as saprobes on dead stems of diverse herbaceous plants, polluted lake water and soil, and as weak or noxious pathogens on *Fabaceae*, especially on peas, also on *Apiaceae*, *Caryophyllaceae*, *Lamiaceae*, *Liliaceae*, *Oleaceae* and *Juglandaceae*.

Disease symptoms: Black stem, stem spots, fruit (bean pods) lesions, leaf spots, seed-borne diseases.

Notes: Libert (1830) established the asexually typified genus *Ascochyta*, based on its type species *A. pisi*, to accommodate some phytopathogenic species characterised by producing predominately uniseptate hyaline conidia and phialidic conidiogenous cells. Species in *Ascochyta* are highly similar to *Phoma* spp. in morphology, physiology, pathogenicity and molecular sequences, resulting in ambiguous generic boundaries (Aveskamp *et al.* 2010). Conidiogenesis and conidial septation were used to discriminate species of *Phoma* and *Ascochyta* in the Saccardoan system (Boerema & Bollen 1975, Aveskamp *et al.* 2010, Chen *et al.* 2015b), but Punithalingam (1979) considered that these characters were not appropriate as taxonomic criteria for distinguishing species. Chen *et al.* (2015b) clarified conidiogenesis to be phialidic in both genera. Recent molecular phylogenetic studies revealed both *Ascochyta* and *Phoma*, as traditionally defined, to be highly polyphyletic (Aveskamp *et al.* 2010). A later systematic revision of the *Didymellaceae*, however, redefined both genera as two monophyletic groups based on multi-locus sequence typing (Chen *et al.* 2015b, 2017, Hou *et al.* 2020a).

Currently, 20 species are recognised in the genus *Ascochyta* that are supported by ex-type or representative cultures and DNA

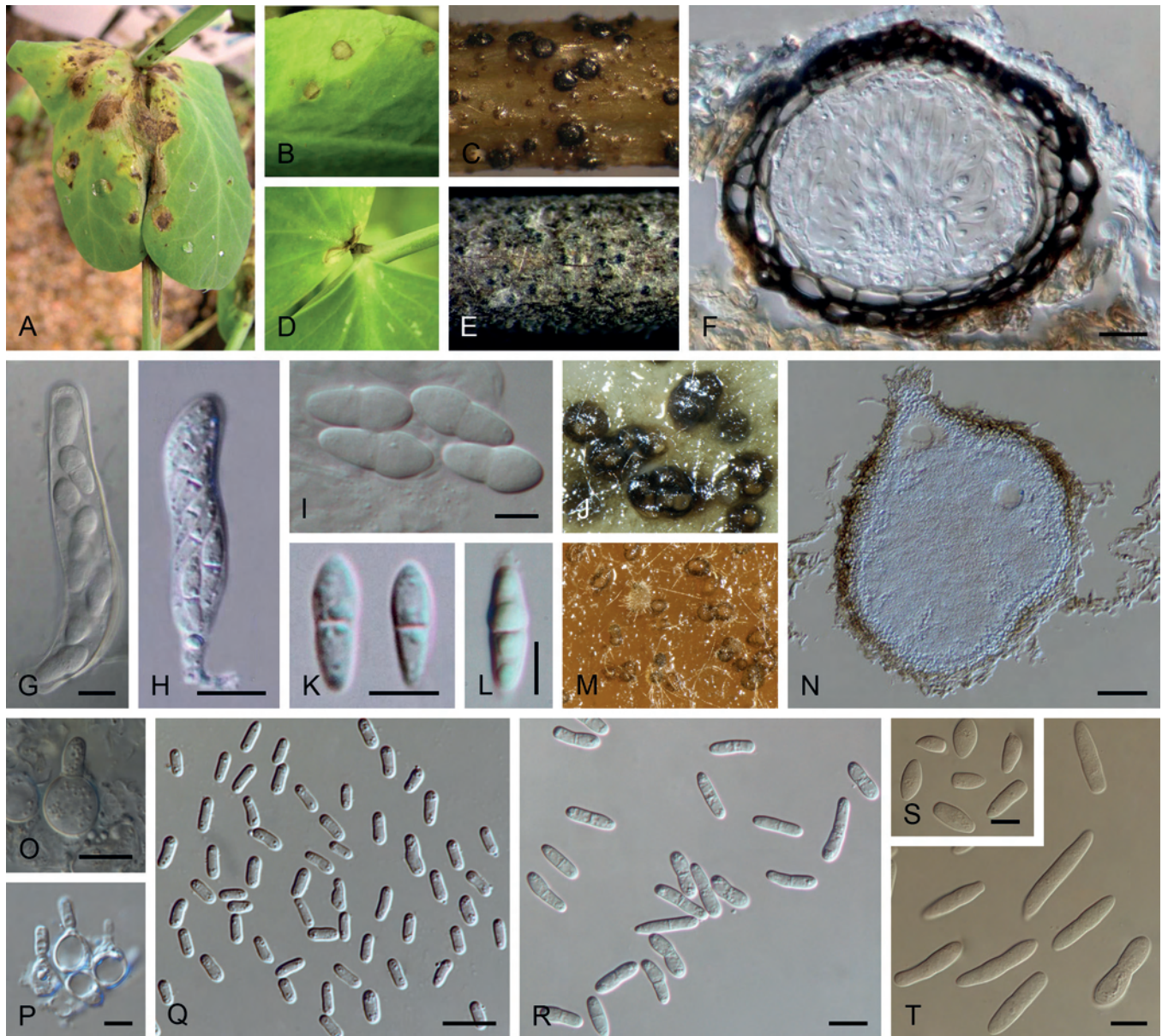


Fig. 1. *Ascochyta* spp. **A, B, D.** Disease symptoms. **A.** Symptoms caused by *Ascochyta koolunga* on field pea seedlings. **B, D.** Symptoms caused by *Ascochyta pisi* on *Pisum sativum* cv. 'Lifter'. **C, E–L.** Sexual morph. **C, E.** Ascomata on host surface. **C.** Ascomata of *Ascochyta pisi* on stem of *Pisum sativum* cv. 'Lifter'. **E.** Ascomata of *Ascochyta clinopodiicola* (holotype MFLU 17-1034) on dead aerial stem of *Clinopodium nepeta*. **F.** Section through ascoma of *Ascochyta clinopodiicola* (holotype MFLU 17-1034). **G, H.** Asci. **G.** *Ascochyta pisi* (WSP 71448). **H.** *Ascochyta clinopodiicola* (holotype MFLU 17-1034). **I, K, L.** Ascospores. **I.** *Ascochyta phacae* (holotype ZT Myc 54988). **K.** *Ascochyta clinopodiicola* (holotype MFLU 17-1034). **L.** *Ascochyta rosae* (ex-type MFLUCC 15-0063). **J, M–T.** Asexual morph. **J, M.** Conidiomata forming on OA. **J.** *Ascochyta benningiorum* (ex-type CBS 144957). **M.** *Ascochyta koolunga* (CBS 372.84). **N.** Section through the conidioma of *Ascochyta benningiorum* (ex-type CBS 144957). **O, P.** Conidiogenous cells. **O.** *Ascochyta koolunga* (CBS 372.84). **P.** *Ascochyta pilosella* (ex-type CBS 583.97). **Q–T.** Conidia. **Q.** *Ascochyta clinopodiicola* (CBS 123526). **R.** *Ascochyta pisi* (ex-epitype CBS 122785). **S, T.** *Ascochyta koolunga* (CBS 372.84). Scale bars: N = 50 µm; F = 15 µm; G, H, O, Q–T = 10 µm; I, K, L, P = 5 µm. Picture A taken from Davidson *et al.* (2009); B–D, G from Chilvers *et al.* (2009); E, F, H, K from Hyde *et al.* (2018); I, R from Chen *et al.* (2015b); L from Tibpromma *et al.* (2017); J, N from Hou *et al.* (2020b); M, O, S, T from Chen *et al.* (2017); P, Q from Hou *et al.* (2020a).

barcodes. Most species in this genus are plant pathogens, on *Fabaceae* and plants in other families (Kaiser *et al.* 1997, Peever *et al.* 2007, Chilvers *et al.* 2009, Hyde *et al.* 2018, Wanasinghe *et al.* 2018a, Hou *et al.* 2020a), while some are saprobes on dead plant tissue, or occur in different environments, such as lake water and soil.

Although names recorded in *Ascochyta* are mostly known only from asexual morphs, some species have both asexual and sexual morphs, such as *A. coronillae-emerii*, *A. fabae*, *A. lentis*, *A. phacae*, *A. pisi*, *A. rabiei* and *A. rosae* (Corbaz 1955, 1957, Corlett 1981,

Jellis & Punithalingam 1991, Trapero-Casas & Kaiser 1992, Kaiser *et al.* 1997, Chilvers *et al.* 2009, Aveskamp *et al.* 2010, Chen *et al.* 2015b, Tibpromma *et al.* 2017, Wanasinghe *et al.* 2018a), while *A. astragalina* (Syn: *Didymella astragalina*) and *A. clinopodiicola* are only observed as sexual morphs (Corbaz 1957, Hyde *et al.* 2018, Hou *et al.* 2020a).

References: Boerema *et al.* 2004 (morphology, distribution and pathogenicity); Aveskamp *et al.* 2010, Chen *et al.* 2015b, 2017, Hou *et al.* 2020a (morphology, phylogeny and pathogenicity).

Table 1. DNA barcodes of accepted *Ascochyta* spp.

Species	Isolates ¹	GenBank accession numbers ²				References
		LSU	ITS	<i>rpb2</i>	<i>tub2</i>	
<i>Ascochyta astragalina</i>	CBS 113797	KT389699	KT389482	MT018257	KT389776	Chen <i>et al.</i> (2015b), Hou <i>et al.</i> (2020a)
<i>A. benningiorum</i>	CBS 144957 ^T	MN823432	MN823581	MN824606	MN824755	Hou <i>et al.</i> (2020b)
<i>A. clinopodiicola</i>	CBS 123524	MN943793	MN973587	—	MT005693	Hou <i>et al.</i> (2020a)
	MFLUCC 18-0344 ^T	MH017429	MH017431	—	—	Hyde <i>et al.</i> (2018)
<i>A. coronillae-emerii</i>	MFLUCC 13-0820 ^T	MH069667	MH069661	MH069679	MH069686	Wanasinghe <i>et al.</i> (2018)
<i>A. fabae</i>	CBS 524.77	GU237963	GU237880	MT018241	GU237526	Aveskamp <i>et al.</i> (2010), Hou <i>et al.</i> (2020a)
<i>A. flava</i>	CGMCC 3.20067 = LC 13574 ^T	MT229670	MT229693	MT239090	MT249261	Present study
	LC 13575	MT229664	MT229687	MT239084	MT249255	Present study
	LC 13576	MT229665	MT229688	MT239085	MT249256	Present study
	LC 13577	MT229666	MT229689	MT239086	MT249257	Present study
	LC 13578	MT229667	MT229690	MT239087	MT249258	Present study
	LC 13579	MT229668	MT229691	MT239088	MT249259	Present study
	LC 13580	MT229669	MT229692	MT239089	MT249260	Present study
<i>A. herbicola</i>	CBS 629.97	GU238083	GU237898	KP330421	GU237614	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015c)
<i>A. koolunga</i>	CBS 372.84 ^T (<i>Ascochyta boeremae</i>)	KT389697	KT389480	—	KT389774	Chen <i>et al.</i> (2015b)
	DAR 78535 ^T	—	EU338416	EU874849	—	Davidson <i>et al.</i> (2009)
<i>A. lentis</i>	CBS 370.84	KT389691	KT389474	MT018246	KT389768	Chen <i>et al.</i> (2015b), Hou <i>et al.</i> (2020a)
<i>A. medicaginicola</i>	CBS 112.53 ^T	GU238101	GU237749	MT018251	GU237628	Aveskamp <i>et al.</i> (2010), Hou <i>et al.</i> (2020a)
<i>A. nigripycnidia</i>	CBS 116.96 ^T	GU238118	GU237756	MT018253	GU237637	Aveskamp <i>et al.</i> (2010), Hou <i>et al.</i> (2020a)
<i>A. phacae</i>	CBS 184.55 ^T	KT389692	KT389475	MT018255	KT389769	Chen <i>et al.</i> (2015b), Hou <i>et al.</i> (2020a)
<i>A. pilosella</i>	CBS 583.97 ^T	MN943796	MN973590	MT018258	MT005696	Hou <i>et al.</i> (2020a)
<i>A. pisi</i>	CBS 122785 ^{ET}	GU237969	GU237763	MT018244	GU237532	Aveskamp <i>et al.</i> (2010), Hou <i>et al.</i> (2020a)
<i>A. rabiei</i>	CBS 237.37 ^T	KT389696	KT389479	MT018256	KT389773	Chen <i>et al.</i> (2015b), Hou <i>et al.</i> (2020a)
<i>A. rosae</i>	MFLUCC 15-0063 ^T	KY496731	KY496751	KY514409	—	Tibpromma <i>et al.</i> (2017)
<i>A. syringae</i>	CBS 545.72	KT389700	KT389483	MT018245	KT389777	Chen <i>et al.</i> (2015b), Hou <i>et al.</i> (2020a)
<i>A. viciae</i>	CBS 451.68	KT389701	KT389484	KT389562	KT389778	Chen <i>et al.</i> (2015b)
<i>A. viciae-pannonicae</i>	CBS 254.92	KT389702	KT389485	MT018250	KT389779	Chen <i>et al.</i> (2015b), Hou <i>et al.</i> (2020a)
<i>A. viciae-villosae</i>	CBS 255.92	MN943790	MN973584	MT018249	MT005690	Hou <i>et al.</i> (2020a)

¹ CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CGMCC: Chinese General Microbiological Culture Collection Center, Beijing, China; DAR: New South Wales Plant Pathology Herbarium, NSW, Australia; LC: Dr Lei Cai's personal collection deposited in laboratory, housed at Chinese Academy of Sciences (CAS), China; MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand. ^{ET} and ^T indicate ex-epitype and ex-type strains, respectively.

² ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial 28S large subunit nrRNA gene; *rpb2*: partial RNA polymerase II second largest subunit gene; *tub2*: partial β -tubulin gene.

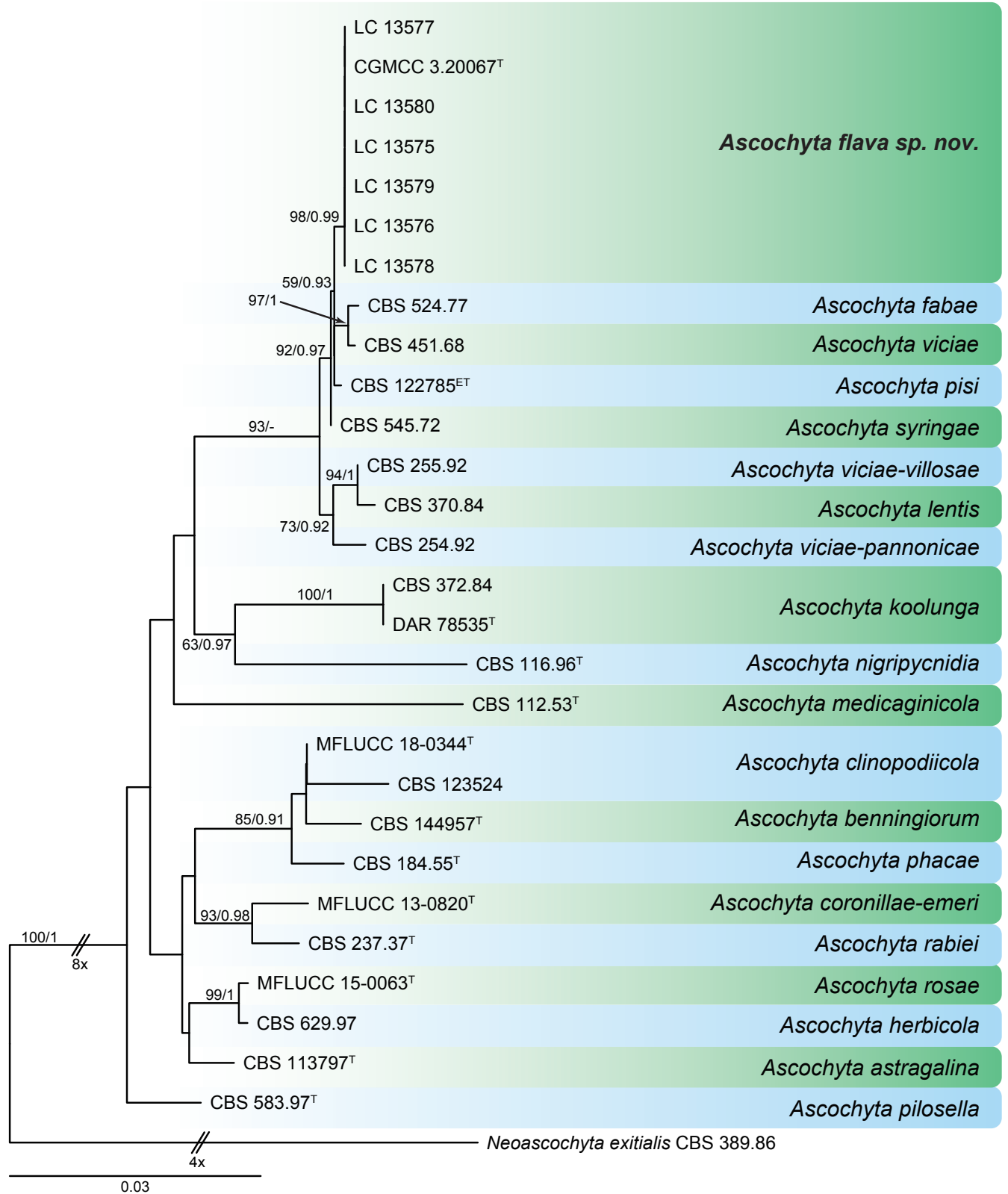


Fig. 2. Phylogenetic tree constructed from LSU (960 bp), ITS (454 bp), *tub2* (333 bp) and *rpb2* (596 bp) sequences of all accepted species of *Ascochyta*. RAxML bootstrap support values (> 70 %) and Bayesian posterior probability scores (> 0.90) are shown at the nodes. The novel taxon is printed in bold. The phylogenetic tree was rooted to *Neoascochyta exitialis* CBS 389.86. GenBank accession numbers are indicated in Table 1. ^T and ^{ET} indicate ex-type and ex-epitype strains, respectively. TreeBASE: S26038.

Ascochyta flava Qian Chen & L. Cai, **sp. nov.** MycoBank MB 834955. Fig. 3.

Etymology: Named after the colour of the colony reverse on OA, flava = yellowish.

Conidiomata pycnidial, mostly aggregated and confluent, globose to subglobose, pale brown, with some hyphal outgrowths, superficial or semi-immersed, ostiolate, 60–380 × 55–330 μm; *ostioles* single, non-papillate; *conidiomatal wall* pseudoparenchymatous 3–5-layered, 12.5–30.5 μm thick, composed of isodiametric cells. *Conidiogenous cells* phialidic, hyaline, smooth, globose,

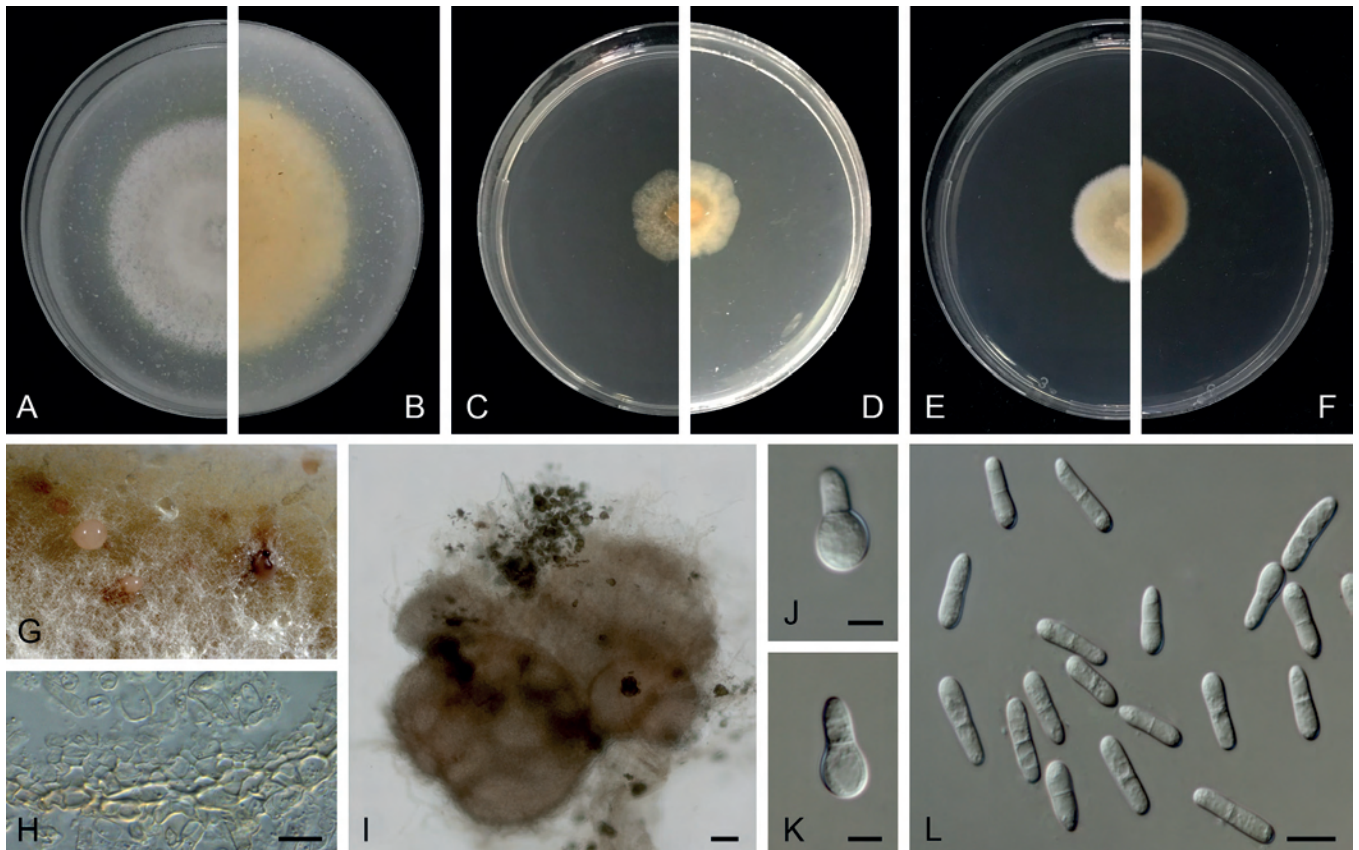


Fig. 3. *Ascochyta flava* (ex-type CGMCC 3.20067). **A, B.** Colony on OA (front and reverse). **C, D.** Colony on MEA (front and reverse). **E, F.** Colony on PDA (front and reverse). **G.** Conidiomata sporulating on OA. **H.** Section of conidiomatal wall. **I.** Conidiomata. **J, K.** Conidiogenous cells. **L.** Conidia. Scale bars: I = 50 µm; H, L = 10 µm; J, K = 5 µm.

ampulliform to obpyriform, 6–12 × 5–9.5 µm. *Conidia* oblong to bacilliform, or narrowly ovoid, always somewhat constricted at the septum, smooth- and thin-walled, hyaline, 0–1-septate, 9–17 × 3.5–5.5 µm, with numerous minute guttules. *Conidial matrix* pale pink.

Culture characteristics: Colonies on OA, 25–30 mm diam after 1 wk, margin regular, floccose to woolly, white; reverse buff. Colonies on MEA 10–15 mm diam after 1 wk, margin regular, floccose to woolly, compact, pale greenish yellow to buff; reverse concolourous. Colonies on PDA, 15–20 mm diam after 1 wk, margin regular, floccose, pale yellow, white near the margin; reverse pale saffron to hazel toward the centre, pale yellow near the margin. Application of NaOH results in a pale saffron discolouration of the agar.

Typus: China, Qinghai, Menyuan County, on leaves of *Angelica dahurica* (*Apiaceae*), 7 Aug. 2019, M.M. Wang (**holotype** HMAS 248350, dried culture, culture ex-type CGMCC 3.20067 = LC 13574).

Additional materials examined: China, Qinghai, Menyuan, on leaves of *Vicia sativa* (*Fabaceae*), 7 Aug. 2019, L.W. Hou, culture LC 13575; *ibid.* culture LC 13576; *ibid.* culture LC 13577; *ibid.* culture LC 13578; *ibid.* culture LC 13579; *ibid.* culture LC 13580.

Notes: *Ascochyta flava* is phylogenetically closely related to *A. pisi* and *A. fabae* (Fig. 2), but differs from *A. pisi* in producing larger conidiogenous cells (6–12 × 5–9.5 µm vs 5.5–8.5 × 4.5–8 µm, Chen *et al.* 2015b), and from *A. fabae* in the shorter conidia [9–17 × 3.5–5.5 µm vs (14–)16–25 × 3.5–6 µm, Punithalingam 1975, Jellis & Punithalingam 1991].

Genome sequenced strain: *Ascochyta pisi*. **The Netherlands**, on *Pisum sativum*, date unknown, M.M.J. Dorenbosch, culture ex-epitype CBS 122785. This Whole Genome Shotgun project has been deposited at GenBank under the accession JALRMB000000000 (BioProject : PRJNA827019, BioSample : SAMN27594410; present study).

Authors: Q. Chen & L. Cai

Cadophora Lagerb. & Melin, Svensk Skogsvårdsfören.Tidskr. 2 (2): 263. 1927. Fig. 4.

Classification: *Leotiomyces*, *Leotiomycetidae*, *Helotiales*, *Ploettnerulaceae*.

Type species: *Cadophora fastigiata* Lagerberg & Melin. Holotype and ex-type strain: A168, CBS 307.49.

DNA barcode (genus): ITS.

DNA barcodes (species): ITS, *tef1* and *tub2*. Table 2. Fig. 5.

Ascomata apothecial, arising singly or in small groups, sessile, slightly erumpent from the substrate, black when fresh. **Receptacle** cupulate, black. **Disc** concave, black. **Ectal excipulum** in lower flanks or in margins and upper flanks, composed of, thin-walled, palebrown to hyaline cells of *textura angularis*, or thick-walled, blackish cells of *textura globulosa*. **Medullary excipulum** in lower flanks, composed of thin-walled, hyaline cells of *textura porrecta*, or in upper flanks, composed of narrow, long, thin-walled, hyaline cells of *textura epidermoidea*. **Hymenium** hyaline. **Paraphyses**

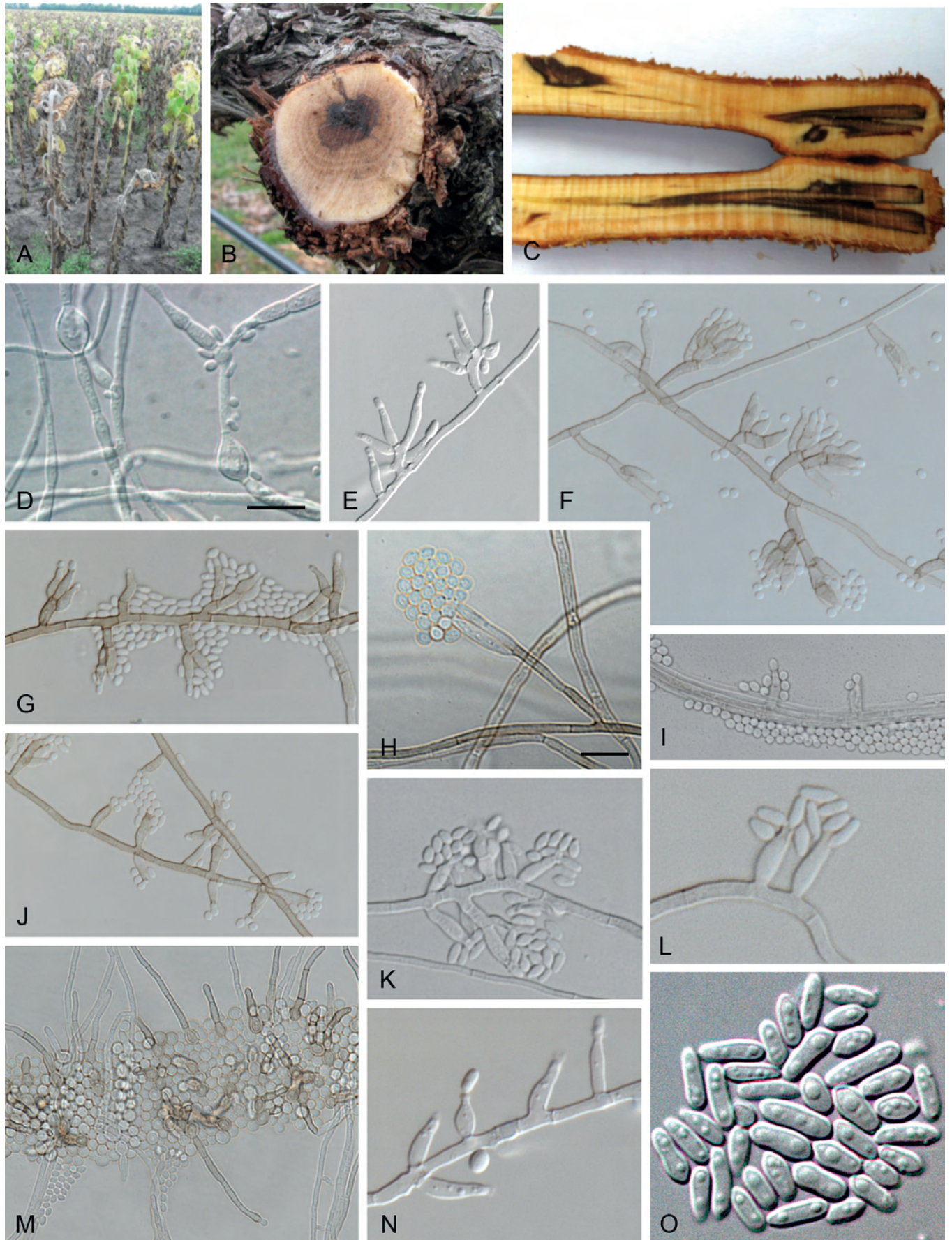


Fig. 4. *Cadophora* spp. **A–C.** Disease symptoms. **A.** Yellowing, leaf necrosis and sudden death caused by *Cadophora helianthi* in a sunflower field. **B.** Black spots and central necrosis on grapevine caused by *Cadophora vinacea*. **C.** Wood discolouration on plum trees caused by *Cadophora domestica*. **D–O.** Asexual morph. **D.** Hyphal swellings of *Cadophora luteo-olivacea* (ex-type CBS 128576). **E–H.** Conidiophores. **E.** *Cadophora helianthi* (ex-type CBS 144752). **F, G.** *Cadophora novi-eboraci* (ex-type OCR1). **H.** *Cadophora rotunda* (ex-type CBS 146264). **I–L, N.** Phialides. **I.** *Cadophora rotunda* (ex-type CBS 146264). **J.** *Cadophora novi-eboraci* (ex-type OCR1). **K, L.** *Cadophora viticola* (ex-type CBS 139.517). **M.** Over-mature conidia of *Cadophora rotunda* (ex-type CBS 146264). **N.** *Cadophora helianthi* (ex-type CBS 144752). **O.** Conidia of *Cadophora luteo-olivacea* (ex-type CBS 128576). Scale bars: D, H = 10 µm; O = 5 µm. D applies to E–G, I, J; H applies to K–N. Pictures D and O taken from Gramaje *et al.* (2011); E and N from Crous *et al.* (2019).

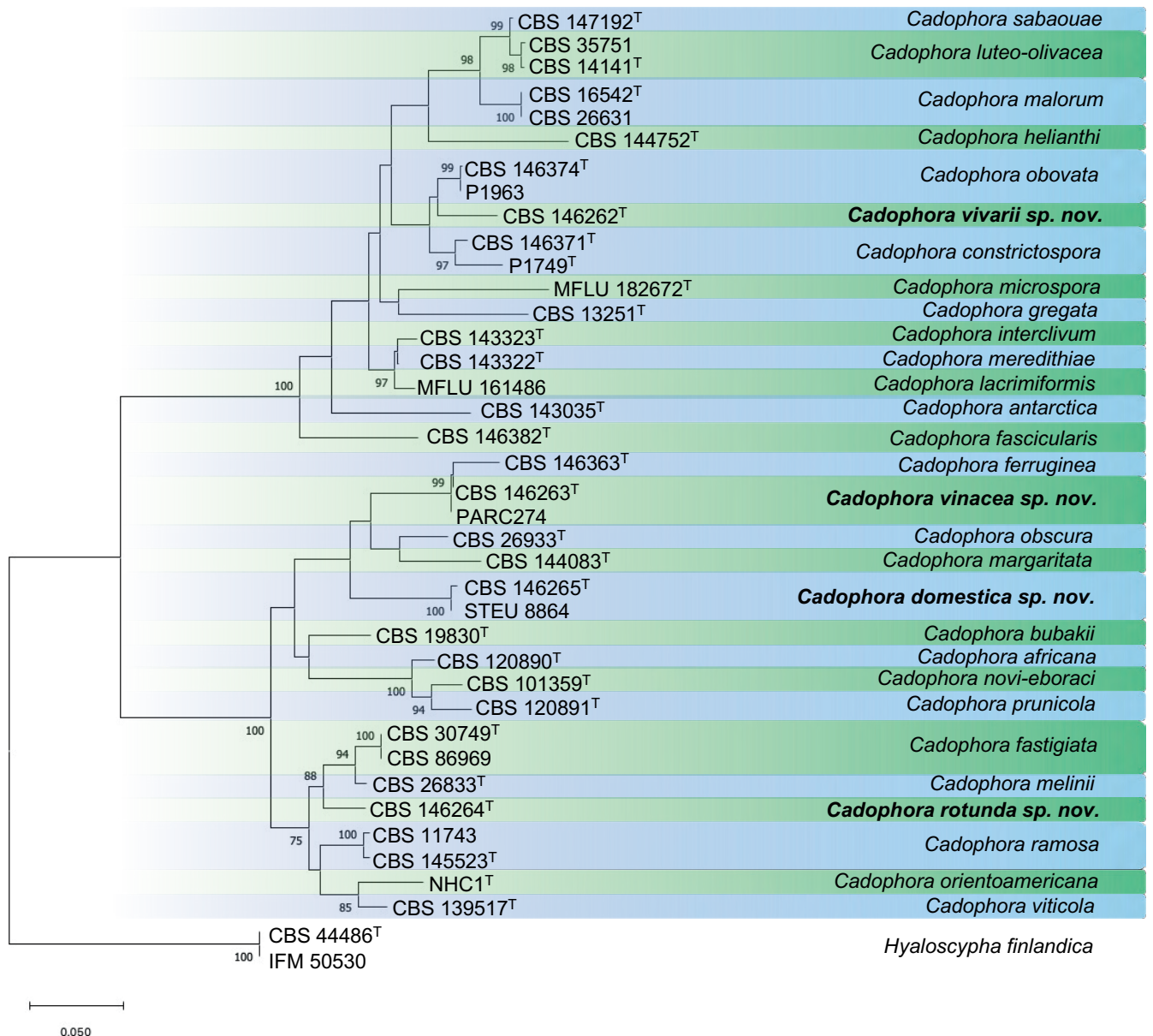


Fig. 5. Maximum likelihood (ML) phylogram obtained from the ITS (500 bp), *tef1* (352 bp) and *tub2* (544 bp) sequences of all accepted species of *Cadophora*. Bootstrap support values (> 70 %) are shown at the nodes. The novel taxa are printed in **bold**. The phylogenetic tree was rooted to *VHyaloscypha finlandica* CBS 44486 and IFM 50530. GenBank accession numbers are indicated in Table 2. ^T indicates ex-type strain. TreeBASE: S25577.

numerous, filiform, branched, septate, hyaline, acute at the apex or obtuse and slightly swollen at the apex, not exceed asci in length. *Asci* 8-spored, unitunicate, cylindrical-clavate, rounded or medium conical at the apex, amyloid, stipitate base, arising from croziers. *Ascospores* 1–2-seriate or multi-seriate, teardrop-shaped, fusoid to ellipsoid or fusoid-clavate, aseptate or sometimes 1-septate, hyaline, guttulate. *Hyphae* single or in bundles of up to 13, branched, septate, tuberculate with warts up to 3 µm diam, verruculose to smooth, hyaline or medium brown. *Conidiophores* mostly short, unbranched or branched, arising from aerial or submerged hyphae, erect to flexuous, up to 7-septate, pale brown. *Phialides* terminal or lateral, mostly single, smooth to verruculose or obclavate, mostly hyaline, but some vinaceous buff to fawn. *Collarettes* short, flaring, cup-shaped, cylindrical, subcylindrical, elongate-ampulliform, attenuated at the base or navicular, mostly hyaline. *Conidia* guttulate, sometimes aggregated in slimy heads, pyriform, ovoid, cylindrical or oblong ellipsoidal, aseptate, mostly hyaline, but some pale hazel.

Cultural characteristics: Colonies on MEA white or vinaceous buff to fawn, brown to pale brown, olivaceousblack or greyolivaceous, flat, felty, with an even edge. Some species produce aerial tufts of hyphae toward the centre and yellow pigmentation on PDA and/or MEA plates.

Optimal media and cultivation conditions: 2 % MEA at 25 °C to induce sporulation of the asexual morph.

Distribution: Worldwide.

Hosts: The known *Cadophora* species occur in several habitats such as soil (Kerry 1990, Aislabie *et al.* 2001, Arenz *et al.* 2006, Hujšlová *et al.* 2010, Crous *et al.* 2017b), decaying wood (Nilsson 1973, Morrell & Zabel 1985, Blanchette *et al.* 2004, Held *et al.* 2005, Arenz *et al.* 2006), or as plant pathogens (Halleen *et al.* 2003, Di Marco *et al.* 2004, Gramaje *et al.* 2011, Spadaro *et al.* 2011, Úrbez-Torres *et al.* 2014, Travadon *et al.* 2015, Crous *et al.* 2019a). The most prominent diseases in which *Cadophora* spp.

Table 2. DNA barcodes of accepted *Cadophora* spp.

Species	Isolates ¹	GenBank accession numbers ²			References
		ITS	<i>tub2</i>	<i>tef1</i>	
<i>Cadophora africana</i>	CBS 120890 ^T	MN232936	MN232967	MN232988	Bien & Damm (2020)
<i>Ca. antarctica</i>	CBS 143035 ^T	MG385664	MK993426	MK993427	Crous <i>et al.</i> (2017)
<i>Ca. bubakii</i>	CBS 198.30 ^T	MH855111	—	MN232989	Bien & Damm (2020)
<i>Ca. constrictospora</i>	CBS 146371	KT269023	—	MN325874	Macià-Vicente <i>et al.</i> (2020)
<i>Ca. domestica</i>	CBS 146265 ^T	MN873024	MN873028	MN873031	Present study
<i>Ca. fascicularis</i>	CBS 146382 ^T	KT269992	—	MN325918	Macià-Vicente <i>et al.</i> (2020)
<i>Ca. fastigiata</i>	CBS 307.49 ^T	AY249073	KM497131	KM497087	Harrington & McNew (2003), Travadon <i>et al.</i> (2015)
<i>Ca. ferruginea</i>	CBS 146363 ^T	KT268618	—	MN325861	Macià-Vicente <i>et al.</i> (2020)
<i>Ca. gregata</i>	ATCC 11073 ^T	U66731	MF677920	MF979586	Harrington & McNew (2003)
<i>Ca. helianthi</i>	CBS 144.752 ^T	MK813837	MH733391	MH719029	Crous <i>et al.</i> (2019a)
<i>Ca. interclivum</i>	CBS 143323 ^T	MF979577	MF677917	MF979583	Walsh <i>et al.</i> (2018)
<i>Ca. lacrimiformis</i>	MFLU 16-1486	MK585003	—	—	Ekanayaka <i>et al.</i> (2019)
<i>Ca. luteo-olivacea</i>	CBS 141.41 ^T	AY249066	KM497133	KM497089	Harrington & McNew (2003)
<i>Ca. malorum</i>	CBS 165.42 ^T	AY249059	KM497134	KM497090	Gams (2000)
<i>Ca. margaritata</i>	CBS 144083 ^T	KJ702027	MH327786	—	Linnakoski <i>et al.</i> (2018)
<i>Ca. melinii</i>	CBS 268.33 ^T	AY249072	KM497132	KM497088	Harrington & McNew (2003), Travadon <i>et al.</i> (2015)
<i>Ca. meredithiae</i>	CBS 143322 ^T	MF979574	MF677914	MF979580	Walsh <i>et al.</i> (2018)
<i>Ca. microspora</i>	MFLU 18-2672	MK591966	—	—	Ekanayaka <i>et al.</i> (2019)
<i>Ca. novi-eboraci</i>	NYC14 ^T	KM497037	KM497118	KM497074	Travadon <i>et al.</i> (2015)
<i>Ca. obovata</i>	CBS 146374 ^T	KT269230	—	MN325888	Macià-Vicente <i>et al.</i> (2020)
<i>Ca. obscura</i>	CBS 269.33	MN232948	—	MN232996	Bien & Damm (2020)
<i>Ca. orientoamericana</i>	NHC1 ^T	KM497018	KM497099	KM497055	Travadon <i>et al.</i> (2015)
<i>Ca. prunicola</i>	CBS 120891 ^T	MN232949	MN232979	MN232997	Bien & Damm (2020)
<i>Ca. ramosa</i>	CBS 145523 ^T	MN232956	MN232984	MN233002	Bien & Damm (2020)
<i>Ca. rotunda</i>	CBS 146264 ^T	MN873023	MN873029	MN873030	Present study
<i>Ca. sabaouae</i>	CBS 147192 ^T	MT644187	MT646749	MT646746	Aigoun-Mouhous <i>et al.</i> (2021)
<i>Ca. vinacea</i>	CBS 146263 ^T	MN873025	MN873027	MN873032	Present study
<i>Ca. viticola</i>	CBS 139.517 ^T	HQ661096	HQ661066	HQ661081	Crous <i>et al.</i> (2015c)
<i>Ca. vivarii</i>	CBS 146262 ^T	KY312633	MN873026	MN873033	Present study

¹ ATCC: American Type Culture Collection, Virginia, USA; CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; MFLU: Mae Fah Luang University Herbarium, Chiang Rai, Thailand; NYC: New York Collection, New York, USA; NHC: New Hampshire Collection, New Hampshire, USA; UAMH: Centre for Global Microfungal Biodiversity, University of Toronto, Toronto, Canada. ^T indicates ex-type strain.

² ITS: internal transcribed spacers and intervening 5.8S nrDNA; *tef1*: partial translation elongation factor 1- α gene; *tub2*: partial β -tubulin gene.

are involved are Petri disease and esca, which occur on young and mature grapevines (*Vitaceae*), respectively.

Disease symptoms: Brown wood vascular streaking, plant decline, fruit skin pitting and brown spot, fruit rot.

Notes: The genus *Cadophora* was recently included within the family *Ploettnerulaceae* (Ekanayaka *et al.* 2019). It has morphological similarities with *Mollisia*, *Phialocephala* and *Collembolispora*. *Mollisia* can be differentiated from *Cadophora* by its phialocephala-like asexual morphs (Walsh *et al.* 2018). *Phialocephala* often produces densely packed head of phialides while *Cadophora* produces phialides singly or in groups of two or three (Day *et al.* 2012). *Collembolispora* differs from *Cadophora* in producing septate

macroconidia (Crous *et al.* 2012a). Species delimitation based on morphology alone is limited since many species have overlapping characters. Moreover, the morphology of the sexual morph cannot be used because only two taxa are known to have a sexual morph. The three loci used most frequently for phylogenetic analyses are ITS, translation elongation factor 1- α (*tef1*) and partial beta-tubulin (*tub2*) genes (Crous *et al.* 2015c, 2019a, Travadon *et al.* 2015). Phylogenetic analyses combining these three regions allow for the resolution of almost all currently known *Cadophora* species (Fig. 5).

References: Gams 2000, Harrington & McNew 2003, Gramaje *et al.* 2011, Day *et al.* 2012 (morphology); Halleen *et al.* 2007, Gramaje *et al.* 2010, 2011, 2014, Úrbez-Torres *et al.* 2014, Travadon *et al.*

2015 (pathogenicity); Agustí-Brisach *et al.* 2011, 2013, Gramaje *et al.* 2011 (epidemiology); Gramaje *et al.* 2014 (population genetics); Day *et al.* 2012, Travadon *et al.* 2015, Crous *et al.* 2015c, 2019a, Linnakoski *et al.* 2018, Walsh *et al.* 2018, Ekanayaka *et al.* 2019, Bien & Damm 2020, Maciá-Vicente *et al.* 2020, Aigoun-Mouhous *et al.* 2021, Koukol & Maciá-Vicente 2022 (taxonomy and phylogeny); Navarrete *et al.* 2011, Spadaro *et al.* 2011, Úrbez-Torres *et al.* 2015, Maldonado-González *et al.* 2020 (detection and identification); Rédou *et al.* 2016, Knapp *et al.* 2018 (genome sequence).

Cadophora domestica L. Mostert, R. van der Merwe, Halleen & Gramaje, *sp. nov.* MycoBank MB 833823. Fig. 6.

Etymology: Named after its host, *Prunus domestica*.

Mycelium composed of branched, septate hyphae occurring singly or in bundles of up to 7; hyphae tuberculate with warts up to 2 µm diam, verruculose to smooth, olivaceous brown, 2.5–3.5 µm diam. *Conidiophores* mostly short, usually branched, arising from aerial or submerged hyphae, erect to flexuous, up to 4-septate, hyaline to pale brown, (7.5–)9.5–38(–48) (av. = 17) µm long and 2–3 (av. = 2.5) µm wide. *Phialides* terminal or lateral, mostly monophialidic, smooth to verruculose, hyaline, with 1.5–3.5 µm long, 2–2.5 µm wide, mostly cylindrical collarettes, (4.5–)6.5–13.5(–14.5) × 1.5–3(–4) (av. = 8 × 2.5) µm. *Conidia* hyaline, oblong ellipsoidal, (3–)3.5–5.5 × 1.5–2.5 (av. = 4.5 × 2) µm.

Culture characteristics: Colonies reaching 19–25 mm after 8 d at 25 °C. The minimum temperature for growth was 5 °C, the optimum 20–25 °C and the maximum 30 °C. Colonies on MEA flat, felty,

with even margins after 16 d, straw with a purple stripe close to the centre; reverse concolourous. Colonies on PDA flat, felty, with even margins after 16 d, white to umber toward the centre; reverse concolourous.

Typus: **South Africa**, Western Cape Province, Montagu, from necrotic tissues from crown of *Prunus domestica* (*Rosaceae*) nursery tree, 2017, R. van der Merwe (**holotype** CBS H-24306, culture ex-type STEU 8865 = CBS 146265).

Additional material examined: **South Africa**, Western Cape Province, Montagu, from necrotic tissues from crown of *Prunus domestica* nursery tree, 2017, R. van der Merwe, culture STEU 8864.

Notes: The two strains of *Ca. domestica* that were evaluated here exhibited very similar morphological characteristics. Conidiophores of strain STEU 8864 are on average longer (av. = 21 µm) than those of STEU 8865 (av. = 17 µm).

Cadophora rotunda L. Mostert, R. van der Merwe, Halleen & Gramaje, *sp. nov.* MycoBank MB 833822. Fig. 7.

Etymology: Latin, *rotundum*, meaning circular. In reference to the circular conidia.

Mycelium composed of branched, septate hyphae occurring singly or in bundles of up to 8; hyphae tuberculate with warts up to 2.5 µm diam, verruculose to smooth, olivaceous brown, 2.5–3.0 µm diam. *Conidiophores* usually branched, arising from aerial or submerged hyphae, erect to flexuous, up to 6-septate, pale brown

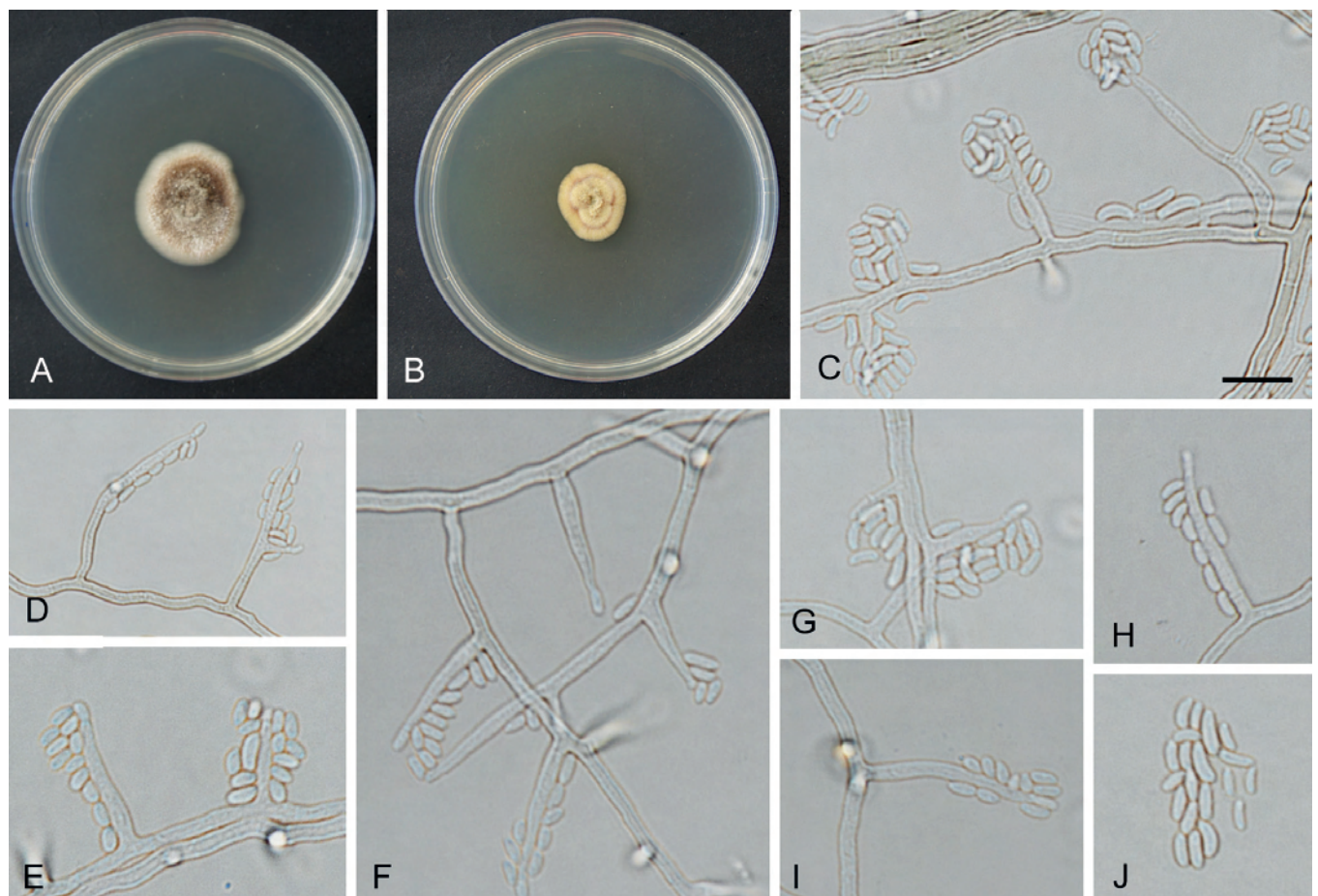


Fig. 6. *Cadophora domestica* (ex-type CBS 146265). **A.** Colony on PDA. **B.** Colony on MEA. **C, D.** Conidiophores and phialides. **E–I.** Phialides. **J.** Conidia. Scale bars: C = 10 µm. C applies to D–J.

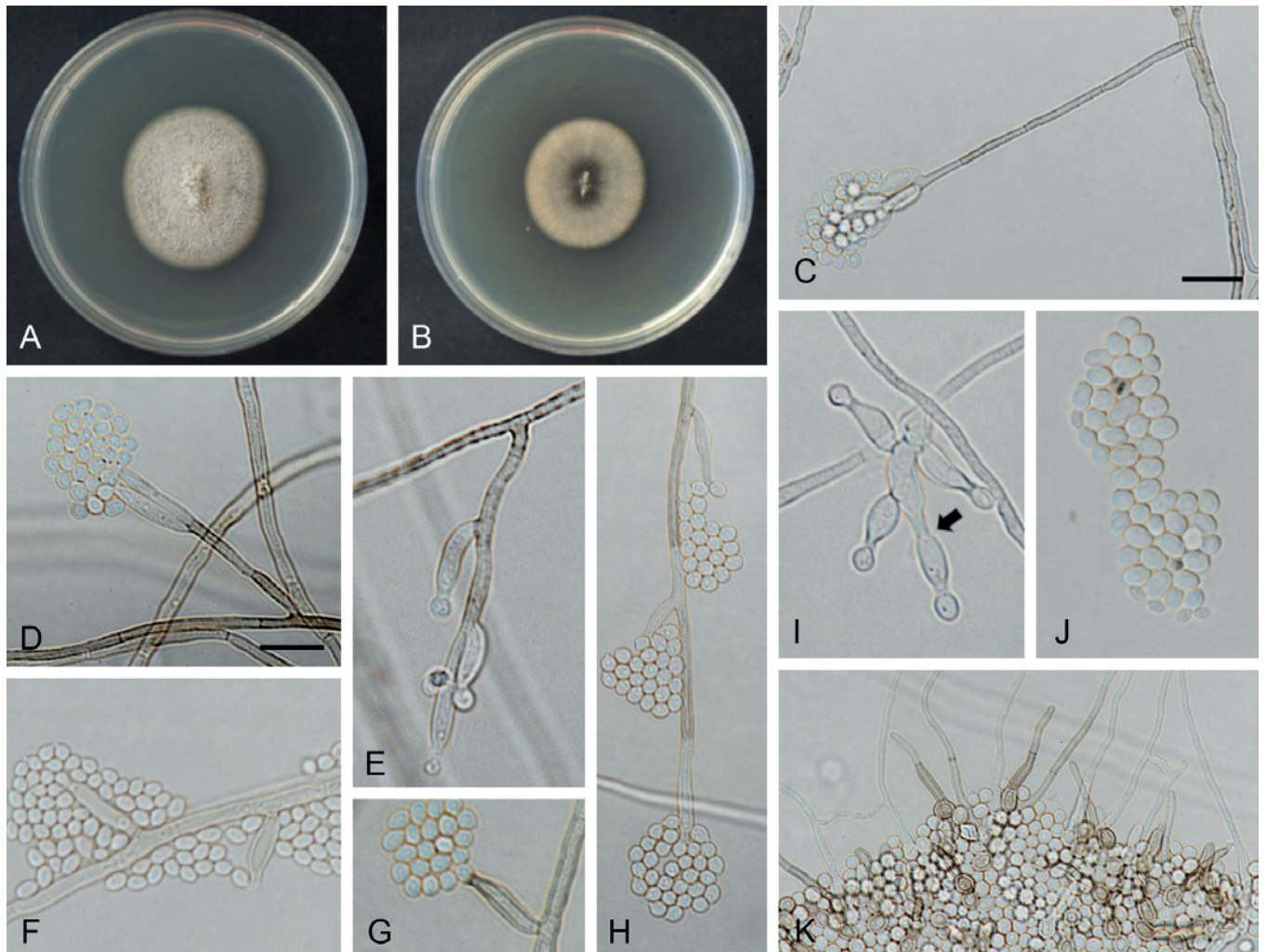


Fig. 7. *Cadophora rotunda* (ex-type CBS 146264). **A.** Colony on PDA. **B.** Colony on MEA. **C–E.** Conidiophores. **F–I.** Phialides. **I.** Percurrently proliferated phialide (indicated by arrow). **J.** Conidia. **K.** Over-mature conidia, some aggregating, some germinating. Scale bars: C, D = 10 μm . C applies to K; D applies to E–J.

to brown, (10–)12.5–59(–71) (av. = 35) μm long and 2–3.5 (av. = 2.5) μm wide. *Phialides* terminal or lateral, mostly monopialidic, smooth, hyaline, with 2–3 μm long, 2–3 μm wide, mostly cylindrical collarettes, some elongate-ampulliform, attenuated at the base or navicular, (3.5–)6–13.5(–15) \times 1.5–3(–3.5) (av. = 8 \times 2.5) μm . Phialides sometimes produce more than one collarette as a result of percurrent proliferation. *Conidia* hyaline, spherical, (3–)3.5–5.5 \times 2.5–3.5 (av. = 4.5 \times 3) μm .

Culture characteristics: Colonies reaching 27–28 mm diam after 8 d at 25 $^{\circ}\text{C}$. The minimum temperature for growth was 5 $^{\circ}\text{C}$, the optimum 20–25 $^{\circ}\text{C}$ and the maximum 35 $^{\circ}\text{C}$. Colonies on MEA flat, felty, with even margins after 16 d, white to grey olivaceous close to the centre; reverse concolourous. Colonies on PDA flat, felty, with even margins after 16 d, white to pale grey; reverse concolourous.

Typus: **South Africa**, Western Cape Province, Montagu, from necrotic tissues from crown of *Prunus domestica* (*Rosaceae*) nursery tree, 2017, R. van der Merwe (**holotype** CBS H-24306, culture ex-type STEU 8862 = CBS 146264).

Notes: *Cadophora rotunda* is currently only known from a single isolate that is phylogenetically related to *Ca. melinii* and *Ca. fastigiata* (Fig. 5). *Cadophora rotunda* differs from *Ca. melinii* in the length of the conidiophores (*Ca. rotunda*: av. 35 μm long; *Ca. melinii*: av. 18.8 μm long) and the conidial morphology (*Ca. rotunda*: spherical; *Ca. melinii*:

cylindrical to oblong ellipsoidal; Travadon *et al.* 2015). A total of 60 bp polymorphisms can distinguish *Ca. rotunda* from *Ca. melinii*: 23 bp in *tef1* locus, 28 bp in *tub2* locus, and 9 bp in ITS. *Cadophora rotunda* differs from *Ca. fastigiata* in the colony growth (*Ca. rotunda*: 27–28 mm after 8 d; *Ca. fastigiata*: 23–25 mm after 10 d) and the presence of light brown phialides in *Ca. fastigiata* (Cole & Kendrick 1973). A total of 78 bp polymorphisms can distinguish *Ca. rotunda* from *Ca. fastigiata*: 23 bp in *tef1* locus, 43 bp in the *tub2* locus, and 12 bp in ITS.

Cadophora vinacea J.R. Úrbez-Torres, D.T. O’Gorman & Gramaje, *sp. nov.* MycoBank MB 833825. Fig. 8.

Etymology: Latin, *vinum*, meaning wine. In reference to the red vinaceous colour of colonies on PDA.

Mycelium composed of branched, septate hyphae occurring singly or in bundles of up to 10; hyphae tuberculate with warts up to 2.5 μm diam, verruculose to smooth, olivaceous brown, 2.5–3 μm diam. *Conidiophores* mostly short, usually branched, arising from aerial or submerged hyphae, erect to flexuous, up to 5-septate, hyaline to pale brown, (8–)9.5–35.5(–44) (av. = 19) μm long and 2–3.5 (av. = 2.5) μm wide. *Phialides* terminal or lateral, mostly monopialidic, smooth to verruculose, hyaline, with 1.5–2.5 μm long, 2–2.5 μm wide, mostly cylindrical collarettes, (5–)7.5–15.5(–18) \times 1.5–3(–3.5) (av. = 11 \times 2.5) μm . *Conidia* hyaline, ovoid to oblong ellipsoidal, (3–)4–5.5 \times 1.5–2.5 (av. = 4.5 \times 2) μm .

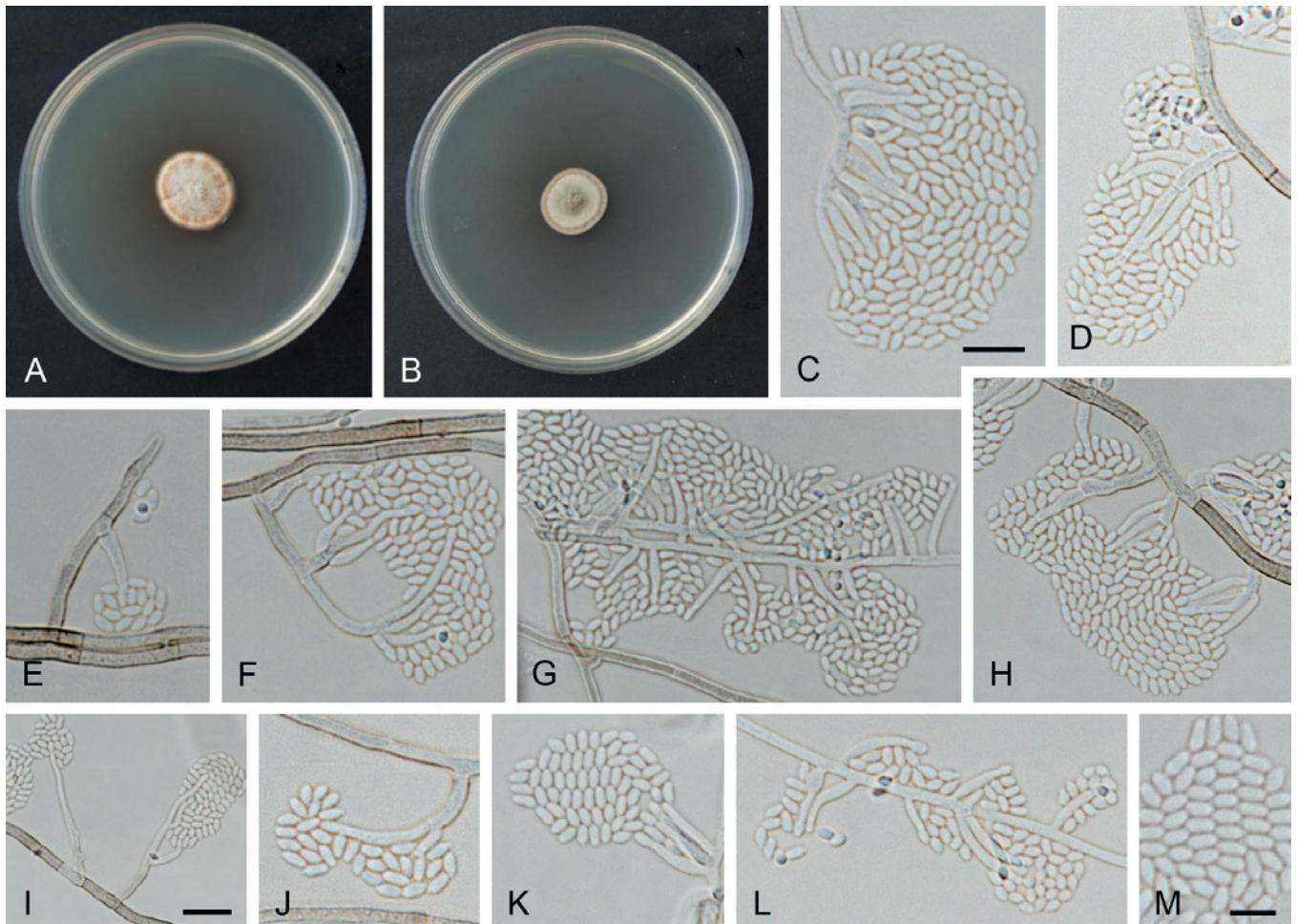


Fig. 8. *Cadophora vinacea* (ex-type CBS 146263). **A.** Colony on PDA. **B.** Colony on MEA. **C–L.** Conidiophores and phialides. **M.** Conidia. Scale bars: C, I = 10 µm; M = 5 µm. C applies to D–H, J–L.

Culture characteristics: Colonies reaching 21–24 mm after 8 d at 25 °C. The minimum temperature for growth was 5 °C, the optimum 20–25 °C and the maximum 30 °C. Colonies on MEA flat, felty, with even margins, after 16 d, buff with a vinaceous stripe near the centre; reverse concolourous. Colonies on PDA flat, felty, with even margins, after 16 d, buff to vinaceous toward the margin; reverse concolourous.

Typus: **Canada**, British Columbia, Okanagan Valley, from necrotic tissue in trunk of *Vitis vinifera* cv. Ehrenfelser (*Vitaceae*), 2011, J.R. Úrbez-Torres (**holotype** CBS H-24307, culture ex-type PARC199 = CBS 146263).

Additional material examined: **Canada**, British Columbia, Okanagan Valley, from necrotic tissue in cordon of *V. vinifera* cv. Gewurztraminer, 2011, J.R. Úrbez-Torres, culture PARC274.

Notes: *Cadophora vinacea* is phylogenetically related to *Ca. ferruginea* (Fig. 5). Cultures CBS 146263 (ex-type) and PARC274 differ from *Ca. ferruginea* in its fastest colony growth on PDA (*Ca. vinacea*: 21–24 mm after 8 d; *Ca. ferruginea*: 18–19 mm after 10 d), and the production of reddish globules and mycelium by *Ca. ferruginea* (Macià-Vicente *et al.* 2020). A total of 19 bp polymorphisms can distinguish *Ca. vinacea* from *Ca. ferruginea*: 17 bp in *tef1* locus, and two in ITS.

Cadophora vivarii L. Mostert, Havenga, Halleen & Gramaje, **sp. nov.** MycoBank MB 833824. Fig. 9.

Etymology: Latin, from *vivarium*, meaning “of the nursery”. In reference to the environment where it was collected.

Mycelium composed of branched, septate hyphae occurring singly or in bundles of up to 10; hyphae tuberculate with warts up to 2 µm diam, verruculose to smooth, olivaceous brown, 2.5–4 µm diam. **Conidiophores** mostly short, usually branched, arising from aerial or submerged hyphae, erect to flexuous, up to 4-septate, pale brown to brown, (7.5–)8.5–41(–43) (av. = 18) µm long and 2–3.5 (av. = 2.5) µm wide. **Phialides** terminal or lateral, mostly monophialidic, smooth to verruculose, hyaline, with 1.5–3 µm long, 2–3 µm wide, mostly cylindrical collarettes, some elongate-ampulliform, attenuated at the base or navicular, (3.5–)5.5–10(–12) × 1.5–3(–4) (av. = 6.5 × 2.5) µm. **Conidia** hyaline, ovoid or oblong ellipsoidal, 3–5 × 1.5–2.5 (av. = 4 × 2) µm.

Culture characteristics: Colonies reaching 17–22 mm after 8 d at 25 °C. The minimum temperature for growth was 5 °C, the optimum 20–25 °C and the maximum 35 °C. Colonies on MEA flat, felty, with entire to undulate margin, producing yellow pigment, after 16 d, pale yellow toward the edge; reverse concolourous. Colonies on PDA flat, felty, with entire to undulate margin, after 16 d white to buff close to the centre; reverse concolourous.

Typus: **South Africa**, Western Cape Province, Kouebokkeveld, from necrotic tissue of bud union of *Malus domestica* (*Rosaceae*) nursery tree, 2015, M. Havenga (**holotype** CBS H-24304, culture ex-type STEU 8310 = CBS 146262).

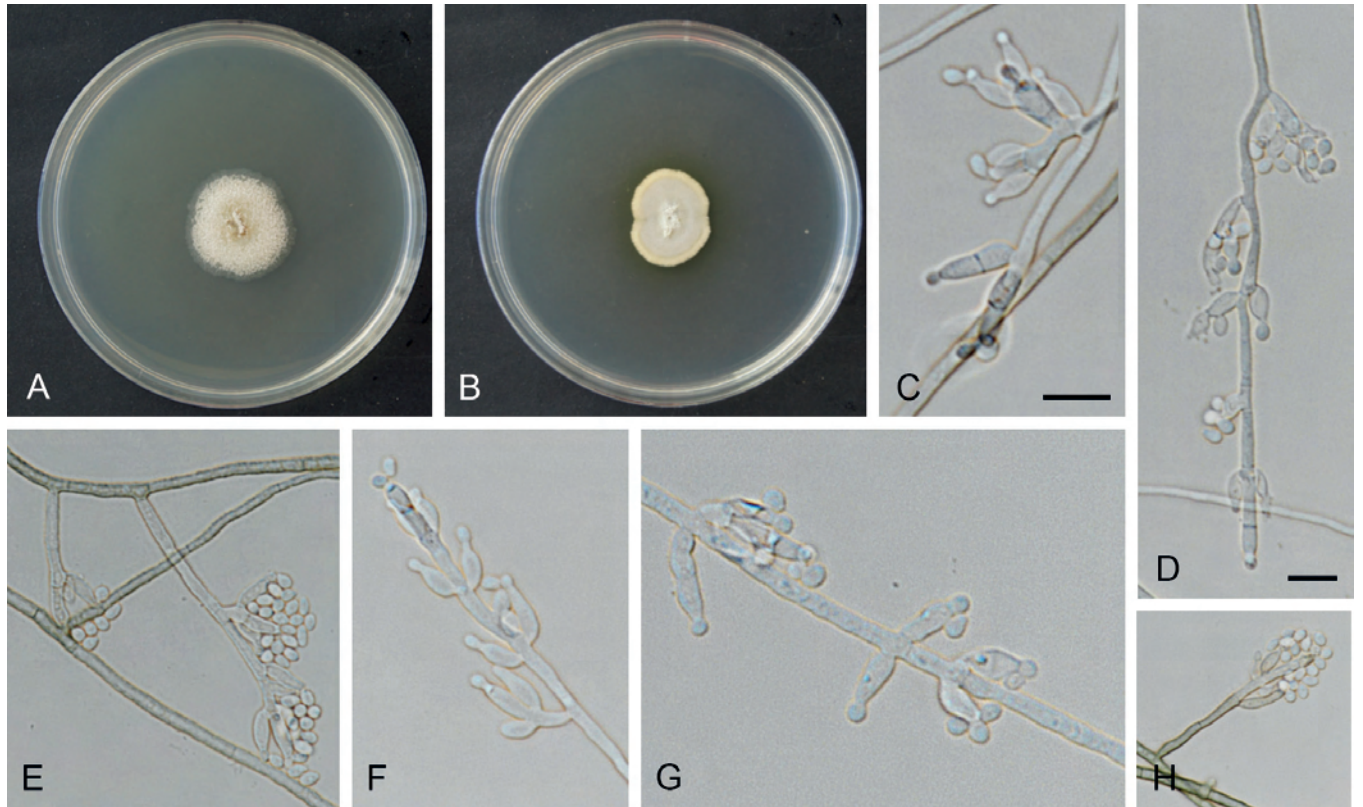


Fig. 9. *Cadophora vivarii* (ex-type CBS 146262). **A.** Colony on PDA. **B.** Colony on MEA. **C–H.** Conidiophores, phialides and conidia. Scale bars: C, D = 10 μ m. C applies to F–G; D applies to E, H.

Notes: *Cadophora vivarii* is currently only known from a single isolate that is phylogenetically related to *Ca. obovata* (Fig. 5). *Cadophora vivarii* differs from *Ca. obovata* in conidial morphology (*Ca. vivarii*: ovoid or oblong ellipsoidal; *Ca. obovata*: obovate) and the absence of conidiophores in *Ca. obovata*.

Genome sequenced strain: *Cadophora luteo-olivacea*. **Spain**, Valencia, grapevine rootstock 110 Richter, 2007, D. Gramaje, culture ex-type CBS 128576 = Clo-18. This Whole Genome Shotgun project has been deposited at GenBank under the accession JALRMC000000000 (BioProject: PRJNA827019, BioSample: SAMN27594411; present study).

Authors: D. Gramaje, J.R. Úrbez-Torres, L. Mostert & F. Halleen

Celoporthe Nakab. *et al.*, Stud. Mycol. 55: 261. 2006. Fig. 10.

Classification: Sordariomycetes, Sordariomycetidae, Diaporthales, Cryphonectriaceae.

Type species: *Celoporthe dispersa* Nakab. *et al.* Holotype and ex-type strains: PREM 58896, CBS 118782 = CMW 9976.

DNA barcode (genus): ITS.

DNA barcodes (species): *tub1*, *tub2*, *tef1*. Table 3. Fig. 11.

Ascomata pseudothecial, semi-immersed to immersed in bark, erumpent, mostly gregarious or single, recognisable by papilla (short emerged perithecial necks). *Stromatic tissues* surrounding perithecia except for the base, orange to umber, pseudoparenchymatous to prosenchymatous depending on regions. *Perithecia* valsoid, bases

immersed, globose to ellipsoidal. *Perithecial walls* dark olivaceous brown to black, pseudoparenchymatous. *Perithecial necks* black, embedded in stromatic tissue. *Asci* 8-spored, unitunicate, fusoid to ellipsoid, clavate to cylindrical, with a non-amyloid refractive ring in apex. *Ascospores* hyaline, oblong to ellipsoidal, straight or slightly curved, 1-median septate. *Conidiomata* superficial to immersed, single or gregarious, orange to umber when young, fuscous to black when mature, globose to conical, pulvinate, with or without short attenuated neck, uni- or multilocular, convoluted. *Stromatic tissues* pseudoparenchymatous to prosenchymatous. *Conidiophores* hyaline, branched irregularly at base, branching out along the length just below septum. *Conidiogenous cells* enteroblastic, cylindrical to lageniform with or without attenuated apices. *Paraphyses* or *cylindrical sterile cells* present or absent. *Conidia* hyaline, aseptate, oblong to cylindrical or ovoid, occasionally allantoid, exuded as bright luteous to orange tendrils or droplets.

Culture characteristics: Colonies grown on 2 % MEA in dark showing abundant floccose aerial mycelia, white, yellow white, pale luteous, and umber when immature, with age turning to sulfur yellow, luteous, umber, hazel, chestnut, or greenish black.

Optimal media and cultivation conditions: *Celoporthe* spp. display optimal growth on 2 % MEA between 25 °C and 30 °C: *Cel. borbonica*, *Cel. cerciana* *Cel. dispersa* and *Cel. woodiana* at 25 °C; *Cel. eucalypti*, *Cel. fontana* *Cel. guangdongensis*, *Cel. hauoliensis*, *Cel. hawaiiensis*, *Cel. indonensiensis*, *Cel. paradisiaca*, *Cel. syzygii* and *Cel. tibouchinae* at 30 °C.

Distribution: China, Indonesia, La Réunion, South Africa, USA (Hawaii), Zambia.



Fig. 10. *Celoporthe* spp. **A–C.** Disease symptoms caused by *Celoporthe cerciana* on *Eucalyptus grandis* hybrid. **A.** Bark cracks of tree. **B.** Fruiting structures on canker. **C.** Close-up of canker. **D–G.** Asexual morph. **D, E.** *Celoporthe tibouchinae* (ex-type CMW 44126 = PPRI 25130). **D.** Conidiomata. **E.** Vertical section of conidioma. **F.** Paraphyses in conidioma of *Celoporthe borbonica* (CMW 44139). **G.** Conidia of *Celoporthe borbonica* (ex-type CMW 44128). **H–L.** Sexual morph of *Celoporthe borbonica* (ex-type CMW 44128). **H, I.** Ascostromata. **J.** Vertical section of ascostroma and perithecium. **K.** Ascus. **L.** Ascospores with some germinating. Scale bars: D = 500 µm; H, I = 250 µm; E, J = 100 µm; K, L = 10 µm; F, G = 5 µm. Picture B taken from Wang *et al.* (2018); F, J, K from Ali *et al.* (2018).

Hosts: *Eucalyptus*, *Heteropyxis*, *Psidium*, *Syzygium* (Myrtaceae), *Melastoma* and *Tibouchina* (Melastomataceae).

Disease symptoms: Cankers, branch dieback and leaf spots.

Notes: *Celoporthe* was introduced to accommodate a fungus that is closely related to *Chrysoporthe* and *Holocryphia* but distinctly different based on DNA sequence data and morphology (Nakabonge *et al.* 2006). The most notable difference between *Celoporthe* and *Chrysoporthe* is in the lengths of perithecial necks; *Celoporthe*

with short necks appearing as papillae and *Chrysoporthe* with a long and easily distinguishable necks. *Celoporthe* accommodates 14 species, including the new species presented here (references in Table 3). Three species, *Cel. dispersa*, *Cel. borbonica* and *Cel. syzygii* are known from both sexual and asexual morphs (Nakabonge *et al.* 2006, Chen *et al.* 2011, Ali *et al.* 2018). Only asexual morphs are known for the remaining species.

The morphologies and characteristics of growth in culture overlap for various species of *Celoporthe*. Although species can be distinguished using a combination of morphological

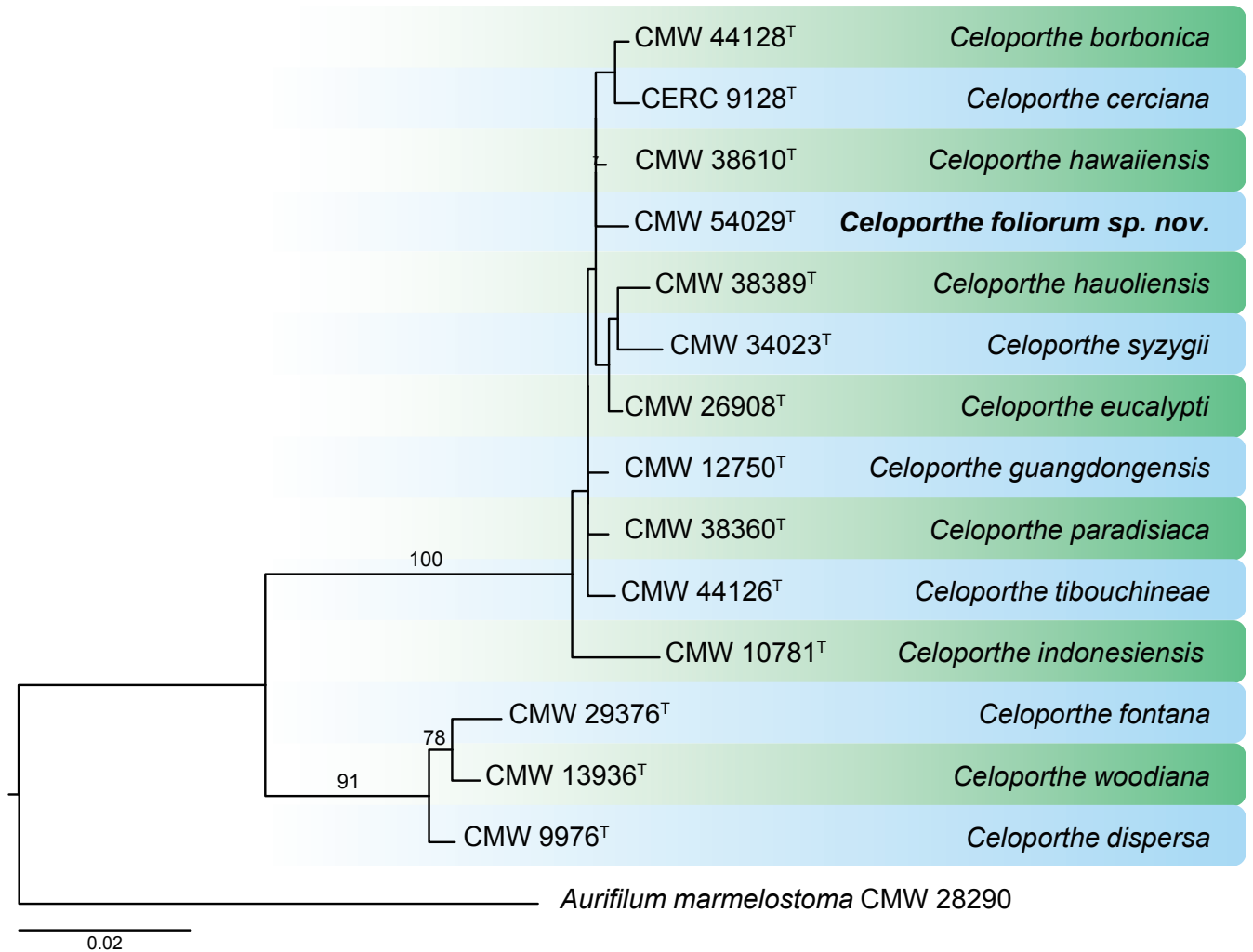


Fig. 11. Maximum likelihood (ML) phylogram constructed using the combined dataset of the ITS (506 bp), *tub1* (434 bp), and *tub2* (399 bp) gene regions of all accepted species of *Celoporthe*. Bootstrap support values (> 70 %) are indicated at the nodes. The novel taxon is printed in bold. The phylogenetic tree was rooted to *Aurifilum marmelostoma* CMW28290. GenBank accession numbers are indicated in Table 3. ^T indicates ex-type strain. TreeBASE: S28873.

Table 3. DNA barcodes of accepted *Celoporthe* spp.

Species	Isolates ¹	GenBank accession numbers ²					References
		LSU	ITS	<i>tub1</i>	<i>tub2</i>	<i>tef1</i>	
<i>Celoporthe borbonica</i>	CMW 44128 = PPRI 25133 ^T	—	MG585741	MG585725	—	—	Ali <i>et al.</i> (2018)
<i>Cel. cerciana</i>	CERC 9128 ^T	—	MH084352	MH084382	MH084412	MH084442	Wang <i>et al.</i> (2018)
<i>Cel. dispersa</i>	CMW 9976 = CBS 118782 ^T	HQ730853	DQ267130	DQ267136	DQ267142	HQ730840	Nakabonge <i>et al.</i> (2006)
<i>Cel. eucalypti</i>	CMW 26908 = CBS 127190 ^T	HQ730863	HQ730837	HQ730817	HQ730827	HQ730850	Chen <i>et al.</i> (2011)
<i>Cel. foliorum</i>	CMW 54029 = PPRI 27961 ^T	—	LC537846	LC537847	LC537848	—	Present study
<i>Cel. fontana</i>	CMW 29376 = CBS 132008 ^T	—	GU726941	GU726953	GU726953	JQ824074	Vermeulen <i>et al.</i> (2013)
<i>Cel. guangdongensis</i>	CMW 12750 = CBS 128341 ^T	HQ730856	HQ730830	HQ730810	HQ730820	HQ730843	Chen <i>et al.</i> (2011)
<i>Cel. hauoliensis</i>	CMW 38389 = CBS 140640 ^T	—	KJ027502	KJ027478	—	—	Roux <i>et al.</i> (2020)
<i>Cel. hawaiiensis</i>	CMW 38610 = CBS 140642 ^T	—	KJ027499	KJ027475	—	—	Roux <i>et al.</i> (2020)

Table 3. (Continued).

Species	Isolates ¹	GenBank accession numbers ²					References
		LSU	ITS	<i>tub1</i>	<i>tub2</i>	<i>tef1</i>	
<i>Cel. indonesiensis</i>	CMW 10781 = CBS 115844 ^T	HQ730855	AY084009	AY084033	AY084021	HQ730842	Chen <i>et al.</i> (2011)
<i>Cel. paradisiaca</i>	CMW 38360 = CBS 147170 ^T	—	KJ027498	KJ027474	—	—	Roux <i>et al.</i> (2020)
<i>Cel. syzygii</i>	CMW 34023 = CBS 127218 ^T	HQ730857	HQ730831	HQ730811	HQ730821	HQ730844	Chen <i>et al.</i> (2011)
<i>Cel. tibouchinae</i>	CMW 44126 = PPRI 25130 ^T	—	MG585747	MG585731	LC537849	—	Ali <i>et al.</i> (2018)
<i>Cel. woodiana</i>	CMW 13936 = CBS 118785 ^T	—	DQ267131	DQ267137	DQ267143	JQ824071	Vermeulen <i>et al.</i> (2013)

¹ CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CERC: Culture Collection of China Eucalypt Research Center, Guangdong Province, China; CMW: Tree Protection Co-operative Program, Forestry and Agricultural Biotechnology Institute, University of Pretoria, South Africa; PPRI: Culture collection of the South African National Collection of Fungi (NCF), Roodeplaat, Pretoria, South Africa. ^T indicates ex-type strain.

² ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial 28S large subunit nrRNA gene; *tef1*: partial translation elongation factor 1- α gene; *tub1*, *tub2*: partial β -tubulin gene.

characteristics such as sizes of conidia or ascospores and optimal growth temperature, DNA sequence data are essential to confirm identifications. The ITS and *tef1* regions do not provide accurate species resolution when used alone (Vermeulen *et al.* 2013, Wang *et al.* 2018). The *tub1* and *tub2* regions are most useful for species resolution, but provide stronger support in combination with ITS and *tef1* data. *Celoporthes* spp. are all tree pathogens but they have been shown to vary in pathogenicity in controlled inoculation tests on *Eucalyptus* clones (Nakabonge *et al.* 2006, Chen *et al.* 2011, Vermeulen *et al.* 2013, Ali *et al.* 2018, Wang *et al.* 2018).

References: Gryzenhout *et al.* 2009 (classification); Nakabonge *et al.* 2006, Chen *et al.* 2011, Vermeulen *et al.* 2013, Ali *et al.* 2018, Wang *et al.* 2018 (morphology, nomenclature, phylogeny and pathogenicity).

Celoporthes foliorum H. Suzuki, Marinc. & M.J. Wingf., *sp. nov.* MycoBank MB 835419. Fig. 12.

Etymology: The name refers to its habitat, occurring on leaves.

Asexual morph observed on 2 % MEA grown in dark for 30 d. *Conidiomata* stromatic, gregarious, formed among aerial mycelium or on the medium, uni- or multi-locular, oozing a yellow and murky spore mass; *conidiomatal walls* pseudoparenchymatous, consisting of a few layers of thick-walled cells, pigmented, 5–21 μ m thick (av. 11.2 μ m), the outermost layer prosenchymatous. *Conidiophores* borne along locular walls, upright, simple, branched at basal cell or lateral, 12–30 μ m long (av. 17.5 μ m). *Paraphyses* not observed. *Conidiogenous cells* enteroblastic, hyaline, flask-shaped, abruptly attenuated toward apex, 4–12.5 \times 1–2 μ m (av. 6.9 \times 1.8 μ m). *Conidia* hyaline, aseptate, oblong to ellipsoidal with a pointed base, 3–4 \times 1–2 μ m (av. 3.6 \times 1.5 μ m). **Sexual morph** not observed.

Culture characteristics: On 2 % MEA showing optimum growth at 30 °C at 14.2 mm / d, followed by at 25 °C at 12.6 mm/d, showing slower growth at 15, 20, 35 °C. Cultures circular with uneven margin, aerial mycelium floccose, white when young, umber to hazel to chestnut when mature.

Typus: **Indonesia**, Riau, isolated from a leaf spot of a native *Syzygium* sp. (*Myrtaceae*), Oct. 2018, M.J. Wingfield (**holotype** PREM 62887, culture ex-type CMW 54029 = PPRI 27961).

Additional material examined: **Indonesia**, Riau, isolated from a leaf spot of a native *Syzygium* sp., Oct. 2018, M.J. Wingfield, PREM 62886, living culture CMW 54028 = PPRI 27960.

Note: Unlike the other *Celoporthes* spp. isolated from bark tissue, *Cel. foliorum* was isolated from leaf spots. Due to the scarcity of specimens, *in vivo* characteristics were not observed. A distinctive morphological feature of *Cel. foliorum* is a lack of paraphyses among conidiophores that is reported present in other species. Long paraphysis-like structures were occasionally observed but they were atypical conidiogenous cells. *Celoporthes hawaiiensis* is a phylogenetic closest relative to *Cel. foliorum* (Fig. 11). *Celoporthes hawaiiensis* was reported from Hawaii on *Psidium* and *Syzygium* infected by *Austropuccinia psidii* (Roux *et al.* 2020). They are morphologically similar to each other based on the observation of *in vitro* cultures with *Eucalyptus* stem sections: their optimal growth temperature is 30 °C and conidial dimensions are 2.5–4 \times 1–1.5 μ m in *Cel. hawaiiensis* and 3–4 \times 1–2 μ m in *Cel. foliorum*. However, conical conidiomata with necks which were present in *Cel. hawaiiensis* were not observed in *Cel. foliorum*. *Celoporthes foliorum* is the second *Celoporthes* sp. to be reported from Indonesia. The other species from this region, *Cel. indonesiensis* was isolated from *Syzygium aromaticum* from North Sumatra in 1997 (Chen *et al.* 2011).

Genome sequenced strain: *Celoporthes dispersa*. **South Africa**, on *Syzygium cordatum*, 2001, M. Gryzenhout, culture ex-type CBS 118782. This Whole Genome Shotgun project has been deposited at GenBank under the accession WAID00000000 (BioProject: PRJNA574566, BioSample: SAMN12860070; Liu *et al.* 2019).

Authors: H. Suzuki, S. Marincowitz, S.F. Chen, B.D. Wingfield, M.J. Wingfield

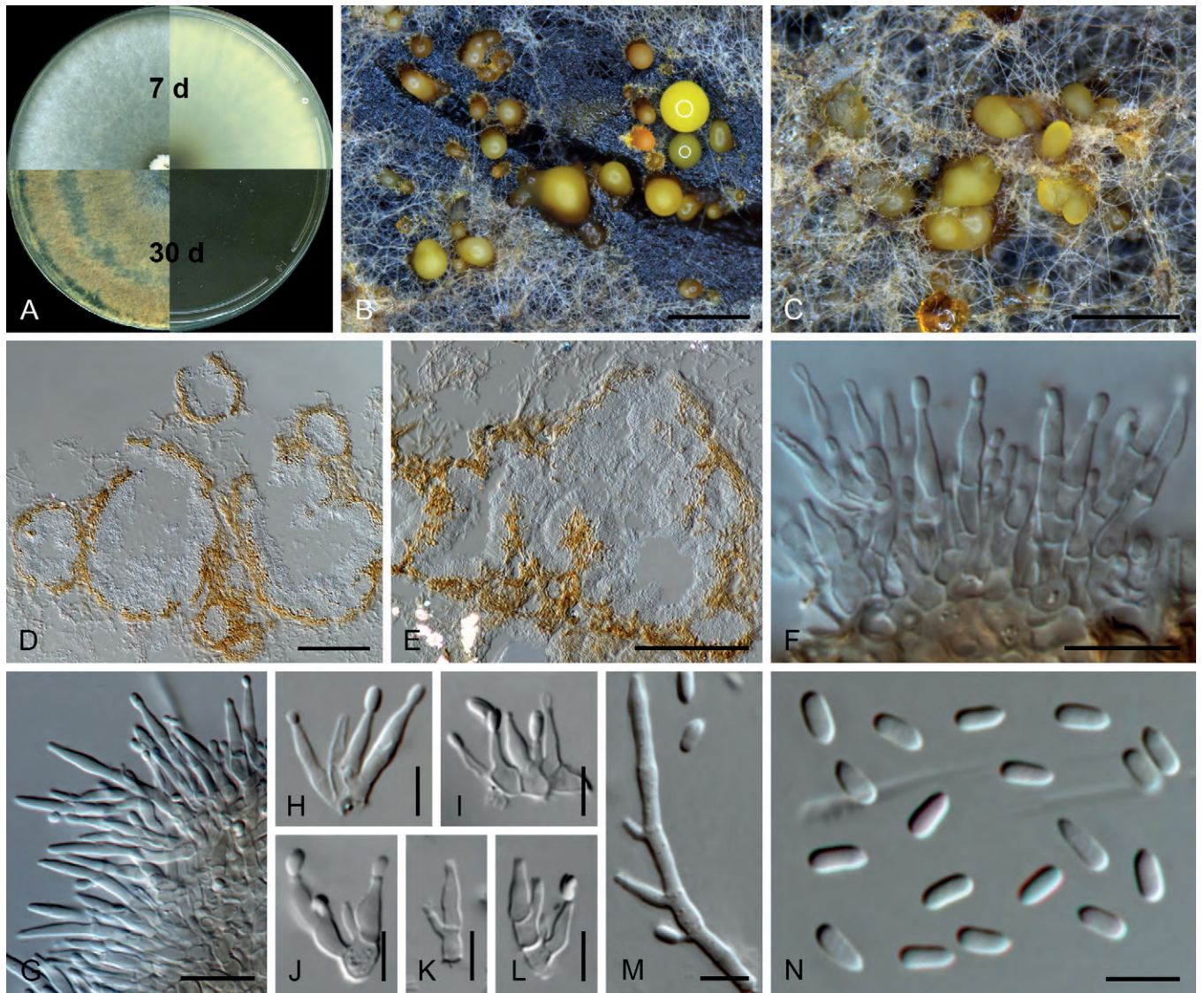


Fig. 12. *Celosporthe foliorum* (ex-type CMW 54029). **A.** Culture grown on 2 % MEA in 7 d and 30 d in dark (left: front, right: reverse). **B, C.** Conidiomata formed on agar surface (B) and on mycelial mass (C) with yellow oozing conidial mass. **D, E.** Vertical section through conidiomata showing multilocular, lobated chambers. **F, G.** Conidiophores. **H–M.** Conidiophores and conidiogenous cells. **N.** Conidia. Scale bars: B, C = 500 μ m; D, E = 50 μ m; F, G = 10 μ m; H–N = 5 μ m.

Cercospora Fresen. ex Fuckel, *Fungi Rhen. Exs.*: No. 117. 1863; *Hedwigia* 2: 133. Apr–Jun 1863, *nom. cons. prop.* Fig. 13.
Synonyms: *Virgasporium* Cooke, *Grevillea* 3: 182. 1875.
Cercosporina Speg., *Anales Mus. Nac. Buenos Aires* 3, 13: 424. 1911.

Classification: *Dothideomycetes*, *Dothideomycetidae*, *Mycosphaerellales*, *Mycosphaerellaceae*.

Type species: *Cercospora apii* Fresen., *typ. cons. prop.* Lectotype designated by Groenewald *et al.* (2005): Fuckel, *Fungi rhen.* 117, in HAL. Epitype designated by Groenewald *et al.* (2005), ex-epitype strain: CBS 116455 = CPC 11556.

DNA barcodes (genus): LSU, ITS, *rpb2*.

DNA barcodes (species): *actA*, *cmdA*, *gapdh*, *his3*, *tef1*, *tub2*. Table 4. Fig. 14.

Hyphomycetous. *Mycelium* internal, rarely external; hyphae branched, septate, hyaline or almost so to usually pigmented, thin-

walled, smooth, rarely faintly rough-walled. *Stromata* lacking to well-developed, substomatal, intraepidermal to deeply immersed, mostly pigmented, composed of *textura angulata* or *textura globosa*. *Conidiophores* macronematous, mononematous, solitary or fasciculate, in small to large fascicles, rarely in sporodochial conidiomata, emerging through stomata or erumpent, very rarely arising from superficial hyphae, erect, continuous to pluriseptate, mostly pigmented, pale olivaceous to dark brown, rarely hyaline or almost so, straight or flexuous, sometimes geniculate, unbranched or rarely branched, wall smooth to somewhat rough, thin to moderately thick. *Conidiogenous cells* integrated, terminal or intercalary, sometimes conidiophores aseptate, *i.e.* reduced to conidiogenous cells, monoblastic, determinate to usually polyblastic, proliferation sympodial, rarely percurrent. *Conidiogenous loci* (scars) conspicuous, thickened and darkened-refractive, planate with minute central pore. *Conidia* solitary, rarely in short chains (mainly under high humidity), mostly scolecosporous, obclavate cylindrical, acicular, filiform and pluriseptate, rarely amero- to phragmosporous, broadly ellipsoid-ovoid to broadly obclavate-cylindrical, but always hyaline or subhyaline (with a pale green tinge), thin-walled, smooth or almost so, hila thickened and

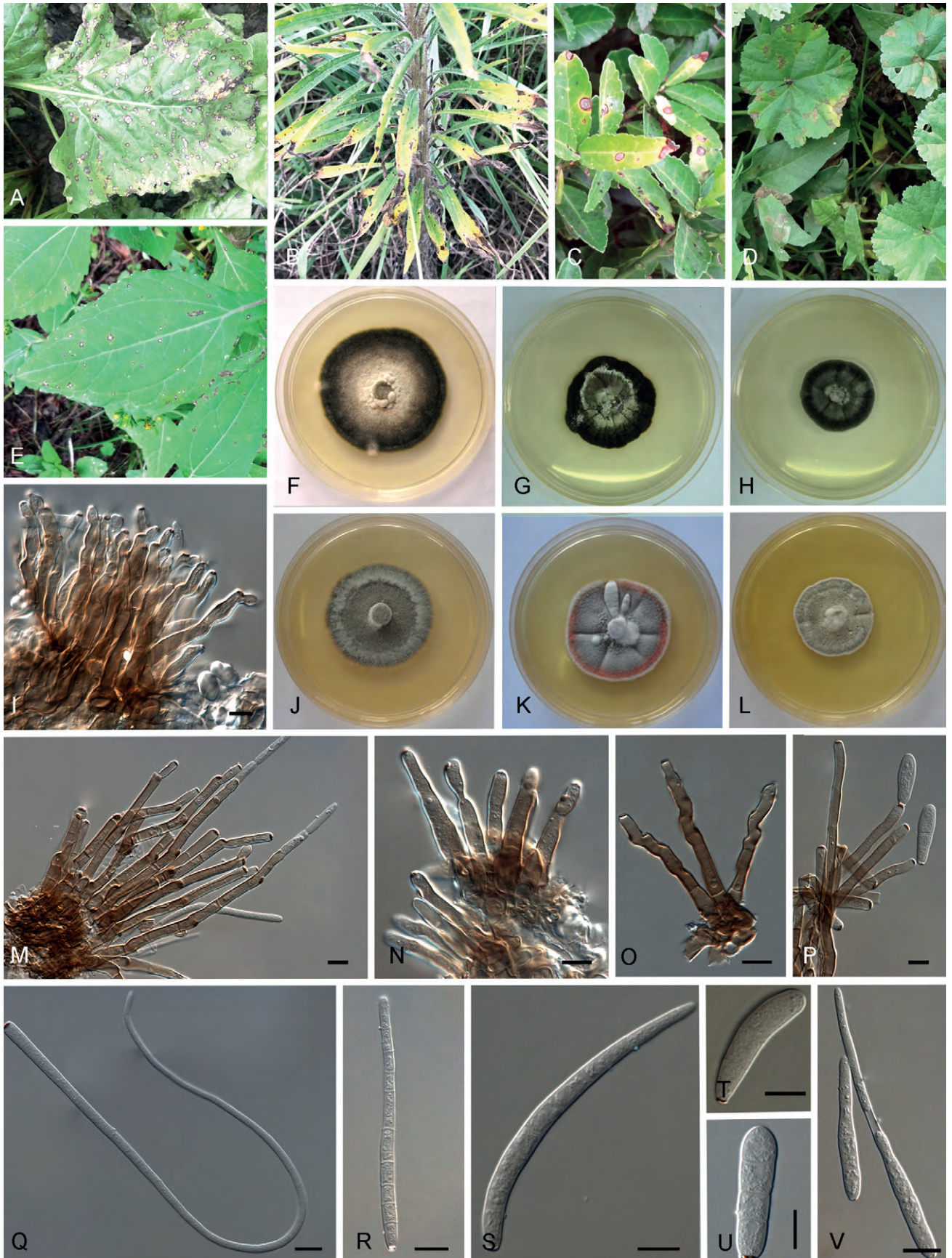


Fig. 13. *Cercospora* spp. **A–E.** Disease symptoms. **A.** *Cercospora beticola* on *Beta vulgaris*. **B.** *Cercospora conyzae-canadensis* on *Conyza canadensis*. **C.** *Cercospora* cf. *flagellaris* on *Buxus microphylla*. **D.** *Cercospora gamsiana* on *Malva neglecta*. **E.** *Cercospora* cf. *richardiicola* on *Bidens tripartita*. **F–H, J–L.** Colonies on MEA. **F.** *Cercospora althaeina* (IRAN 2674C). **G.** *Cercospora cylindracea* (ex-type IRAN 2654C). **H.** *Cercospora pseudochenopodii* (ex-type IRAN 2649C). **J.** *Cercospora uwebrauniana* (ex-type CBS 138581). **K.** *Cercospora* cf. *flagellaris* (IRAN 2668C). **L.** *Cercospora* cf. *flagellaris* (IRAN 2648C). **I, M–P.** Conidiophores. **I.** *Cercospora* cf. *gossypii* (CBS 136137). **M.** *Cercospora beticola* (CCTU 1135). **N.** *Cercospora rautensis* (CBS 136134). **O.** *Cercospora cylindracea* (ex-type CBS 138580). **P.** *Cercospora uwebrauniana* (ex-type CBS 138581). **Q–V.** Conidia. **Q.** *Cercospora beticola* (CCTU 1135). **R.** *Cercospora cylindracea* (ex-type CBS 138580). **S.** *Cercospora sorghicola* (ex-type CBS 136448). **T.** *Cercospora chenopodii* (CCTU 1033). **U.** *Cercospora uwebrauniana* (ex-type CBS 138581). **V.** *Cercospora gamsiana* (CBS 144962). Scale bars = 10 µm. Pictures D, I, M, P, Q, U, V taken from Bakhshi et al. (2018); O, R–T from Bakhshi et al. (2015a); N from Bakhshi (2019).

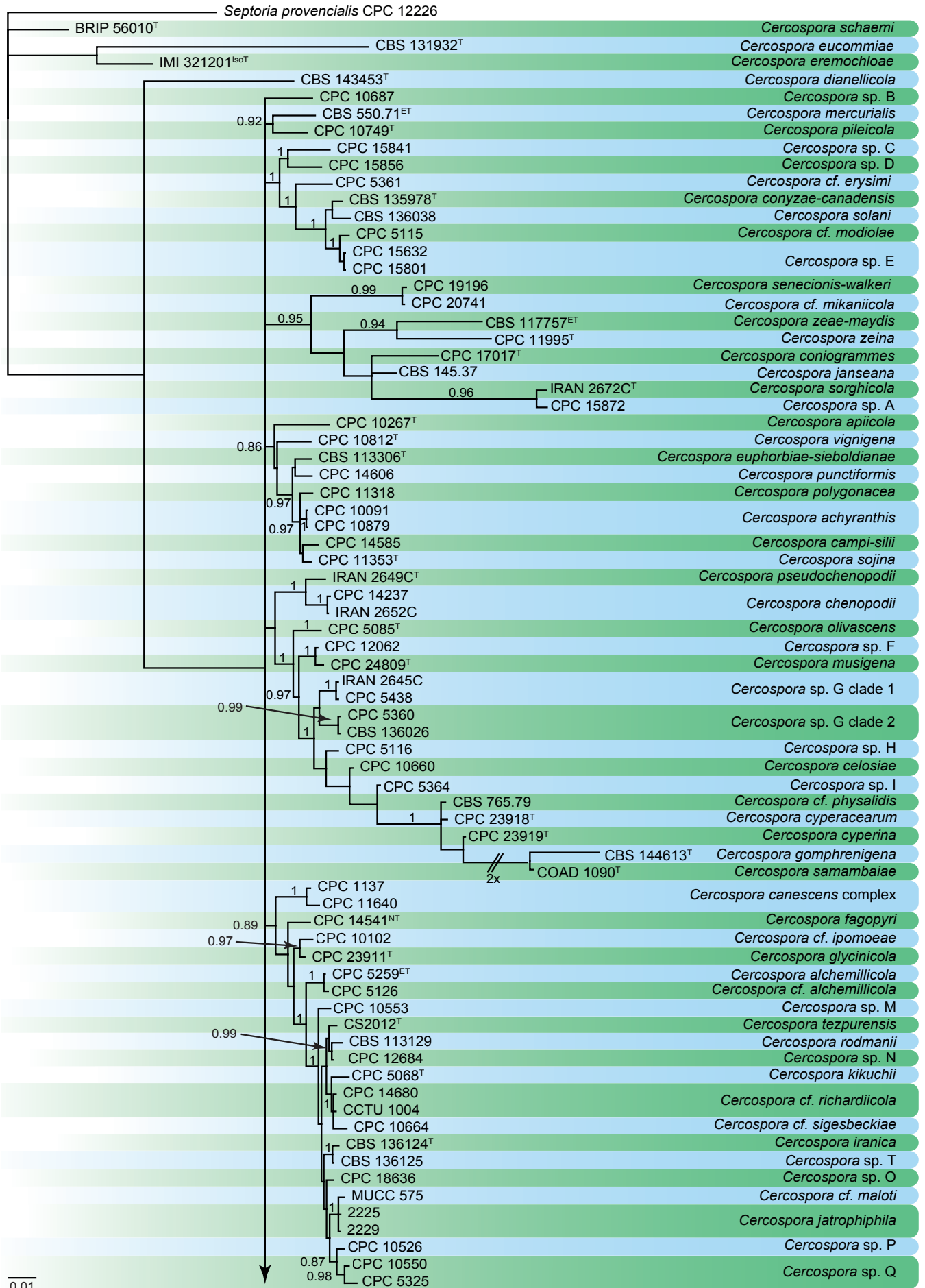


Fig. 14. Bayesian phylogram constructed from ITS (478 bp), *actA* (209 bp), *cmdA* (259 bp), *gapdh* (870 bp), *his3* (363 bp), *rpb2* (1 230 bp), *tef1* (352 bp) and *tub2* (415 bp) sequences of all accepted species of *Cercospora*. Bayesian posterior probability scores (≥ 0.85) are shown at the nodes. The novel taxon is printed in bold. The phylogenetic tree was rooted to *Septoria provencialis* CPC 12226. ^T and ^{ET} indicate ex-type and ex-epitype strains, respectively. TreeBASE: S26138.

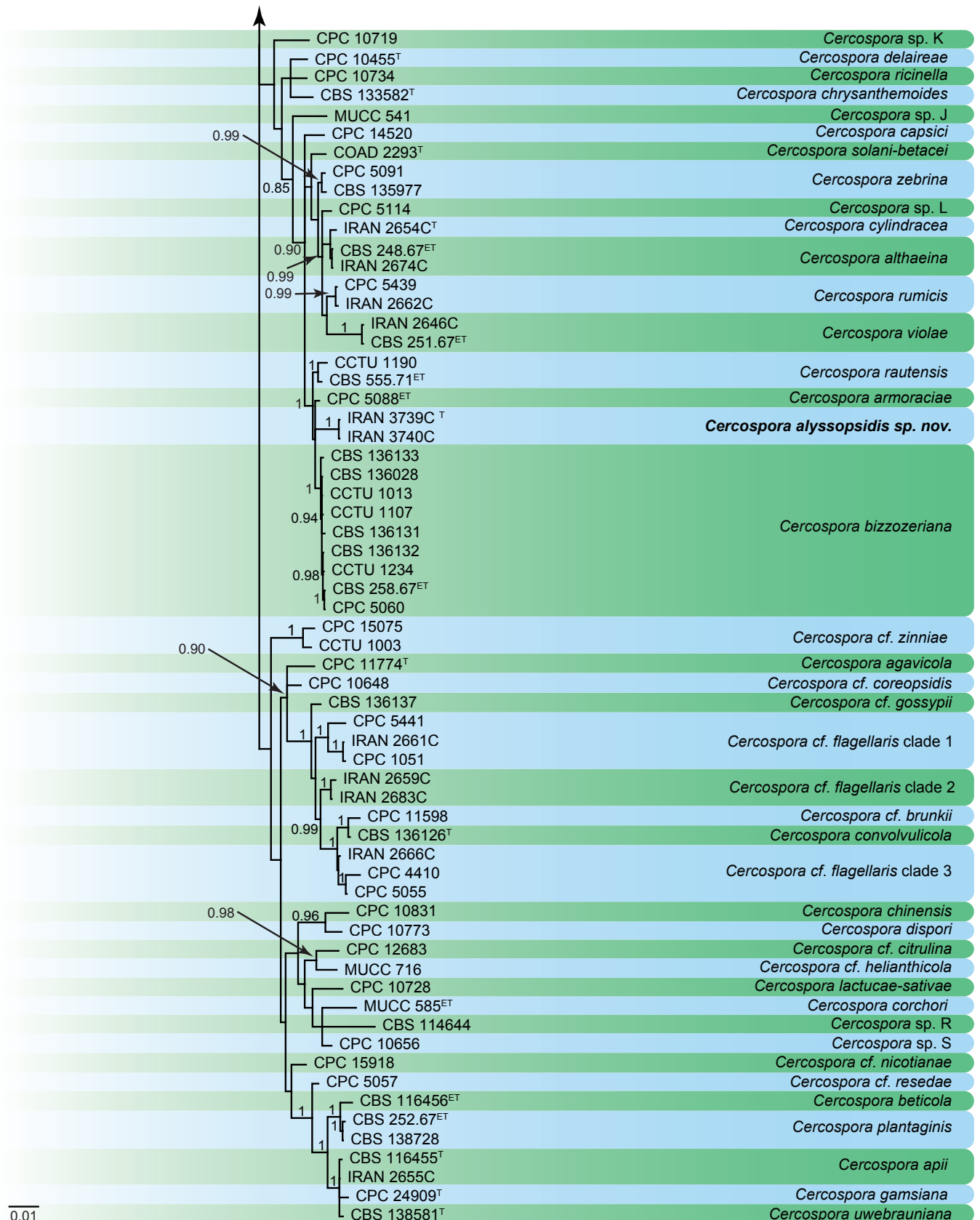


Fig. 14. (Continued).

darkened, conidial secession schizolytic. *Sexual morph* unknown (adapted from Ellis 1971, Crous & Braun 2003, Braun *et al.* 2013).

Cultural characteristics: Colonies on MEA, flat to folded, with smooth, even margins and sparse to moderate aerial mycelium, sometimes radially striated, surface white, olivaceous green, smoke grey,

sometimes with different colour (e.g. vinaceous grey) in outer region, reverse olivaceous grey to iron grey. Colony colour sometimes changes with subculturing.

Optimal media and cultivation conditions: MEA incubated at 25 °C in dark for 2–4 wk, to determine growth rates, colour and shape of the colony.

Table 4. DNA barcodes of accepted *Cercospora* spp.

Species	Isolates ¹	GenBank accession numbers ²										References		
		ITS	actA	cmdA	gapdh	his3	rbp2	tef1	tub2					
<i>Cercospora achyranthis</i>	CBS 132613 = CPC 10879	JX143523	JX143031	JX142785	—	JX142539	—	JX143277	—	—	—	—	—	Groenewald et al. (2013)
	CPC 10091	JX143524	JX143032	JX142786	—	JX142540	—	JX143278	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. agavicola</i>	CBS 117292 = CPC 11774 ^T	AY647237	AY966898	AY966899	—	AY966900	—	AY966897	—	—	—	—	—	Groenewald et al. (2013)
	CPC 5259 ^{ET}	JX143525	JX143033	JX142787	—	JX142541	—	JX143279	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. cf. alchemillicola</i>	CPC 5126	JX143526	JX143034	JX142788	—	JX142542	—	JX143280	—	—	—	—	—	Groenewald et al. (2013)
	CBS 248.67 = CPC 5117 ^{ET}	JX143530	JX143038	JX142792	MH496170	JX142546	—	JX143284	MH496340	—	—	—	—	Groenewald et al. (2013), Bakhshi et al. (2018)
<i>Cer. althaeina</i>	CCTU 1194 = IRAN 2674C	KJ886397	KJ885914	KJ885753	MH496171	KJ886075	MH511837	KJ886236	MH496341	—	—	—	—	Bakhshi et al. (2015a, 2018)
	IRAN 3739C ^T	MT338042	MT334647	MT334651	MT334649	MT334645	—	MT334643	—	—	—	—	—	Present study
<i>Cer. alyssopsisidis</i>	IRAN 3740C	MT338043	MT334648	MT334652	MT334650	MT334646	—	MT334644	—	—	—	—	—	Present study
	CBS 116455 = CPC 11556 ^T	AY840519	AY840450	AY840417	MH496173	AY840384	—	AY840486	MH496343	—	—	—	—	Groenewald et al. (2013), Bakhshi et al. (2018)
<i>Cer. apii</i>	CCTU 1086 = CBS 136037 = IRAN 2655C	KJ886411	KJ885928	KJ885767	MH496176	KJ886089	—	KJ886250	MH496346	—	—	—	—	Bakhshi et al. (2015a, 2018)
	CBS 116457 = CPC 10267 ^T	AY840536	AY840467	AY840434	—	AY840401	—	AY840503	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. amoraciae</i>	CBS 250.67 = CPC 5088 ^{ET}	JX143545	JX143053	JX142807	MH496181	JX142561	—	JX143299	MH496351	—	—	—	—	Groenewald et al. (2013), Bakhshi et al. (2018)
	CBS 116456 = CPC 11557 ^{ET}	AY840527	AY840458	AY840425	MH496185	AY840392	—	AY840494	MH496355	—	—	—	—	Groenewald et al. (2013), Bakhshi et al. (2018)
<i>Cer. bizzozzeriana</i>	CBS 258.67 = CPC 5061 ^{ET}	JX143546	JX143054	JX142808	MH496198	JX142562	—	JX143300	MH496368	—	—	—	—	Groenewald et al. (2013), Bakhshi et al. (2018)
	CBS 540.71 = IMI 161110 = CPC 5060	JX143548	JX143056	JX142810	MH496199	JX142564	—	JX143302	MH496369	—	—	—	—	Groenewald et al. (2013), Bakhshi et al. (2018)
<i>Cer. cf. brunkii</i>	CCTU 1013	KJ886414	KJ885931	KJ885770	MH496192	KJ886092	—	KJ886253	MH496362	—	—	—	—	Bakhshi et al. (2015a, 2018)
	CCTU 1022 = CBS 136028	KJ886415	KJ885932	KJ885771	MH496193	KJ886093	—	KJ886254	MH496363	—	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. campii-silii</i>	CCTU 1040 = CBS 136131	KJ886416	KJ885933	KJ885772	MH496200	KJ886094	—	KJ886255	MH496370	—	—	—	—	Bakhshi et al. (2015a, 2018)
	CCTU 1107	KJ886417	KJ885934	KJ885773	MH496197	KJ886095	—	KJ886256	MH496367	—	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. canescens complex</i>	CCTU 1117 = CBS 136132	KJ886418	KJ885935	KJ885774	MH496195	KJ886096	—	KJ886257	MH496365	—	—	—	—	Bakhshi et al. (2015a, 2018)
	CCTU 1127 = CBS 136133	KJ886420	KJ885937	KJ885775	MH496194	KJ886098	—	KJ886259	MH496364	—	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. cf. brunkii</i>	CCTU 1234	KJ886419	KJ885936	KJ885776	MH496196	KJ886097	—	KJ886258	MH496366	—	—	—	—	Bakhshi et al. (2015a, 2018)
	CBS 132657 = CPC 11598	JX143559	JX143067	JX142821	—	JX142575	—	JX143313	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. campii-silii</i>	CBS 132625 = CPC 14585	JX143561	JX143069	JX142823	—	JX142577	—	JX143315	—	—	—	—	—	Groenewald et al. (2013), Videira et al. (2017)
	CBS 111133 = CPC 1137	AY260065	DQ835103	DQ835130	—	DQ835157	—	DQ835084	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. capsici</i>	CPC 11640 = IMI 186563	JX143566	JX143074	JX142828	—	JX142582	—	DQ835084	—	—	—	—	—	Groenewald et al. (2013)
	CBS 132622 = CPC 14520	JX143568	JX143077	JX142831	—	JX142585	—	JX143320	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. celosiae</i>	CBS 132600 = CPC 10660	JX143570	JX143080	JX142834	—	JX142588	—	JX143326	—	—	—	—	—	Groenewald et al. (2013)
	CBS 132620 = CPC 14237	JX143571	JX143081	JX142835	—	JX142589	—	JX143327	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. chenopodii</i>	CCTU 1060 = IRAN 2652C	KJ886438	KJ885955	KJ885794	MH496201	KJ886116	MH511862	KJ886277	MH496371	—	—	—	—	Bakhshi et al. (2015a, 2018)
	CBS 132612 = CPC 10831	JX143578	JX143088	JX142842	—	JX142596	—	JX143334	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. chinensis</i>	CBS 133582 = CPC 20529 ^T	KC005779	KC005764	KC005767	—	—	—	KC005813	—	—	—	—	—	Crous et al. (2012a)
	CBS 132669 = CPC 12683	EU514223	JX143090	JX142844	—	JX142598	—	JX143336	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. cf. citrulina</i>	CBS 132634 = CPC 17017 ^T	JX143583	JX143095	JX142849	—	JX142603	—	JX143341	—	—	—	—	—	Groenewald et al. (2013)
	CCTU 1083 = CBS 136126 ^T	KJ886441	KJ885958	KJ885797	MH496204	KJ886119	MH511865	KJ886280	MH496374	—	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. conyzae-canadensis</i>	CCTU 1119 = CBS 135978 ^T	KJ886445	KJ885962	KJ885801	MH496207	KJ886123	MH511868	KJ886284	MH496377	—	—	—	—	Bakhshi et al. (2015a, 2018)

Table 4. (Continued).

Species	Isolates ¹	GenBank accession numbers ²										References	
		ITS	actA	cmdA	gapdh	his3	rpb2	tef1	tub2				
<i>Cer. corchori</i>	MUCC 585 = MUCNS 72 = MAFF 238191 ^{ET}	JX143584	JX143096	JX142850	—	JX142604	—	JX143342	—	—	—	—	Groenewald et al. (2013)
<i>Cer. cf. coreopsisidis</i>	CBS 132598 = CPC 10648	JX143585	JX143097	JX142851	—	JX142605	—	JX143343	—	—	—	—	Groenewald et al. (2013)
<i>Cer. cylindracea</i>	CCTU 1081 = CBS 138580 = IRAN 2654C ^T	KJ886449	KJ885966	KJ885805	MH496211	KJ886127	MH511872	KJ886288	MH496381	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. cyperacearum</i>	CPC 23918 ^T	KT193667	—	KT193727	—	—	—	—	—	—	—	—	Nguanhom et al. (2016)
<i>Cer. cyperina</i>	CPC 23919 ^T	KT193669	—	KT193729	—	—	—	—	—	—	—	—	Nguanhom et al. (2016)
<i>Cer. delaireae</i>	CBS 132595 = CPC 10455 = GV2 PPRI number: C558 ^T	JX143587	JX143099	JX142853	—	JX142607	—	JX143345	—	—	—	—	Groenewald et al. (2013)
<i>Cer. dianellicola</i>	CBS 143453 = CPC 32597 ^T	MG386075	MG674152	MG674153	—	—	—	—	—	—	—	—	Crous et al. (2017b)
<i>Cer. dispori</i>	CBS 132608 = CPC 10773	JX143591	JX143103	JX142857	—	JX142611	—	JX143349	—	—	—	—	Groenewald et al. (2013)
<i>Cer. eremochloae</i>	IMI 321201 ^{set}	HM235405	—	—	—	—	—	—	—	—	—	—	Crous et al. (2011a)
<i>Cer. cf. erysimi</i>	CBS 115059 = CPC 5361	JX143592	JX143104	JX142858	—	JX142612	—	JX143350	—	—	—	—	Groenewald et al. (2013)
<i>Cer. eucommiae</i>	CBS 131932 = CPC 10802 ^T	GU269851	GU320555	—	—	—	—	GU384563	—	—	—	—	Crous et al. (2013)
<i>Cer. euphorbiae-sieboldianae</i>	CBS 113306 ^T	JX143593	JX143105	JX142859	—	JX142613	MF951462	JX143351	—	—	—	—	Groenewald et al. (2013), Videira et al. (2017)
<i>Cer. fagopyri</i>	CBS 132623 = CPC 14541 ^{NT}	JX143594	JX143106	JX142860	—	JX142614	MF951463	JX143352	—	—	—	—	Groenewald et al. (2013), Videira et al. (2017)
<i>Cer. cf. flagellaris</i> clade 1	CCTU 1128 = CBS 136141 = IRAN 2661C	KJ886476	KJ885993	KJ885832	MH496223	KJ886154	MH511884	KJ886315	MH496393	—	—	—	Bakhshi et al. (2015a, 2018)
	CPC 1051	AY260069	JX143121	JX142875	MH496225	JX142629	MH511886	JX143367	MH496395	—	—	—	Bakhshi et al. (2015a, 2018)
	CPC 5441	JX143611	JX143124	JX142878	MH496217	JX142632	MH511878	JX143370	MH496387	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. cf. flagellaris</i> clade 2	CCTU 1115 = CBS 136139 = IRAN 2659C	KJ886473	KJ885990	KJ885829	MH496232	KJ886151	MH511893	KJ886312	MH496402	—	—	—	Bakhshi et al. (2015a, 2018)
	CCTU 1223 = CBS 136154 = IRAN 2683C	KJ886512	KJ886029	KJ885868	MH496236	KJ886190	MH511897	KJ886351	MH496406	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. cf. flagellaris</i> clade 3	CBS 115482 = A207 Bs+ = CPC 4410	AY260070	DQ835114	DQ835141	MH496249	DQ835168	MH511910	DQ835095	MH496419	—	—	—	Bakhshi et al. (2015a, 2018)
	CBS 143.51 = CPC 5055	JX143607	JX143119	JX142873	MH496246	JX142627	MH511907	JX143365	MH496416	—	—	—	Bakhshi et al. (2015a, 2018)
	CCTU 1140 = CBS 136143 = IRAN 2666C	KJ886481	KJ885998	KJ885837	MH496248	KJ886159	MH511909	KJ886320	MH496418	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. gamsiana</i>	CCTU 1074 = CPC 24909 ^T	KJ886426	KJ885943	KJ885782	MH496276	KJ886104	MH511937	KJ886265	MH496446	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. glycinicola</i>	CPC 23911 ^T	KT193670	—	KT193730	—	—	—	—	—	—	—	—	Nguanhom et al. (2016)
<i>Cer. gomphrenigena</i>	CBS 144613 = CPC 32470 ^T	MK442573	—	MK442650	—	MK442658	—	MK442690	MK442728	—	—	—	Crous et al. (2019b)
<i>Cer. cf. gossypii</i>	CCTU 1070 = CBS 136137	KJ886467	KJ885984	KJ885823	MH496282	KJ886145	MH511943	KJ886306	MH496452	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. cf. helianthicola</i>	MUCC 716	JX143615	JX143128	JX142882	—	JX142636	—	JX143374	—	—	—	—	Groenewald et al. (2013)
<i>Cer. cf. ipomoeae</i>	CBS 132639 = CPC 10102	JX143616	JX143129	JX142883	—	JX142637	—	JX143375	—	—	—	—	Groenewald et al. (2013)
<i>Cer. iranica</i>	CCTU 1137 = CBS 136124 ^T	KJ886513	KJ886030	KJ885869	MH496285	KJ886191	MH511946	KJ886352	MH496455	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. ischaemi</i>	BRIP 56010 ^T	KM055428	—	—	—	—	—	—	—	—	—	—	Shivas et al. (2015)
<i>Cer. jansseana</i>	CBS 145.37, IMI 303642	KF251314	—	—	—	—	MF951464	—	—	—	—	—	Videira et al. (2017)
<i>Cer. jatrophiophila</i>	CMHUB 21035 Strain 2225	KJ186790	—	KJ186792	—	KJ186794	—	—	—	—	—	—	Dianese et al. (2014)
	CMHUB 21035 Strain 2229	KJ186791	—	KJ186793	—	KJ186795	—	—	—	—	—	—	Dianese et al. (2014)

Table 4. (Continued).

Species	Isolates ¹	GenBank accession numbers ²										References		
		ITS	actA	cmdA	gapdh	his3	rbp2	tef1	tub2					
<i>Cer. kikuchii</i>	CBS 128.27 = CPC 5068 ^T	DQ835070	DQ835107	DQ835134	—	DQ835161	—	DQ835088	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. lactucae-sativae</i>	CBS 132604 = CPC 10728	JX143621	JX143134	JX142888	—	JX142642	—	JX143380	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. cf. malloti</i>	MUCC 575 = MUCNS 582 = MAFF 237872	JX143625	JX143138	JX142892	—	JX142646	—	JX143384	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. mercurialis</i>	CBS 550.71 ^{ET}	JX143628	JX143141	JX142895	—	JX142649	—	JX143387	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. cf. mikaniicola</i>	CPC 20741	KT193693	—	KT193753	—	—	—	—	—	—	—	—	—	Nguanhom et al. (2016)
<i>Cer. cf. modiolae</i>	CPC 5115	JX143630	JX143143	JX142897	—	JX142651	—	JX143389	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. musigena</i>	CPC 24809 ^T	KT193698	—	KT193758	—	—	—	—	—	—	—	—	—	Nguanhom et al. (2016)
<i>Cer. cf. nicotianae</i>	CBS 132632 = CPC 15918	JX143631	JX143144	JX142898	—	JX142652	—	JX143390	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. olivascens</i>	CBS 253.67 = IMI 124975 = CPC 5085 ^T	JX143632	JX143145	JX142899	—	JX142653	—	JX143391	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. cf. physalidis</i>	CBS 765.79	JX143633	JX143146	JX142900	—	JX142654	—	JX143392	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. pileicola</i>	CBS 132607 = CPC 10749 ^T	JX143634	JX143147	JX142901	—	JX142655	—	JX143393	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. plantaginis</i>	CBS 252.67 = CPC 5084 ^{ET}	DQ233318	DQ233368	DQ233394	MH496291	DQ233420	—	DQ233342	MH496461	—	—	—	—	Groenewald et al. (2013), Bakhshi et al. (2018)
<i>Cer. polygonacea</i>	CCTU 1082 = CBS 138728	KJ886402	KJ885919	KJ885758	MH496286	KJ886080	MH511947	KJ886241	MH496456	—	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. pseudochenopodii</i>	CBS 132614 = CPC 11318	JX143637	JX143150	JX142904	—	JX142658	—	JX143396	—	—	—	—	—	Groenewald et al. (2013)
	CCTU 1038 = CBS 136022 = IRAN 2649C ^T	KJ886516	KJ886033	KJ885872	MH496294	KJ886194	MH511954	KJ886355	MH496464	—	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. punctiformis</i>	CBS 132626 = CPC 14606	JX143638	JX143151	JX142905	—	JX142659	—	JX143397	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. rautensis</i>	CBS 555.71 = IMI 161117 = CPC 5082 ^{ET}	JX143550	JX143058	JX142812	MK531772	JX142566	—	JX143304	MK531770	—	—	—	—	Groenewald et al. (2013), Bakhshi (2019)
	CCTU 1190 = CBS 136134	KJ886422	KJ885939	KJ885778	MK531771	KJ886100	MK564169	KJ886261	MK531769	—	—	—	—	Bakhshi et al. (2015a), Bakhshi (2019)
<i>Cerc. cf. resedae</i>	CBS 257.67 = CPC 5057	DQ233319	DQ233369	DQ233395	—	DQ233421	—	DQ233343	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. cf. richardicola</i>	CBS 132627 = CPC 14680	JX143640	JX143153	JX142907	—	JX142661	—	JX143399	—	—	—	—	—	Groenewald et al. (2013)
	CCTU 1004	KJ886519	KJ886036	KJ885875	MH496295	KJ886197	MH511955	KJ886358	MH496465	—	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. ricinella</i>	CBS 132605 = CPC 10734	JX143646	JX143159	JX142913	—	JX142667	—	JX143405	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. rodmanii</i>	CBS 113129 = RC397 = WH9-BR	DQ835081	DQ835127	DQ835154	—	DQ835181	—	AF146143	—	—	—	—	—	Groenewald et al. (2013)
	CCTU 1129 = IRAN 2662C	KJ886522	KJ886039	KJ885878	MH496297	KJ886200	MH511957	KJ886361	MH496467	—	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. rumicis</i>	CPC 5439	JX143648	JX143161	JX142915	—	JX142669	—	JX143407	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. samambatae</i>	CPC 24673 = COAD 1090 ^T	KT037508	KT037590	KT037457	—	—	—	KT037468	—	—	—	—	—	Guatimosim et al. (2016)
<i>Cer. senecionis-walkeri</i>	CBS 132636 = CPC 19196	JX143649	JX143162	JX142916	—	JX142670	MF951466	JX143408	—	—	—	—	—	Groenewald et al. (2013), Videira et al. (2017)
<i>Cer. cf. sigesbeckiae</i>	CBS 132601 = CPC 10664	JX143650	JX143163	JX142917	—	JX142671	—	JX143409	—	—	—	—	—	Groenewald et al. (2013)
<i>Cer. sojina</i>	CBS 132615 = CPC 11353 ^T	JX143659	JX143173	JX142927	—	JX142681	—	JX143419	KX288419	—	—	—	—	Groenewald et al. (2013), Videira et al. (2017)
	CCTU 1043 = CBS 136038	KJ886523	KJ886040	KJ885879	MH496299	KJ886201	MH511959	KJ886362	MH496469	—	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cer. solani-betacei</i>	COAD 2293 ^T	MH223464	MH445457	MH428037	—	—	—	—	—	—	—	—	—	Crous et al. (2018a)
<i>Cer. sorghicola</i>	CCTU 1173 = CBS 136448 = IRAN 2672C ^T	KJ886525	KJ886042	KJ885881	MH496301	KJ886203	MH511961	KJ886364	MH496471	—	—	—	—	Bakhshi et al. (2015a, 2018)
<i>Cercospora</i> sp. A	CBS 132631 = CPC 15872	JX143675	JX143189	JX142943	—	JX142697	—	JX143435	—	—	—	—	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. B	CBS 132602 = CPC 10687	JX143676	JX143190	JX142944	—	JX142698	—	JX143436	—	—	—	—	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. C	CBS 132629 = CPC 15841	JX143677	JX143191	JX142945	—	JX142699	—	JX143437	—	—	—	—	—	Groenewald et al. (2013)

Table 4. (Continued).

Species	Isolates ¹	GenBank accession numbers ²							References	
		ITS	actA	cmdA	gapdh	his3	rbp2	tef1		tub2
<i>Cercospora</i> sp. D	CBS 132630 = CPC 15856	JX143678	JX143192	JX142946	—	JX142700	—	JX143438	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. E	CBS 132628 = CPC 15632	JX143679	JX143193	JX142947	—	JX142701	—	JX143439	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. F	CBS 132618 = CPC 12062	DQ185071	DQ185095	DQ185107	—	DQ185119	—	DQ185083	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. G clade 1	CCTU 1015 = CBS 136024 = IRAN 2645C	KJ886528	KJ886045	KJ885884	MH496303	KJ886206	MH511963	KJ886367	MH496473	Bakhshi et al. (2015a, 2018)
<i>Cercospora</i> sp. G clade 2	CPC 5438	JX143682	JX143196	JX142950	MH496304	JX142704	—	JX143442	MH496474	Groenewald et al. (2013), Bakhshi et al. (2018)
	CBS 115518 = CPC 5360	JX143681	JX143195	JX142949	MH496310	JX142703	—	JX143441	MH496480	Groenewald et al. (2013), Bakhshi et al. (2018)
	CCTU 1030 = CBS 136026	KJ886530	KJ886047	KJ885886	MH496311	KJ886208	MH511969	KJ886369	MH496481	Bakhshi et al. (2015a, 2018)
<i>Cercospora</i> sp. H	CBS 115205 = CPC 5116	JX143683	JX143197	JX142951	—	JX142705	—	JX143443	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. I	CBS 114815 = CPC 5364	JX143685	JX143199	JX142953	—	JX142707	—	JX143445	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. J	MUCC 541	JX143695	JX143209	JX142963	—	JX142717	—	JX143455	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. K	CBS 132603 = CPC 10719	JX143696	JX143210	JX142964	—	JX142718	—	JX143456	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. L	CBS 115477 = CPC 5114	JX143699	JX143213	JX142967	—	JX142721	—	JX143459	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. M	CBS 132596 = CPC 10553	JX143700	AY752203	AY752234	—	AY752265	—	AY752175	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. N	CBS 132619 = CPC 12684	EU514224	JX143214	JX142968	—	JX142722	—	JX143460	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. O	CBS 132635 = CPC 18636	JX143701	JX143215	JX142969	—	JX142723	—	JX143461	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. P	CBS 116365 = CPC 10526	AY752141	AY752204	AY752235	—	AY752266	—	AY752176	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. Q	CBS 113997 = CPC 5325	JX143717	JX143230	JX142984	JX142521	JX142738	—	JX143476	JX142478	Groenewald et al. (2013)
	CPC 10550	AY752139	AY752200	AY752231	JX142533	AY752262	—	AY752172	JX142484	Groenewald et al. (2013)
<i>Cercospora</i> sp. R	CBS 114644	JX143732	JX143245	JX142999	—	JX142753	—	JX143491	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. S	CBS 132599 = CPC 10656	JX143733	JX143246	JX143000	—	JX142754	—	JX143492	—	Groenewald et al. (2013)
<i>Cercospora</i> sp. T	CCTU 1148 = CBS 136125	KJ886541	KJ886058	KJ885897	MH496318	KJ886219	MH511976	KJ886380	MH496488	Bakhshi et al. (2015a, 2018)
<i>Cer. tezepurensis</i>	CS2012 [†]	KC351743	KC355808	KC513745	—	KC355807	—	KC513746	—	Meghvansi et al. (2013)
<i>Cer. uwebrauniana</i>	CCTU 1200 = CBS 138581 [†]	KJ886408	KJ885925	KJ885764	MH496319	KJ886086	MH511977	KJ886247	MH496489	Bakhshi et al. (2015a, 2018)
<i>Cer. vignigena</i>	CBS 132611 = CPC 10812 [†]	JX143734	JX143247	JX143001	—	JX142755	—	JX143493	—	Groenewald et al. (2013)
<i>Cer. violae</i>	CBS 251.67 = CPC 5079 ^{ET}	JX143737	JX143250	JX143004	MH496322	JX142758	—	JX143496	MH496492	Groenewald et al. (2013), Bakhshi et al. (2018)
	CCTU 1025 = IRAN 2646C	KJ886543	KJ886060	KJ885899	MH496321	KJ886221	MH511979	KJ886382	MH496491	Bakhshi et al. (2015a, 2018)
<i>Cer. zeae-maydis</i>	CBS 117757 = JV-WI-02 = A360 ^{ET}	DQ185074	DQ185098	DQ185110	—	DQ185122	—	DQ185086	—	Groenewald et al. (2013)
<i>Cer. zebrina</i>	CBS 108.22 = CPC 5091	JX143744	JX143257	JX143011	MH496324	JX142765	—	JX143503	MH496494	Groenewald et al. (2013), Bakhshi et al. (2018)
	CCTU 1239 = CBS 135977	KJ886551	KJ886068	KJ885907	MH496334	KJ886229	MH511987	KJ886390	MH496504	Bakhshi et al. (2015a, 2018)
<i>Cer. zeina</i>	CBS 118820 = CPC 11995 [†]	DQ185081	DQ185105	DQ185117	—	DQ185129	MF951469	DQ185093	—	Groenewald et al. (2013)
<i>Cer. cf. zinniae</i>	CBS 132676 = CPC 15075	JX143757	JX143273	JX143027	—	JX142781	—	JX143519	—	Groenewald et al. (2013)
	CCTU 1003	KJ886552	KJ886069	KJ885908	MH496335	KJ886230	MH511988	KJ886391	MH496505	Bakhshi et al. (2015a, 2018)

¹ BRIP: Queensland Herbarium, Brisbane, Australia; CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CCTU: Culture Collection of Tabriz University, Tabriz, Iran; COAD: Coleção Octávio Almeida Drummond, Universidade Federal de Viçosa, Viçosa, Brazil; CPC: Culture collection of Pedro Crous, housed at CBS; IMI: International Mycological Institute, Kew, UK; IRAN: Iranian Fungal Culture Collection, Iranian Research Institute of Plant Protection, Tehran, Iran; MAFF: Ministry of Agriculture, Forestry and Fisheries, Tsukuba, Ibaraki, Japan; MUCC: Murdoch University, Perth, Western Australia. ^{T, ET, ISOT, and NT} indicate ex-type, ex-epitype, ex-isotype and ex-neotype strains, respectively.

² ITS: internal transcribed spacers and intervening 5.8S nrDNA; actA: partial actin gene; cmdA: partial calmodulin gene; gapdh: partial glyceraldehyde-3-phosphate dehydrogenase gene; his3: partial histone H3 gene; rpb2: partial RNA polymerase II second largest subunit gene; tef1: partial translation elongation factor 1- α gene; tub2: partial beta-tubulin gene.

Not sporulating well in culture. The descriptions are based on fungal structures *in planta*.

Distribution: Worldwide, but mostly in humid, tropical and subtropical climates.

Hosts: A wide range of woody and herbaceous plants including agricultural crops, cereals, vegetables, ornamentals, oil crops, forest trees and weeds of different plant families (Crous & Braun 2003, Groenewald *et al.* 2013, Bakhshi *et al.* 2018).

Disease symptoms: Often associated with leaf spots, but also causing necrotic lesions on flowers, fruits, bracts, seeds and pedicels.

Notes: Species of *Cercospora* are morphologically similar and hard to differentiate from one another. The most relevant differential morphological traits are the presence or absence of external mycelium, conidiophore morphology and conidial shape and size, but they are not always reliable as too much intraspecific variation exists (Crous & Braun 2003). Chupp (1954) provided the first monograph of the genus and stated that species of *Cercospora* are commonly host-specific and each plant host genus or family would have its own *Cercospora* species. At the moment, the connection between a *Cercospora* isolate and the host plant from which it was isolated, is still a major factor in the taxonomic description of most *Cercospora* species. Crous & Braun (2003) reassessed Chupp's work and recognised 659 species as true species of *Cercospora* using morphological criteria, with a further 281 species names reduced to synonyms under *Cer. apii* s. *lat.* since they were morphologically not or barely distinguishable from *Cer. apii* s. *str.* on celery. In recent years, Braun *et al.* (2013, 2014, 2015a, b, 2016) published a series of papers to produce a modern monograph of *Cercospora* and allied genera in a stepwise approach at plant family level based on morphological features and host data. However, as there are only few distinctive morphological characters useful for species discrimination and since specialised as well as plurivorous species are involved, molecular data are essential for accurate identification of species within this genus.

The ITS barcode has limited discriminatory power to distinguish *Cercospora* species (Stewart *et al.* 1999, Crous *et al.* 2000, 2009a, b, Goodwin *et al.* 2001), making multi-locus sequence analysis with several protein-coding loci essential for accurate species identification in this genus. Groenewald *et al.* (2013) provided a backbone phylogeny for *Cercospora* spp. based on a multi-locus DNA sequence dataset of five genomic loci (ITS, *actA*, *cmdA*, *his3* and *tef1*) of a large sampling of species. Since then, numerous molecular examinations of *Cercospora* species have been carried out based on multi-gene approaches (Dianese *et al.* 2014, Bakhshi *et al.* 2015a, Shivas *et al.* 2015, Soares *et al.* 2015, Albu *et al.* 2016, Guatimosim *et al.* 2016, Nguanhom *et al.* 2016, Guillin *et al.* 2017). Bakhshi *et al.* (2018) applied three more potential candidate gene regions including *gapdh*, *rpb2*, and *tub2* to perform an eight-gene phylogeny (ITS, *actA*, *cmdA*, *gapdh*, *his3*, *rpb2*, *tef1* and *tub2*) for *Cercospora* species. With the classifications presented by Groenewald *et al.* (2013) and Bakhshi *et al.* (2018), none of the genes analysed provided an effective barcode on its own across the entire genus. However, *gapdh* emerged as a strong candidate for improved species delimitation in *Cercospora* and provides better insight, especially into species complexes (Bakhshi *et al.* 2018, Bakhshi 2019). However, the *gapdh* marker has not yet been applied for the phylogeny of most of the reference taxa studied by Groenewald *et al.* (2013).

Based on molecular studies done in recent years, we have several issues in *Cercospora* taxonomy: 1. *Cercospora* collections

on certain hosts with agreeing morphology found in different geographical regions do often not belong to a single species, thus most of the clades treated as "cf." based on their morphological similarities to existing species and pending comparison of those species with DNA sequence data of (epi-)type material from the original country and host; 2. Most of the *Cercospora* clades studied, have uncertain identity (*Cercospora* sp. A–T) (Groenewald *et al.* 2013, Bakhshi *et al.* 2015a), and it was not possible to unequivocally assign a species name since these clades contained isolates from multiple hosts and/or countries and the same hosts occurred in multiple clades, or the host information was not available. The speciation within *Cercospora* s. *str.*, above all is more complicated than previously presumed and beside specialised species, the genus includes many complex species with a wide host range, often with overlapping host ranges between different taxa. Therefore, typification and epitypification of the species within this genus is essential to stabilise the names of different taxa, and to provide connections between specimens assessed through morphological and molecular methods.

At the generic level, the genus *Cercospora* is well distinguished from other cercosporoid genera by the smooth hyphae (*vs Stenella* s. *lat.*), conspicuous, thickened and darkened conidiogenous loci and conidial hila (*vs Pseudocercospora* s. *lat.*) and hyaline or subhyaline conidia (*vs Passalora* s. *lat.*) (Crous & Braun 2003). However, the monophyly of *Cercospora* s. *str.* was rejected by Bakhshi *et al.* (2015b) who introduced the genus *Neocercospora* with cercospora-like morphology, clustering in a clade in *Mycosphaerellaceae* apart from *Cercospora* s. *str.*, suggesting that also at generic level, molecular identification is practically mandatory for the classification of cercospora-like taxa.

Cercospora is a very successful pathogenic genus that causes disease on a great number of agricultural crops, including cereals, vegetables, ornamentals, oil crops and forest trees, but is rarely saprobic or a secondary invader (Crous & Braun 2003, Groenewald *et al.* 2013). Species of the genus are commonly described causing leaf spots, but are also associated with necrotic lesions on flowers, fruits, seeds, bracts and pedicels of many cultivated and native plants in a range of climates worldwide (Crous & Braun 2003, Groenewald *et al.* 2013). Some species are considered potential biocontrol agents of weeds, including *Cer. caricis* on *Cyperus rotundus* and *Cer. rodmanii* on *Eichhornia crassipes* (Inglis *et al.* 2001, Tessmann *et al.* 2001, Praveena & Naseema 2004). Examples of the most relevant plant pathogens are *Cer. apii* on celery (Groenewald *et al.* 2006a), *Cer. beticola* on sugar beet (Groenewald *et al.* 2008), *Cer. canescens* on beans (Chand *et al.* 2015, Duangsong *et al.* 2016), *Cer. carotae* on carrots (Kushalappa *et al.* 1989), *Cer. kikuchii* on soybean (Sautua *et al.* 2019), *Cer. zaeae-maydis* and *Cer. zeina* on maize (Crous *et al.* 2006a) and *Cer. zonata* on faba beans (Kimber 2011). Some of these pathogens produce a photo-activated perylinquinone toxin called cercosporin, which helps the fungus to obtain its nourishment by killing host cells (Daub 1982, Chen 2007, Santos Rezende *et al.* 2020). Elucidation of the draft genome sequence of *Cercospora* species, especially the plant pathogenic taxa, will provide insights to better understand the genes involved in various biosynthesis pathways including cercosporin (secondary metabolites) production, pathogenicity, virulence and other important molecular functions. In addition, it will enable the proper classification of *Cercospora* spp.

References: Ellis 1971, Chupp 1954, Crous & Braun 2003, Braun *et al.* 2013, 2014, 2015a, b, 2016 (morphology and host range); Groenewald *et al.* 2006b, 2008, Soares *et al.* 2015, Albu *et al.* 2016, Vaghefi *et al.* 2018, Santos Rezende *et al.* 2020 (pathogenicity);

Greenewald *et al.* 2013, Bakhshi *et al.* 2015a, 2018, Guatimosim *et al.* 2016, Nguanhom *et al.* 2016 (morphology and phylogeny).

Cercospora alyssopsidis M. Bakhshi, Zare & Crous, *sp. nov.*
Mycobank MB 835420. Fig. 15.

Etymology: Name derived from the host genus, *Alyssopsis*.

Leaf spots amphigenous, circular, 3–6 mm, grey with definite border and yellow halo. *Mycelium* internal. *Caespituli* amphigenous, brown. *Conidiophores* aggregated in moderately dense fascicles, arising from a moderately developed, brown stroma, to 55 µm diam; conidiophores brown, 1–5-septate, straight to geniculate-sinuuous due to sympodial proliferation, simple, sometimes branched, uniform in width, sometimes constricted at the proliferating point, (40–)130–210(–240) × 3–5 µm. *Conidiogenous cells* integrated, terminal or lateral, pale brown to brown, proliferating sympodially, 15–30 × 3–5 µm, multi-local; loci distinctly thickened, darkened and somewhat refractive, apical, lateral or formed on shoulders caused by geniculation, 1.5–3 µm diam. *Conidia* solitary, obclavate-cylindrical, straight to slightly curved, hyaline, (25–)35–70(–105) × 3–6 µm, 3–10-septate, with obtuse to subobtuse apices and subtruncate or obconically truncate bases; hila thickened, darkened, refractive, 1.5–3 µm diam.

Culture characteristics: Colonies on MEA slow-growing, reaching 18 mm diam after 20 d at 25 °C in the dark; raised, folded, with smooth, even margins and sparse aerial mycelium, radially striated, surface grey olivaceous, reverse iron grey. Colonies on PDA reaching 27 mm diam after 20 d at 25 °C, flat, with smooth, even margins and moderate aerial mycelium, surface grey olivaceous, reverse iron grey.

Typus: Iran, Golestan Province, Gorgan, 36°50'26.22"N, 54°27'24.98"E, 150 m a.s.l., on leaves of *Alyssopsis mollis* (*Brassicaceae*), 1 Nov. 2017, M. Bakhshi (*holotype* IRAN 17628F, culture ex-type IRAN 3739C).

Additional material examined: Iran, Golestan Province, Gorgan, on *Alyssopsis mollis*, Oct. 2018, M. Bakhshi (IRAN 17629F, culture IRAN 3740C).

Notes: Based on the results of the combined phylogenetic tree, two isolates obtained from *Alyssopsis mollis* cluster in a distinct well-supported clade (Fig. 14). No *Cercospora* species is presently known from *Alyssopsis* (Crous & Braun 2003, Farr & Rossman 2022). As *Arabis secunda*, *Nasturtium sagittatum* and *Sisymbrium molle* are synonyms of *Alyssopsis mollis*, we also checked the *Cercospora* species reported on these genera. *Cercospora armoraciae*, *Cer. cruciferarum*, *Cer. kuznetzoviana* and *Cer. nasturtii* are species of *Cercospora* that have been described from these plant genera (Crous & Braun 2003, Farr & Rossman 2022). *Cercospora alyssopsidis* is phylogenetically distinct from *Cer. armoraciae*. Among the other candidate species, no type material could be located for *Cer. kuznetzoviana*, but possibly this species is allied to *Pseudocercospora capsellae* (Crous & Braun 2003). *Cercospora cruciferarum* is in the *Cer. apii* s. lat. complex (Crous & Braun 2003) and causes different leaf spots (0.5–2 mm diam, white centre, pale to dark brown border). *Cercospora nasturtii* also differs morphologically from this species by the shorter and somewhat wider conidiophores (20–100 × 4–6.5 µm) and indistinctly septate conidia (Hsieh & Goh 1990). *Cercospora alyssopsidis* is the first *Cercospora* species reported until now on the host genus *Alyssopsis* and appears to be specific to *Alyssopsis mollis*.

Genome sequenced strain: *Cercospora apii*. **Germany**, Heilbron, Landwirtschaftsamt, on *Apium graveolens* (*Apiaceae*), 10 Aug. 2004, K. Schrameyer, culture ex-epitype CBS 116455 = CPC 11556. This Whole Genome Shotgun project has been deposited at GenBank under the accession JALRMD000000000 (BioProject: PRJNA827019, BioSample: SAMN27594412; present study).

Authors: M. Bakhshi & R. Zare

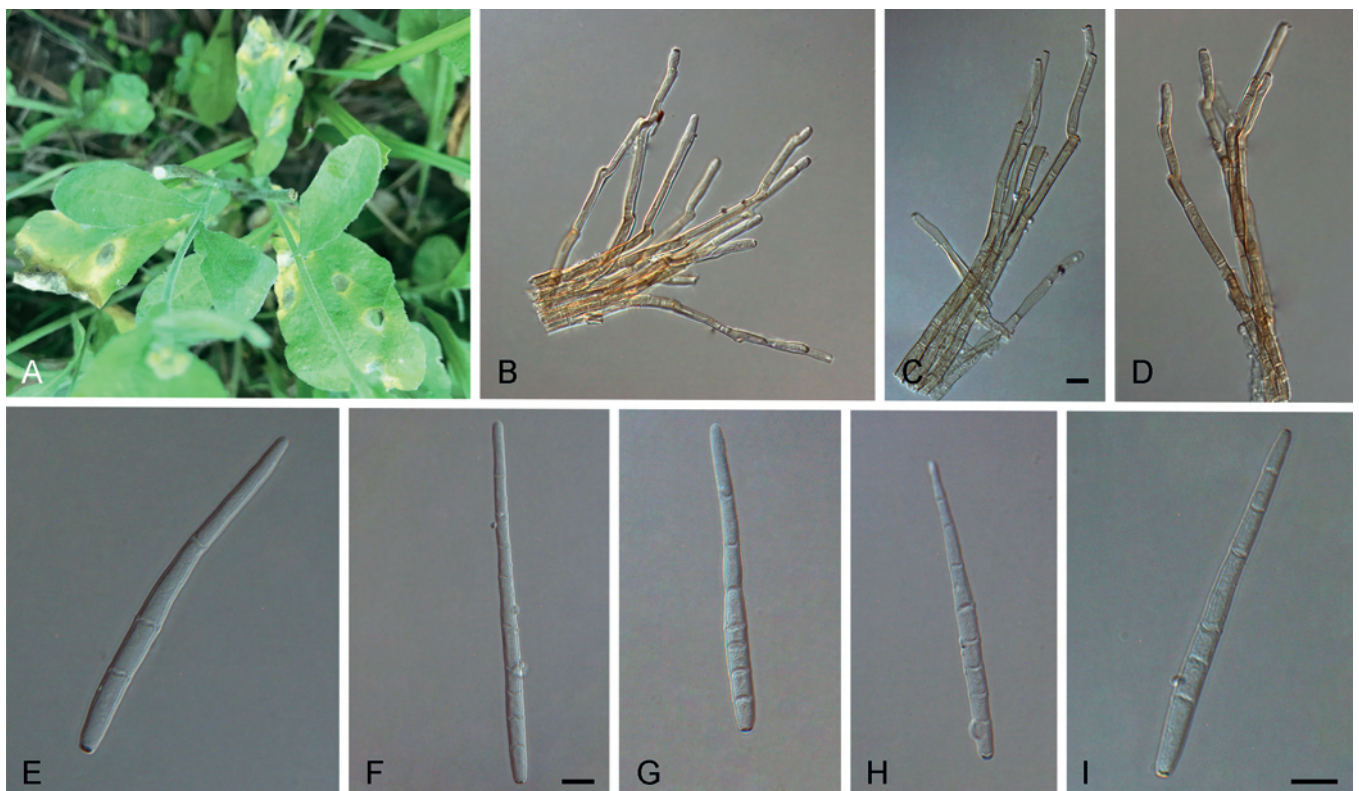


Fig. 15. *Cercospora alyssopsidis* (ex-type IRAN 3739C). **A.** Leaf spots. **B–D.** Fasciculate conidiophores. **E–I.** Conidia. Scale bars = 10 µm.

Coleophoma Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. I, 116: 637. 1907. Fig 16.

Synonyms: *Rhabdostromellina* Höhn., Ann. Mycol. 15: 303. 1917.

Bactropycnis Höhn., Hedwigia 62: 65. 1920.

Xenodomus Petr., in Sydow & Petrak, Ann. Mycol. 20: 206. 1922.

Parafabraea Chen Chen et al., Fungal Biol. 120: 1317. 2016.

Classification: *Leotiomyces*, *Leotiomycetidae*, *Helotiales*, *Dermateaceae*.

Type species: *Coleophoma crateriformis* (Durieu & Mont.) Höhn., basionym: *Ascospora crateriformis* Durieu & Mont. Holotype: FH 00304449, ex-type or reference living culture not available.

DNA barcode (genus): ITS.

DNA barcodes (species): *tef1* and *tub2*. Table 5. Fig. 17.

Mycelium immersed, septate, branched, hyaline to pale brown hyphae. *Ascomata* apothecial, short-stalked, pale to dark brown, sessile to sub-sessile, gregarious or confluent, semi-immersed, cluster on basal stroma. *Disc* pale brown, turbinate. Seta-like structures surrounding apothecia, pale brown, rigid, septate, straight or curved, cylindrical, slightly enlarged at truncate apex. *Stroma* sub-immersed, composed of irregular, pale to brown cells. *Hamathecium* composed of hyaline to pale brown, slender, cylindrical, septate, filamentous paraphyses. *Asci* hyaline to pale brown, clavate to cylindrical-clavate, inoperculate, short-pedicellate, apex rounded, base truncate, 8-spored. *Ascospores* hyaline, fusoid to ellipsoid, thin-walled, rounded ends, guttulate, aseptate, straight or slightly curved. *Conidiomata* pycnidial, black, immersed, globose or flattened at base, with single, non-papillate ostiole; *conidiomata wall* multi-layer, brown, comprised of *textura angularis*, with inner layer thin, pale brown and outer layer thick, brown to dark brown. *Paraphyses* hyaline, cylindrical to long clavate, septate at base, intermingled among conidiophores. *Conidiophores* smooth, thin-walled, septate, branched, hyaline at apex, pale brown at base, formed from inner pycnidial wall, confined to the base or in short

chains. *Conidiogenous cells* determinate, phialidic, integrated and subcylindrical, or discrete and ampulliform to lageniform, hyaline, determinate, smooth, with prominent periclinal thickening, and collarete minute. *Conidia* hyaline, straight, cylindrical, smooth, aseptate, guttulate, apex obtuse, acute at base.

Cultural characteristics: Colonies erumpent, flat, spreading with sparse aerial mycelium, feathery margin and fast growing on OA and PDA as compared to MEA. Colonies on OA, PDA and MEA are olivaceous grey, smoke grey with patches of honey and iron grey with patches of olivaceous grey respectively.

Optimal media and cultivation conditions: OA, PDA or MEA at 25 °C under continuous nuv-light to induce sporulation.

Distribution: Worldwide.

Hosts: Pathogens, saprophytes or endophytes on a variety of hosts such as *Amelanchier lamarkii* (Rosaceae), *Camellia japonica* (Theaceae), *Coptosperma littorale* (Rubiaceae), *Eucalyptus caliginosa*, *E. globulus*, *E. piperita*, *E. gummifera* (Myrtaceae), *Empetrum nigrum*, *Erica cinerea*, *Rhododendron* sp. (Ericaceae), *Helleborus* sp. (Ranunculaceae), *Hedera helix* (Araliaceae), *Hypericum* sp. (Hypericaceae), *Liriodendron tulipifera* (Magnoliaceae), *Protea caffra* (Proteaceae) and *Thuja plicata* (Cupressaceae).

Disease symptoms: Leaf spots or leaf blotch.

Notes: The genus *Coleophoma* typified by *Co. crateriformis* was established by von Höhnel (1907). This genus was previously listed as *incertae sedis* in *Pezizomycotina* in MycoBank and Index Fungorum, with confusing taxonomy. Crous & Groenewald (2016) confirmed it as a polyphyletic genus based on LSU/ITS sequence data and provided a backbone tree for *Coleophoma* employing ITS, *tef1* and *tub2* sequence data. Moreover, they established the sexual-asexual connection between *Coleophoma* and *Parafabraea*, thus reduced *Parafabraea* as synonymy under *Coleophoma*. Presently,

Table 5. DNA barcodes of accepted *Coleophoma* spp.

Species	Isolates ¹	GenBank accession numbers ²			References
		ITS	<i>tef1</i>	<i>tub2</i>	
<i>Coleophoma caliginosa</i>	CBS 124806 ^T	GU973505	—	—	Cheewangkoon et al. (2010)
<i>Co. camelliae</i>	CBS 101376 ^T	KU728481	KU728558	KU728597	Crous & Groenewald (2016)
<i>Co. coptospermatis</i>	CPC 19864 ^T	KU728483	KU728560	KU728599	Crous & Groenewald (2016)
<i>Co. cylindrospora</i>	CBS 449.70	KJ663834	KU728561	KU728600	Crous et al. (2014b), Crous & Groenewald (2016)
	CBS 505.71	KU728485	KU728563	KU728602	Crous & Groenewald (2016)
<i>Co. ericicola</i>	CBS 301.72 ^T	KU728488	KU728566	KU728605	Crous & Groenewald (2016)
<i>Co. eucalypticola</i>	CBS 124810 ^T	GQ303279	—	—	Cheewangkoon et al. (2009)
<i>Co. eucalyptorum</i>	CBS 131314 ^T	JQ044430	KU728567	KU728606	Crous et al. (2011b), Crous & Groenewald (2016)
<i>Co. paracylindrospora</i>	CBS 109074 ^T	KU728491	KU728570	KU728609	Crous & Groenewald (2016)
<i>Co. parafusiformis</i>	CBS 132692 ^T	KU728494	KU728573	KU728612	Crous & Groenewald (2016)
<i>Co. proteae</i>	CBS 132532 ^T	JX069866	KU728574	KU728613	Crous et al. (2012b), Crous & Groenewald (2016)
<i>Co. xanthosiae</i>	CBS 142070 ^T	KY173396	—	KY173598	Crous et al. (2016)

¹ CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CPC: Culture collection of Pedro Crous housed at CBS. ^T indicates ex-type strain.

² ITS: internal transcribed spacers and intervening 5.8S nrDNA; *tef1*: partial translation elongation factor 1- α gene; *tub2*: partial β -tubulin gene.

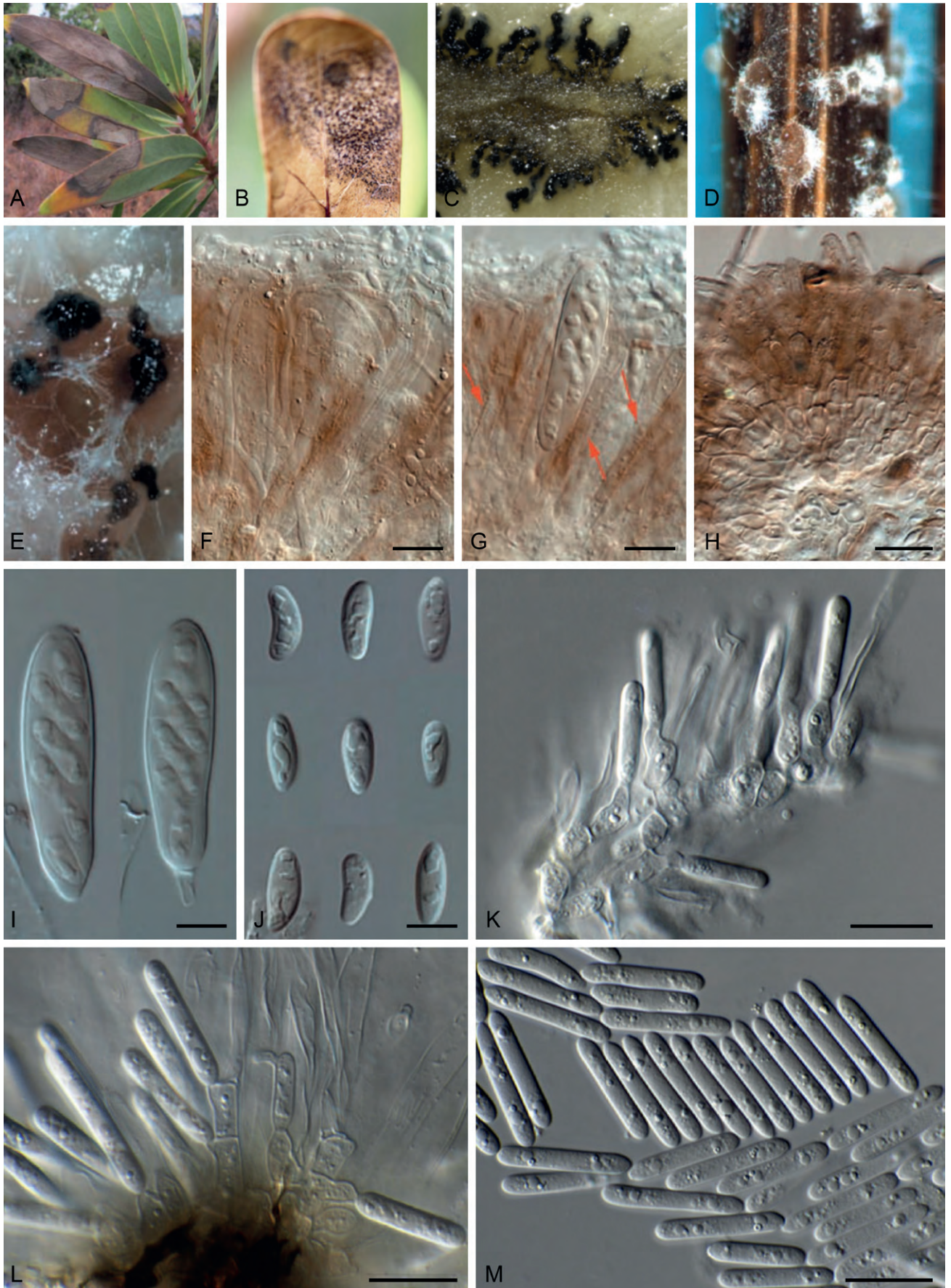


Fig. 16. *Coleophoma* spp. **A, B.** Disease symptoms. **A.** *Coleophoma proteae* (ex-type CBS 132532) on *Protea caffra*. **B.** *Coleophoma coptospermatis* (ex-type CPC 19864) on *Coptosperma littorale*. **C.** Sporulation on OA of *Coleophoma parafusiformis* (CBS 129169). **D, F–J.** Sexual morph (*Coleophoma eucalypticola* = *Neofabraea eucalypti*, ex-type CBS 124810). **D.** Ascomata on pine needle agar. **F.** Paraphyses. **G, H.** Paraphyses, asci and setae-like structures (arrows indicate setae-like structure). **I.** Asci. **J.** Ascospores. **E, K–M.** Asexual morph. **E.** Pycnidia of *Coleophoma eucalypticola* (ex-type CBS 124810) on OA. **K.** Conidiogenous cells and paraphyses of *Coleophoma eucalyptorum* (CPC 19865). **L.** Conidiogenous cells of *Coleophoma coptospermatis* (ex-type CPC 19864). **M.** Conidia of *Coleophoma paracylindrospora* (ex-type CBS 109074). Scale bars = 10 µm. Picture A taken from Crous *et al.* (2012b); B, C, K–M from Crous & Groenewald (2016); D–J from Cheewangkoon *et al.* (2009).

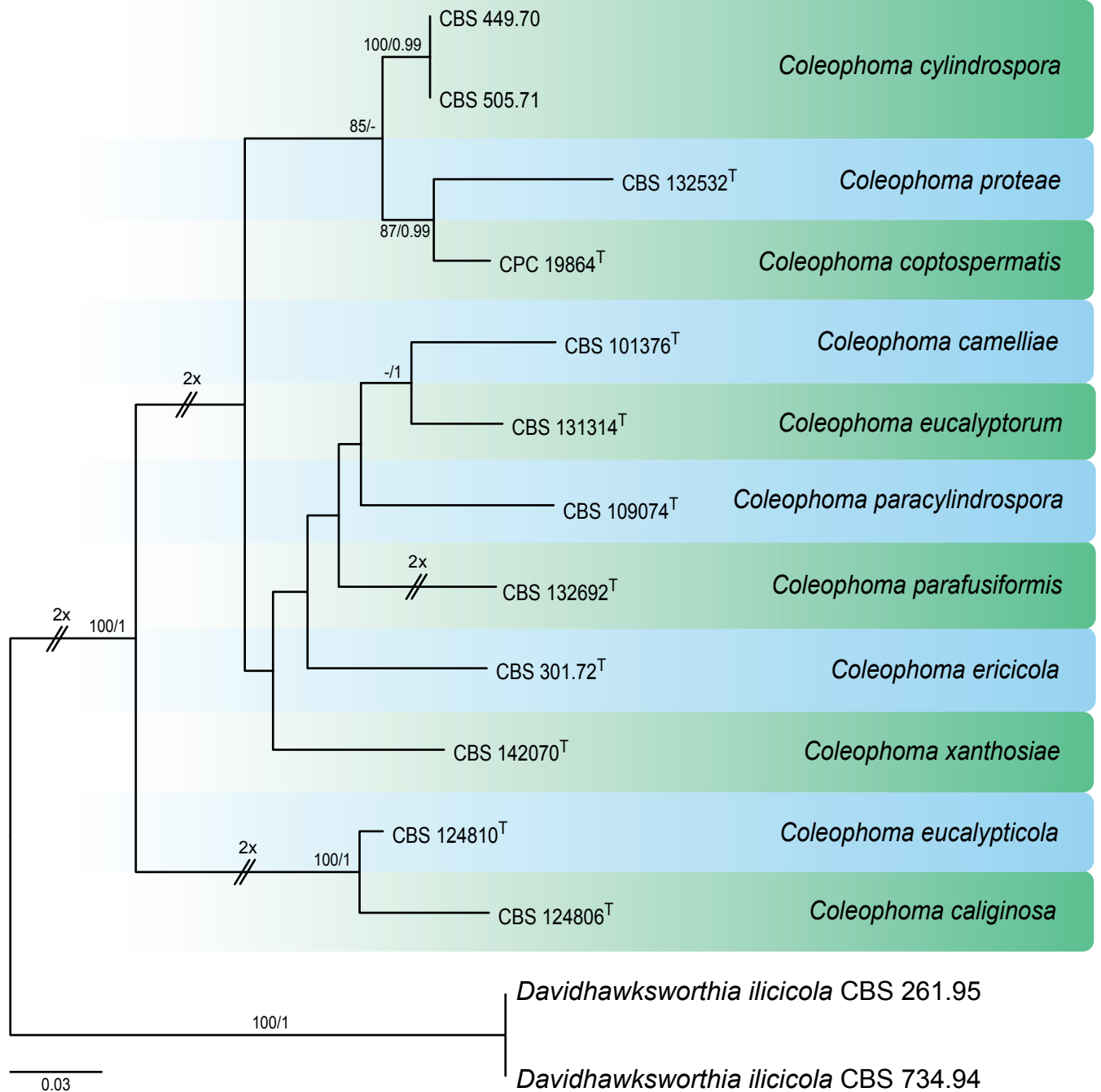


Fig. 17. RAxML phylogram constructed from ITS (528 bp), *tef1* (423 bp) and *tub2* (280 bp) sequences of all accepted species of *Coleophoma*. Maximum likelihood bootstrap support values (> 70 %) and Bayesian posterior probability scores (> 0.95) are indicated on the branches. The phylogenetic tree was rooted to *Davidhawksworthia ilicicola* CBS 261.95 and CBS 734.94. GenBank accession numbers are indicated in Table 5. ^T indicates ex-type strain. TreeBASE; S26189.

Coleophoma is placed in *Dermateaceae* (Johnston *et al.* 2019) but there is no available culture of its type species *Co. crateriformis*. Species of *Coleophoma* are characterised by pycnidial conidiomata, hyaline conidiophores intermingled with paraphyses and integrated phialidic conidiogenous cells with periclinal thickening and hyaline, smooth, straight cylindrical, guttulate conidia with obtuse ends (Sutton 1980, Crous & Groenewald 2016). This genus has been reported as saprobic or endophytic and plant pathogenic (Sutton 1980, Yuan 1996, Duan *et al.* 2007).

References: Sutton 1980, Yuan 1996, Duan *et al.* 2007 (pathogenicity); Cheewangkoon *et al.* 2009 (sexual/asexual connection); Cheewangkoon *et al.* 2009, Crous & Groenewald 2016 (morphology and phylogeny).

Genome sequenced strain: *Coleophoma eucalyptorum*. **Australia**, New South Wales, Blue Mountains, Kurrajong Heights, from leaves of *Eucalyptus piperita*, 16 Nov. 2010, B.A. Summerell, culture ex-type CBS 131314. This Whole Genome Shotgun project has been deposited at GenBank under the accession JALRME000000000 (BioProject: PRJNA827019, BioSample: SAMN27594413; present study).

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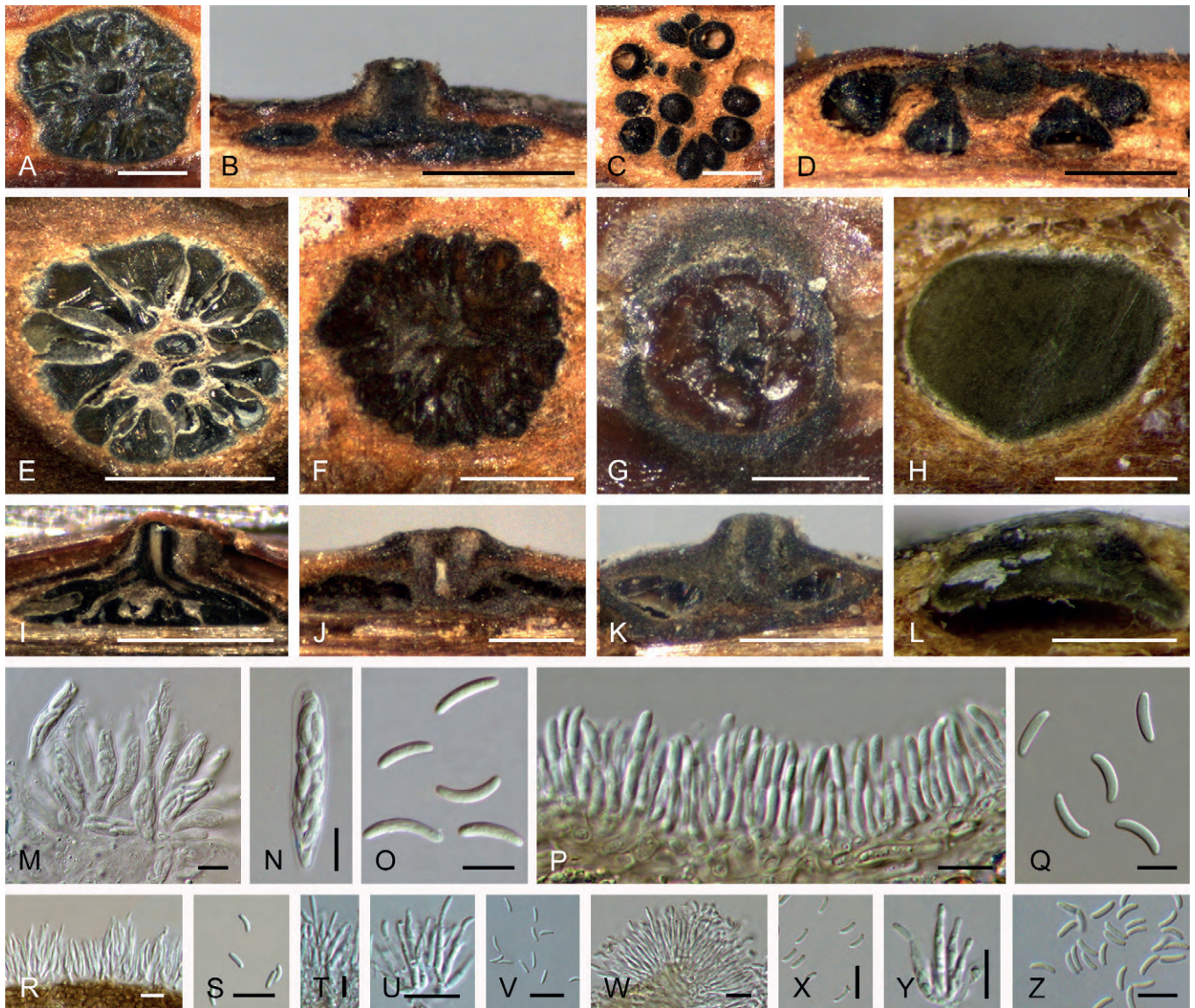


Fig. 18. *Cytospora* spp. **A, B.** Conidiomata of *Cytospora mali* (BJFC-S503) on *Malus pumila*. **C, D.** Ascomata of *Cytospora mali* (BJFC-S503) on *Malus pumila*. **E, I.** Lamyelloid conidioma of *Cytospora ceratosperma* (BJFC-S774) on *Juglans regia*. **F, J.** Cytosporoid conidioma of *Cytospora chrysosperma* (BJFC-S750) on *Populus alba* subsp. *pyramidalis*. **G, K.** Leucostosporoid conidioma of *Cytospora leucostoma* (BJFC-S918) on *Prunus persica*. **H, L.** Cytophomoid conidioma of *Cytospora pruinosa* (BJFC-S636) on *Syringa oblata*. **M–O.** Asci and ascospores of *Cytospora sibiraeae* (BJFC-S783) on *Sibiraea angustata*. **P–Z.** Conidiophores and conidia. **P, Q.** *Cytospora gigaspora* (BJFC-S975) on *Salix psammophila*. **R, S.** *Cytospora ceratosperma* (BJFC-S774) on *Juglans regia*. **T–V.** *Cytospora chrysosperma* (BJFC-S750) on *Populus alba* subsp. *pyramidalis*. **W, X.** *Cytospora leucostoma* (BJFC-S918) on *Prunus persica*. **Y, Z.** *Cytospora pruinosa* (BJFC-S636) on *Syringa oblata*. Scale bars: A–L = 500 µm; M–Z = 10 µm.

Cytospora Ehrenb., Sylvae Mycologicae Berolinenses: 28. 1818. Fig. 18.

Synonyms: *Valsa* Fr., Summa Veg. Scand., Sectio Post. (Stockholm): 410. 1849.

Valsella Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 203. 1870.

Leucocytospora (Pers.) Höhn., Ber. Deutch. Bot. Ges. 35: 352. 1917.

Leucostoma (Nitschke) Höhn., Ber. Deutch. Bot. Ges. 35: 637. 1917.

Valseutypella Höhn., Ann. Mycol. 16: 224. 1919.

Classification: Sordariomycetes, Diaporthales, Diaporthomycetidae, Cytosporaceae.

Type species: *Cytospora chrysosperma* (Pers.) Fr., basionym: *Sphaeria chrysosperma* Pers. (epitypification pending).

DNA barcodes (genus): ITS, LSU.

DNA barcodes (species): ITS, LSU, *act1*, *rpb2*, *tef1* and *tub2*. Table 6. Fig. 19.

Ascstromata solitary, immersed in vascular plant tissues, slightly to strongly erumpent through the bark surface. **Stromatic tissues** prosenchymatous or pseudoparenchymatous, sometimes delimited by a black marginal line (conceptacle). **Ascomata** perithecial inclined to upright, in valsoid or diatrypelloid configurations, immersed, usually embedded in ectostromatic disc, with beaks converging at surface. **Ostioles** numerous per disc, periphysate; walls of perithecia bilayered, narrow, outer layer of *textura epdermoidea* to *textura angularis*. **Paraphyses** may be lacking at maturity but usually present, often collapsed and broad. **Asci** free, narrow, ellipsoid to clavate, apical ring refractive. **Ascospores** hyaline, allantoid, aseptate, thin-walled, smooth, biserial, 4–8 or polysporous per ascus. **Conidiomata** pycnidial,

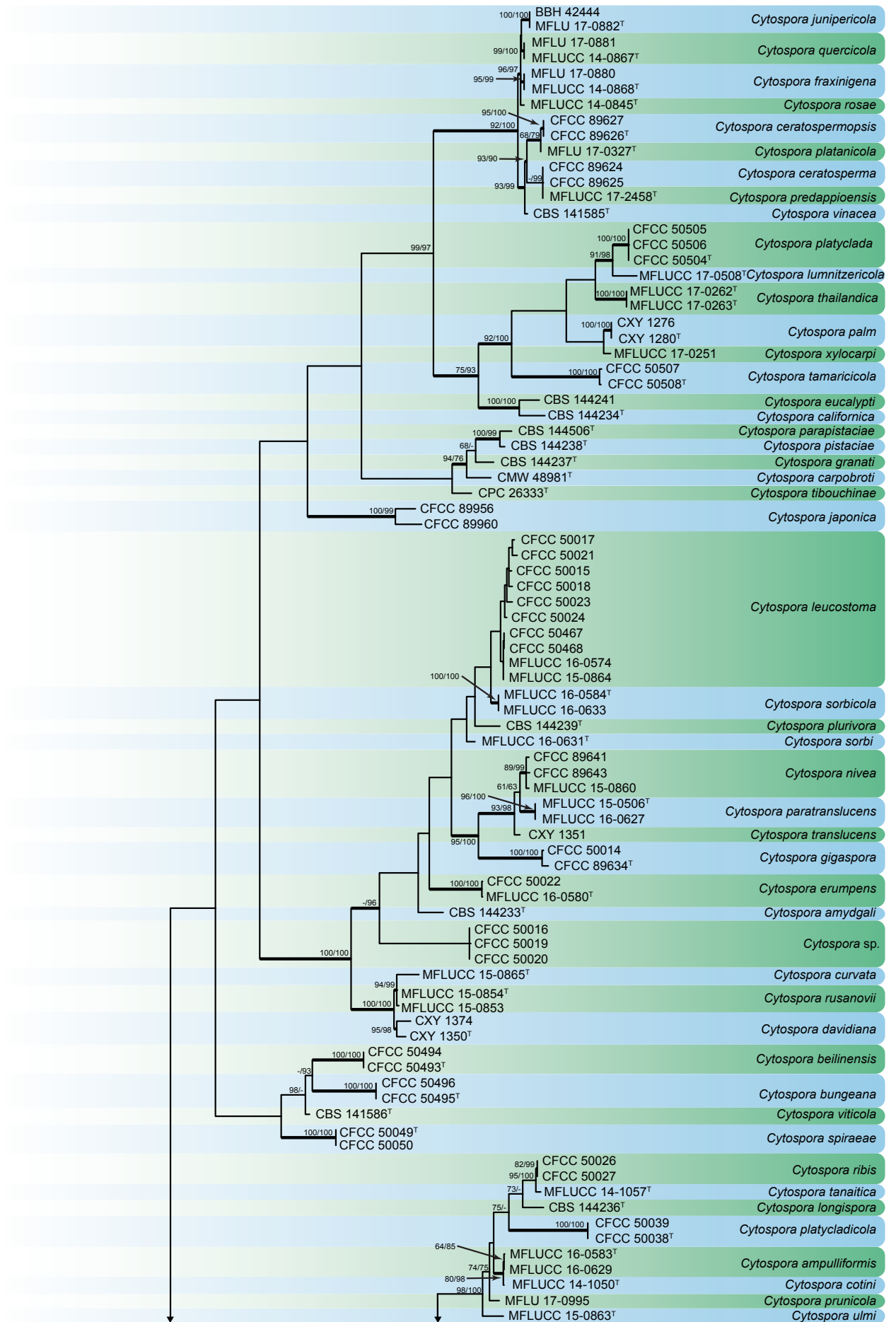


Fig. 19. Maximum parsimony phylogram constructed from ITS (662 bp), LSU (525 bp), *act1* (357 bp), *rpb2* (730 bp), *tef1-α* (796 bp) and *tub2* (635 bp) sequences of all accepted species of *Cytospora*. Maximum parsimony (MP) and Maximum likelihood (ML) bootstrap support values (> 50 %) are shown at the nodes (MP/ML). Thickened branches represent Bayesian posterior probability scores (> 0.95). The phylogenetic tree was rooted to *Diaporthe vaccinii* CBS 160.32. GenBank accession numbers are indicated in Table 6. † indicates ex-type strains. TreeBASE: S26220.

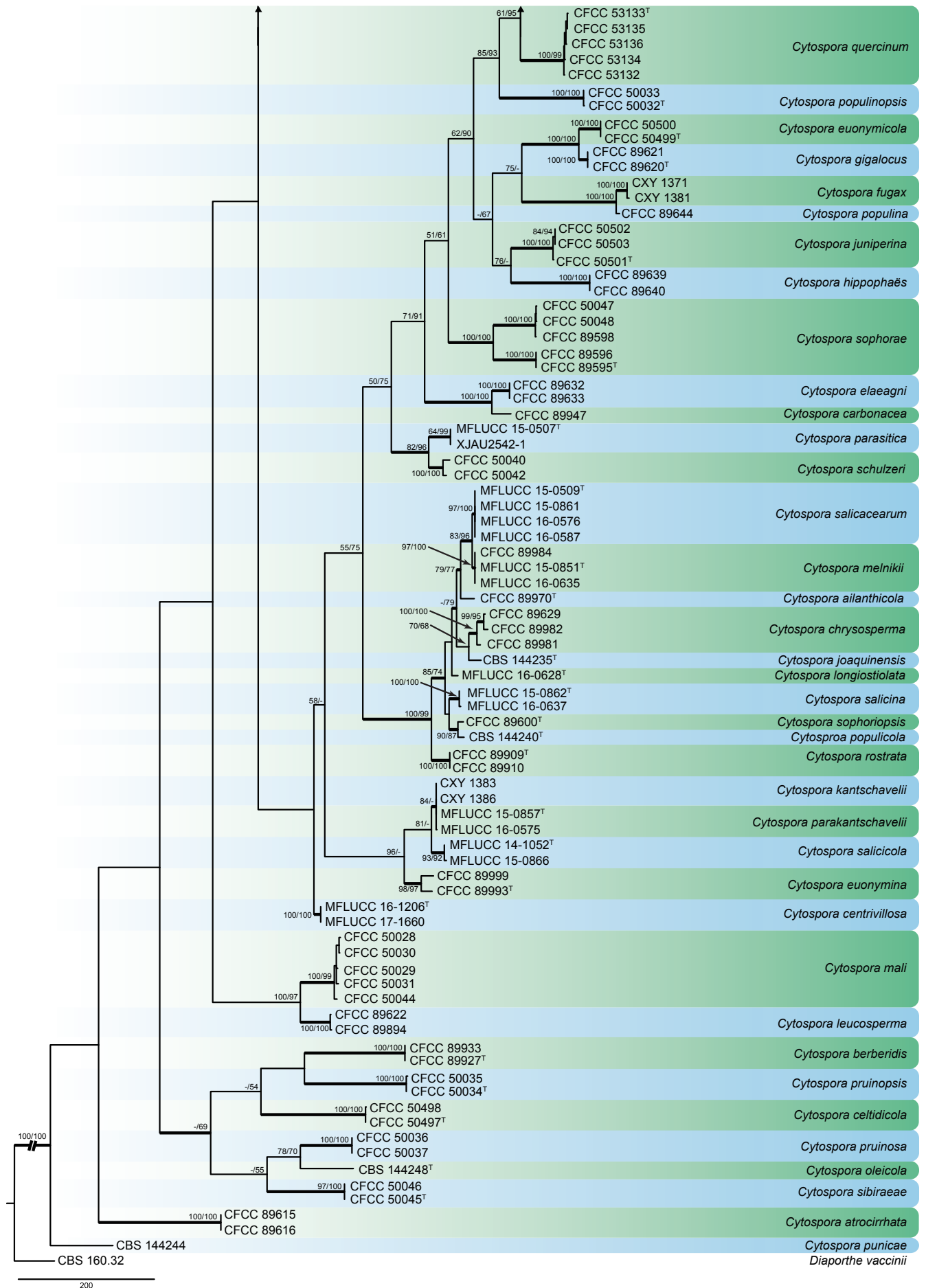


Fig. 19. (Continued).

Table 6. DNA barcodes of accepted *Cytospora* spp.

Species	Isolates ¹	GenBank accession numbers ²						References
		ITS	LSU	<i>act1</i>	<i>rpb2</i>	<i>tef1</i>	<i>tub2</i>	
<i>Cytospora ailanthicola</i>	CFCC 89970 ^T	MH933618	MH933653	MH933526	MH933592	MH933494	MH933565	Fan <i>et al.</i> (2020)
<i>Cy. ampulliformis</i>	MFLUCC 16-0583 ^T	KY417726	KY417760	KY417692	KY417794	—	—	Norphanphoun <i>et al.</i> (2017)
	MFLUCC 16-0629	KY417727	KY417761	KY417693	KY417795	—	—	Norphanphoun <i>et al.</i> (2017)
<i>Cy. amygdali</i>	CBS 144233 ^T	MG971853	—	MG972002	—	MG971659	MG971718	Lawrence <i>et al.</i> (2018)
<i>Cy. atrocirrhatta</i>	CFCC 89615	KR045618	KR045700	KF498673	KU710946	KP310858	KR045659	Fan <i>et al.</i> (2020)
	CFCC 89616	KR045619	KR045701	KF498674	KU710947	KP310859	KR045660	Fan <i>et al.</i> (2020)
<i>Cy. beilinensis</i>	CFCC 50493 ^T	MH933619	MH933654	MH933527	—	MH933495	MH933561	Fan <i>et al.</i> (2020)
	CFCC 50494	MH933620	MH933655	MH933528	—	MH933496	MH933562	Fan <i>et al.</i> (2020)
<i>Cy. berberidis</i>	CFCC 89927 ^T	KR045620	KR045702	KU710990	KU710948	KU710913	KR045661	Fan <i>et al.</i> (2020)
	CFCC 89933	KR045621	KR045703	KU710991	KU710949	KU710914	KR045662	Fan <i>et al.</i> (2020)
<i>Cy. bungeana</i>	CFCC 50495 ^T	MH933621	MH933656	MH933529	MH933593	MH933497	MH933563	Fan <i>et al.</i> (2020)
	CFCC 50496	MH933622	MH933657	MH933530	MH933594	MH933498	MH933564	Fan <i>et al.</i> (2020)
<i>Cy. californica</i>	CBS 144234 ^T	MG971935	—	MG972083	—	MG971645	—	Lawrence <i>et al.</i> (2018)
<i>Cy. carbonacea</i>	CFCC 89947	KR045622	KP310812	KP310842	KU710950	KP310855	KP310825	Fan <i>et al.</i> (2020)
<i>Cy. carpobroti</i>	CMW 48981 ^T	MH382812	MH411216	—	—	MH411212	MH411207	Jami <i>et al.</i> (2018)
<i>Cy. celtidicola</i>	CFCC 50497 ^T	MH933623	MH933658	MH933531	MH933595	MH933499	MH933566	Fan <i>et al.</i> (2020)
	CFCC 50498	MH933624	MH933659	MH933532	MH933596	MH933500	MH933567	Fan <i>et al.</i> (2020)
<i>Cy. centrivillosa</i>	MFLUCC 16-1206 ^T	MF190122	MF190068	—	MF377601	—	—	Senanayake <i>et al.</i> (2017)
	MFLUCC 17-1660	MF190124	MF190070	—	MF377600	—	—	Senanayake <i>et al.</i> (2017)
<i>Cy. ceratosperma</i>	CFCC 89624	KR045645	KR045724	—	KU710976	KP310860	KR045686	Fan <i>et al.</i> (2020)
	CFCC 89625	KR045646	KR045725	—	KU710977	KP31086	KR045687	Fan <i>et al.</i> (2020)
<i>Cy. ceratospermopsis</i>	CFCC 89626 ^T	KR045647	KR045726	KU711011	KU710978	KU710934	KR045688	Fan <i>et al.</i> (2020)
	CFCC 89627	KR045648	KR045727	KU711012	KU710979	KU710935	KR045689	Fan <i>et al.</i> (2020)
<i>Cy. chrysosperma</i>	CFCC 89629	KF765673	KF765689	—	KF765705	—	—	Fan <i>et al.</i> (2020)
	CFCC 89981	MH933625	MH933660	MH933533	MH933597	MH933501	MH933568	Fan <i>et al.</i> (2020)
	CFCC 89982	KP281261	KP310805	KP310835	—	KP310848	KP310818	Fan <i>et al.</i> (2020)
<i>Cy. cotini</i>	MFLUCC 14-1050 ^T	KX430142	KX430143	—	KX430144	—	—	Norphanphoun <i>et al.</i> (2017)
<i>Cy. curvata</i>	MFLUCC 15-0865 ^T	KY417728	KY417762	KY417694	KY417796	—	—	Norphanphoun <i>et al.</i> (2017)
<i>Cy. davidiana</i>	CXY 1350 ^T	KM034870	—	—	—	—	—	Wang <i>et al.</i> (2015)
	CXY 1374	KM034869	—	—	—	—	—	Wang <i>et al.</i> (2015)
<i>Cy. elaeagni</i>	CFCC 89632	KR045626	KR045706	KU710995	KU710955	KU710918	KR045667	Fan <i>et al.</i> (2020)
	CFCC 89633	KF765677	KF765693	KU710996	KU710956	KU710919	KR045668	Fan <i>et al.</i> (2020)
<i>Cy. erumpens</i>	CFCC 50022	MH933627	MH933661	MH933534	—	MH933502	MH933569	Fan <i>et al.</i> (2020)
	MFLUCC 16-0580 ^T	KY417733	KY417767	KY417699	KY417801	—	—	Norphanphoun <i>et al.</i> (2017)
<i>Cy. eucalypti</i>	CBS 144241	MG971907	—	MG972056	—	MG971617	MG971772	Lawrence <i>et al.</i> (2018)
<i>Cy. euonymicola</i>	CFCC 50499 ^T	MH933628	MH933662	MH933535	MH933598	MH933503	MH933570	Fan <i>et al.</i> (2020)
	CFCC 50500	MH933629	MH933663	MH933536	MH933599	MH933504	MH933571	Fan <i>et al.</i> (2020)
<i>Cy. euonymina</i>	CFCC 89993 ^T	MH933630	MH933664	MH933537	MH933600	MH933505	MH933590	Fan <i>et al.</i> (2020)
	CFCC 89999	MH933631	MH933665	MH933538	MH933601	MH933506	MH933591	Fan <i>et al.</i> (2020)
<i>Cy. fraxinigena</i>	MFLUCC 14-0868 ^T	MF190133	MF190078	—	—	—	—	Senanayake <i>et al.</i> (2017)
	MFLU 17-0880	MF190134	MF190079	—	—	—	—	Senanayake <i>et al.</i> (2017)

Table 6. (Continued).

Species	Isolates ¹	GenBank accession numbers ²						References
		ITS	LSU	<i>act1</i>	<i>rpb2</i>	<i>tef1</i>	<i>tub2</i>	
<i>Cy. fugax</i>	CXY 1371	KM034852	—	—	—	—	KM034891	Wang <i>et al.</i> (2015)
	CXY 1381	KM034853	—	—	—	—	KM034890	Wang <i>et al.</i> (2015)
<i>Cy. gigalocus</i>	CFCC 89620 ^T	KR045628	KR045708	KU710997	KU710957	KU710920	KR045669	Fan <i>et al.</i> (2020)
	CFCC 89621	KR045629	KR045709	KU710998	KU710958	KU710921	KR045670	Fan <i>et al.</i> (2020)
<i>Cy. gigaspora</i>	CFCC 50014	KR045630	KR045710	KU710999	KU710959	KU710922	KR045671	Fan <i>et al.</i> (2020)
	CFCC 89634 ^T	KF765671	KF765687	KU711000	KU710960	KU710923	KR045672	Fan <i>et al.</i> (2020)
<i>Cy. granati</i>	CBS 144237 ^T	MG971799	—	MG971949	—	MG971514	MG971664	Lawrence <i>et al.</i> (2018)
<i>Cy. hippophaëns</i>	CFCC 89639	KR045632	KR045712	KU711001	KU710961	KU710924	KR045673	Fan <i>et al.</i> (2020)
	CFCC 89640	KF765682	KF765698	KF765730	KU710962	KP310865	KR045674	Fan <i>et al.</i> (2020)
<i>Cy. japonica</i>	CFCC 89956	KR045624	KR045704	KU710993	KU710953	KU710916	KR045665	Fan <i>et al.</i> (2020)
	CFCC 89960	KR045625	KR045705	KU710994	KU710954	KU710917	KR045666	Fan <i>et al.</i> (2020)
<i>Cy. joaquinensis</i>	CBS 144235 ^T	MG971895	—	MG972044	—	MG971605	MG971761	Lawrence <i>et al.</i> (2018)
<i>Cy. junipericola</i>	BBH 42444	—	—	—	—	MF377579	—	Senanayake <i>et al.</i> (2017)
	MFLU 17-0882 ^T	MF190125	MF190072	—	—	MF377580	—	Senanayake <i>et al.</i> (2017)
<i>Cy. juniperina</i>	CFCC 50501 ^T	MH933632	MH933666	MH933539	MH933602	MH933507	—	Fan <i>et al.</i> (2020)
	CFCC 50502	MH933633	MH933667	MH933540	MH933603	MH933508	MH933572	Fan <i>et al.</i> (2020)
	CFCC 50503	MH933634	MH933668	MH933541	MH933604	MH933509	—	Fan <i>et al.</i> (2020)
<i>Cy. kantschavelii</i>	CXY 1383	KM034867	—	—	—	—	—	Wang <i>et al.</i> (2015)
	CXY 1386	KM034866	—	—	—	—	—	Wang <i>et al.</i> (2015)
<i>Cy. leucosperma</i>	CFCC 89622	KR045616	KR045698	KU710988	KU710944	KU710911	KR045657	Fan <i>et al.</i> (2020)
	CFCC 89894	KR045617	KR045699	KU710989	KU710945	KU710912	KR045658	Fan <i>et al.</i> (2020)
<i>Cy. leucostoma</i>	MFLUCC 15-0864	KY417729	KY417763	KY417695	KY417797	—	—	Norphanphoun <i>et al.</i> (2017)
	MFLUCC 16-0574	KY417731	KY417764	KY417696	KY417798	—	—	Norphanphoun <i>et al.</i> (2017)
	CFCC 50015	KR045634	KR045714	KU711002	KU710963	KU710925	KR045675	Fan <i>et al.</i> (2020)
	CFCC 50017	MH933635	MH933669	MH933542	—	MH933510	MH933573	Fan <i>et al.</i> (2020)
	CFCC 50018	MH933636	MH933670	MH933543	—	MH933511	MH933574	Fan <i>et al.</i> (2020)
	CFCC 50021	MH933639	MH933673	MH933546	—	MH933512	MH933575	Fan <i>et al.</i> (2020)
	CFCC 50023	KR045635	KR045715	KU711003	KU710964	KU710926	KR045676	Fan <i>et al.</i> (2020)
	CFCC 50024	MH933640	MH933674	MH933547	MH933605	—	MH933576	Fan <i>et al.</i> (2020)
	CFCC 50467	KT732948	KT732967	—	—	—	—	Fan <i>et al.</i> (2020)
	CFCC 50468	KT732949	KT732968	—	—	—	—	Fan <i>et al.</i> (2020)
<i>Cy. longiostiolata</i>	MFLUCC 16-0628 ^T	KY417734	KY417768	KY417700	KY417802	—	—	Norphanphoun <i>et al.</i> (2017)
<i>Cy. longispora</i>	CBS 144236 ^T	MG971905	—	MG972054	—	MG971615	MG971764	Lawrence <i>et al.</i> (2018)
<i>Cy. lumnitzericola</i>	MFLUCC 17-0508 ^T	MG975778	MH253461	MH253457	MH253453	—	—	Norphanphoun <i>et al.</i> (2018)
<i>Cy. mali</i>	CFCC 50028	MH933641	MH933675	MH933548	MH933606	MH933513	MH933577	Fan <i>et al.</i> (2020)
	CFCC 50029	MH933642	MH933676	MH933549	MH933607	MH933514	MH933578	Fan <i>et al.</i> (2020)
	CFCC 50030	MH933643	MH933677	MH933550	MH933608	MH933524	MH933579	Fan <i>et al.</i> (2020)
	CFCC 50031	KR045636	KR045716	KU711004	KU710965	KU710927	KR045677	Fan <i>et al.</i> (2020)
	CFCC 50044	KR045637	KR045717	KU711005	KU710966	KU710928	KR045678	Fan <i>et al.</i> (2020)
<i>Cy. melnikii</i>	CFCC 89984	MH933644	MH933678	MH933551	MH933609	MH933515	MH933580	Fan <i>et al.</i> (2020)
	MFLUCC 15-0851 ^T	KY417735	KY417769	KY417701	KY417803	—	—	Norphanphoun <i>et al.</i> (2017)
	MFLUCC 16-0635	KY417736	KY417770	KY417702	KY417804	—	—	Norphanphoun <i>et al.</i> (2017)

Table 6. (Continued).

Species	Isolates ¹	GenBank accession numbers ²						References
		ITS	LSU	<i>act1</i>	<i>rpb2</i>	<i>tef1</i>	<i>tub2</i>	
<i>Cy. nivea</i>	CFCC 89641	KF765683	KF765699	KU711006	KU710967	KU710929	KR045679	Fan <i>et al.</i> (2020)
	CFCC 89643	KF765685	KF765701	—	KU710968	KP310863	KP310829	Fan <i>et al.</i> (2020)
	MFLUCC 15-0860	KY417737	KY417771	KY417703	KY417805	—	—	Norphanphoun <i>et al.</i> (2017)
<i>Cy. oleicola</i>	CBS 144248 ^T	MG971944	—	MG972098	—	MG971660	MG971752	Lawrence <i>et al.</i> (2018)
<i>Cy. palm</i>	CXY 1276	JN402990	—	—	—	KJ781296	—	Zhang <i>et al.</i> (2014)
	CXY 1280 ^T	JN411939	—	—	—	KJ781297	—	Zhang <i>et al.</i> (2014)
<i>Cy. parakantschavelii</i>	MFLUCC 15-0857 ^T	KY417738	KY417772	KY417704	KY417806	—	—	Norphanphoun <i>et al.</i> (2017)
	MFLUCC 16-0575	KY417739	KY417773	KY417705	KY417807	—	—	Norphanphoun <i>et al.</i> (2017)
<i>Cy. parapistaciae</i>	CBS 144506 ^T	MG971804	—	MG971954	—	MG971519	MG971669	Lawrence <i>et al.</i> (2018)
<i>Cy. parasitica</i>	MFLUCC 15-0507 ^T	KY417740	KY417774	KY417706	KY417808	—	—	Norphanphoun <i>et al.</i> (2017)
	XJAU 2542-1	MH798884	MH798897	—	—	MH813452	—	Ma <i>et al.</i> (2018)
<i>Cy. paratranslucens</i>	MFLUCC 15-0506 ^T	KY417741	KY417775	KY417707	KY417809	—	—	Norphanphoun <i>et al.</i> (2017)
	MFLUCC 16-0627	KY417742	KY417776	KY417708	KY417810	—	—	Norphanphoun <i>et al.</i> (2017)
<i>Cy. pistaciae</i>	CBS 144238 ^T	MG971802	—	MG971952	—	MG971517	MG971667	Lawrence <i>et al.</i> (2018)
<i>Cy. platanicola</i>	MFLU 17-0327 ^T	MH253451	MH253452	MH253449	MH253450	—	—	Hyde <i>et al.</i> (2018)
<i>Cy. platycladi</i>	CFCC 50504 ^T	MH933645	MH933679	MH933552	MH933610	MH933516	MH933581	Fan <i>et al.</i> (2020)
	CFCC 50505	MH933646	MH933680	MH933553	MH933611	MH933517	MH933582	Fan <i>et al.</i> (2020)
	CFCC 50506	MH933647	MH933681	MH933554	MH933612	MH933518	MH933583	Fan <i>et al.</i> (2020)
<i>Cy. platycladicola</i>	CFCC 50038 ^T	KT222840	MH933682	MH933555	MH933613	MH933519	MH933584	Fan <i>et al.</i> (2020)
	CFCC 50039	KR045642	KR045721	KU711008	KU710973	KU710931	KR045683	Fan <i>et al.</i> (2020)
<i>Cy. plurivora</i>	CBS 144239 ^T	MG971861	—	MG972010	—	MG971572	MG971726	Lawrence <i>et al.</i> (2018)
<i>Cy. populicola</i>	CBS 144240 ^T	MG971891	—	MG972040	—	MG971601	MG971757	Lawrence <i>et al.</i> (2018)
<i>Cy. populina</i>	CFCC 89644	KF765686	KF765702	KU711007	KU710969	KU710930	KR045681	Fan <i>et al.</i> (2020)
<i>Cy. populinopsis</i>	CFCC 50032 ^T	MH933648	MH933683	MH933556	MH933614	MH933520	MH933585	Fan <i>et al.</i> (2020)
	CFCC 50033	MH933649	MH933684	MH933557	MH933615	MH933521	MH933586	Fan <i>et al.</i> (2020)
<i>Cy. predappioensis</i>	MFLUCC 17-2458 ^T	MG873484	MG873480	—	—	—	—	Jayawardena <i>et al.</i> (2019)
<i>Cy. pruinopsis</i>	CFCC 50034 ^T	KP281259	KP310806	KP310836	KU710970	KP310849	KP310819	Fan <i>et al.</i> (2020)
	CFCC 50035	KP281260	KP310807	KP310837	KU710971	KP310850	KP310820	Fan <i>et al.</i> (2020)
<i>Cy. pruinosa</i>	CFCC 50036	KP310800	KP310802	KP310832	—	KP310845	KP310815	Fan <i>et al.</i> (2020)
	CFCC 50037	MH933650	MH933685	MH933558	—	MH933522	MH933589	Fan <i>et al.</i> (2020)
<i>Cy. prunicola</i>	MFLU 17-0995	MG742350	MG742351	MG742353	MG742352	—	—	Hyde <i>et al.</i> (2018)
<i>Cy. punicae</i>	CBS 144244	MG971943	—	MG972091	—	MG971654	MG971798	Lawrence <i>et al.</i> (2018)
<i>Cy. quercicola</i>	MFLU 17-0881	MF190129	MF190074	—	—	—	—	Senanayake <i>et al.</i> (2017)
	MFLUCC 14-0867 ^T	MF190128	MF190073	—	—	—	—	Senanayake <i>et al.</i> (2017)
<i>Cy. quercinum</i>	CFCC 53132	MT360044	MT360032	MT363981	MT363990	MT364000	MT364010	Pan <i>et al.</i> (2021)
	CFCC 53133 ^T	MT360045	MT360033	MT363982	MT363991	MT364001	MT364011	Pan <i>et al.</i> (2021)
	CFCC 53134	MT360046	MT360034	MT363983	MT363992	MT364002	MT364012	Pan <i>et al.</i> (2021)
	CFCC 53135	MT360047	MT360035	MT363984	MT363993	MT364003	MT364013	Pan <i>et al.</i> (2021)
	CFCC 53136	MT360048	MT360036	MT363985	MT363994	MT364004	MT364014	Pan <i>et al.</i> (2021)

Table 6. (Continued).

Species	Isolates ¹	GenBank accession numbers ²						References
		ITS	LSU	<i>act1</i>	<i>rpb2</i>	<i>tef1</i>	<i>tub2</i>	
<i>Cy. ribis</i>	CFCC 50026	KP281267	KP310813	KP310843	KU710972	KP310856	KP310826	Fan <i>et al.</i> (2020)
	CFCC 50027	KP281268	KP310814	KP310844	—	KP310857	KP310827	Fan <i>et al.</i> (2020)
<i>Cy. rosae</i>	MFLUCC 14-0845 ^T	MF190131	MF190076	—	—	—	—	Senanayake <i>et al.</i> (2017)
<i>Cy. rostrata</i>	CFCC 89909 ^T	KR045643	KR045722	KU711009	KU710974	KU710932	KR045684	Fan <i>et al.</i> (2020)
	CFCC 89910	KR045644	KR045723	KU711010	KU710975	KU710933	—	Fan <i>et al.</i> (2020)
<i>Cy. rusanovii</i>	MFLUCC 15-0853	KY417743	KY417777	KY417709	KY417811	—	—	Norphanphoun <i>et al.</i> (2017)
	MFLUCC 15-0854 ^T	KY417744	KY417778	KY417710	KY417812	—	—	Norphanphoun <i>et al.</i> (2017)
<i>Cy. salicacearum</i>	MFLUCC 16-0576	KY417747	KY417781	KY417713	KY417815	—	—	Norphanphoun <i>et al.</i> (2017)
	MFLUCC 15-0509 ^T	KY417746	KY417780	KY417712	KY417814	—	—	Norphanphoun <i>et al.</i> (2017)
	MFLUCC 15-0861	KY417745	KY417779	KY417711	KY417813	—	—	Norphanphoun <i>et al.</i> (2017)
	MFLUCC 16-0587	KY417748	KY417782	KY417714	KY417816	—	—	Norphanphoun <i>et al.</i> (2017)
<i>Cy. salicicola</i>	MFLUCC 14-1052 ^T	KU982636	KU982635	KU982637	—	—	—	Li <i>et al.</i> (2018)
	MFLUCC 15-0866	KY417749	KY417783	KY417715	KY417817	—	—	Norphanphoun <i>et al.</i> (2017)
<i>Cy. salicina</i>	MFLUCC 15-0862 ^T	KY417750	KY417784	KY417716	KY417818	—	—	Norphanphoun <i>et al.</i> (2017)
	MFLUCC 16-0637	KY417751	KY417785	KY417717	KY417819	—	—	Norphanphoun <i>et al.</i> (2017)
<i>Cy. schulzeri</i>	CFCC 50040	KR045649	KR045728	KU711013	KU710980	KU710936	KR045690	Fan <i>et al.</i> (2020)
	CFCC 50042	KR045650	KR045729	KU711014	KU710981	KU710937	KR045691	Fan <i>et al.</i> (2020)
<i>Cy. sibiraeae</i>	CFCC 50045 ^T	KR045651	KR045730	KU711015	KU710982	KU710938	KR045692	Fan <i>et al.</i> (2020)
	CFCC 50046	KR045652	KR045731	KU711015	KU710983	KU710939	KR045693	Fan <i>et al.</i> (2020)
<i>Cy. sophorae</i>	CFCC 50047	KR045653	KR045732	KU711017	KU710984	KU710940	KR045694	Fan <i>et al.</i> (2020)
	CFCC 50048	MH820401	MH820394	MH820409	MH820397	MH820405	MH820390	Fan <i>et al.</i> (2020)
	CFCC 89598	KR045654	KR045733	KU711018	KU710985	KU710941	KR045695	Fan <i>et al.</i> (2020)
<i>Cy. sophoricola</i>	CFCC 89595 ^T	KR045655	KR045734	KU711019	KU710986	KU710942	KR045696	Fan <i>et al.</i> (2020)
	CFCC 89596	KR045656	KR045735	KU711020	KU710987	KU710943	KR045697	Fan <i>et al.</i> (2020)
<i>Cy. sophoriopsis</i>	CFCC 89600 ^T	KR045623	KP310804	KU710992	KU710951	KU710915	KP310817	Fan <i>et al.</i> (2020)
<i>Cy. sorbi</i>	MFLUCC 16-0631 ^T	KY417752	KY417786	KY417718	KY417820	—	—	Norphanphoun <i>et al.</i> (2017)
<i>Cy. sorbicola</i>	MFLUCC 16-0584 ^T	KY417755	KY417789	KY417721	KY417823	—	—	Norphanphoun <i>et al.</i> (2017)
	MFLUCC 16-0633	KY417758	KY417792	KY417724	KY417826	—	—	Norphanphoun <i>et al.</i> (2017)
<i>Cytospora</i> sp.	CFCC 50016	MH820400	MH820393	MH820408	—	MH820404	MH820389	Fan <i>et al.</i> (2020)
	CFCC 50019	MH933637	MH933671	MH933544	—	—	—	Fan <i>et al.</i> (2020)
	CFCC 50020	MH933638	MH933672	MH933545	—	—	—	Fan <i>et al.</i> (2020)
<i>Cy. spiraeae</i>	CFCC 50049 ^T	MG707859	MG707643	MG708196	MG708199	—	—	Fan <i>et al.</i> (2020)
	CFCC 50050	MG707860	MG707644	MG708197	MG708200	—	—	Fan <i>et al.</i> (2020)
<i>Cy. tamaricicola</i>	CFCC 50507	MH933651	MH933686	MH933559	MH933616	MH933525	MH933587	Fan <i>et al.</i> (2020)
	CFCC 50508 ^T	MH933652	MH933687	MH933560	MH933617	MH933523	MH933588	Fan <i>et al.</i> (2020)

Table 6. (Continued).

Species	Isolates ¹	GenBank accession numbers ²						References
		ITS	LSU	<i>act1</i>	<i>rpb2</i>	<i>tef1</i>	<i>tub2</i>	
<i>Cy. tanaitica</i>	MFLUCC 14-1057 ^T	KT459411	KT459412	KT459413	—	—	—	Ariyawansa <i>et al.</i> (2015)
<i>Cy. thailandica</i>	MFLUCC 17-0262 ^T	MG975776	MH253463	MH253459	MH253455	—	—	Norphanphoun <i>et al.</i> (2018)
	MFLUCC 17-0263 ^T	MG975777	MH253464	MH253460	MH253456	—	—	Norphanphoun <i>et al.</i> (2018)
<i>Cy. tibouchinae</i>	CPC 26333 ^T	KX228284	KX228335	—	—	—	—	Norphanphoun <i>et al.</i> (2018)
<i>Cy. translucens</i>	CXY 1351	KM034874	—	—	—	—	KM034895	Wang <i>et al.</i> (2015)
<i>Cy. ulmi</i>	MFLUCC 15-0863 ^T	KY417759	—	—	—	—	—	Norphanphoun <i>et al.</i> (2017)
<i>Cy. vinacea</i>	CBS 141585 ^T	KX256256	—	—	—	KX256277	KX256235	Lawrence <i>et al.</i> (2018)
<i>Cy. viticola</i>	CBS 141586 ^T	KX256239	—	—	—	KX256260	KX256218	Lawrence <i>et al.</i> (2018)
<i>Cy. xylocarpi</i>	MFLUCC 17-0251	MG975775	MH253462	MH253458	MH253454	—	—	Norphanphoun <i>et al.</i> (2018)

¹ BBH: BIOTEC Bangkok Herbarium, National Science and Technology Development Agency, Thailand; CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CFCC: China Forestry Culture Collection Centre, Beijing, China; CMW: Tree Protection Co-operative Program, Forestry and Agricultural Biotechnology Institute, University of Pretoria, South Africa; CPC: Culture collection of Pedro Crous, housed at CBS; MFLU: Mae Fah Luang University herbarium, Thailand; MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; XJAU: Xinjiang Agricultural University, Xinjiang, China. ^T indicates ex-type strain.

² ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial 28S large subunit nrRNA gene; *act1*: partial actin gene; *rpb2*: partial RNA polymerase II second largest subunit gene; *tef1*: partial translation elongation factor1- α gene; *tub2*: partial β -tubulin gene.

ostiolate, immersed in vascular plant tissues, slightly to strongly erumpent through the bark surface, sometimes delimited by a black marginal line (conceptacle). *Ectostromatic disc* prominent or lacking, one to few ostioles per disc. *Locules* single, undivided to multiple chambered with invaginations, globoid to flattened toroid, in ectostroma or embedded in entostroma, sometimes with a column; wall bilayered, outer layer prosenchymatous, ultimately sclerenchymatous. *Conidiophores* borne along the locules, hyaline, branched or not, thin-walled, normally embedded in a gelatinous layer. *Conidiogenous cells* enteroblastic, phialidic, sub-cylindrical to cylindrical, tapering towards apices. *Conidia* hyaline, allantoid, eguttulate, smooth, aseptate, thin-walled, relatively small and narrow (adapted from Adams *et al.* 2005, Fan *et al.* 2020).

Culture characteristics: Colonies growing fast on MEA and PDA, covering the medium within 5 d at 25 °C, with surface mycelium flattened, dense and felty. Colonies initially white, becoming cream to yellowish, producing brownish dots with age, with visible solitary conidiomata at maturity on all media.

Optimal media and cultivation conditions: On MEA and PDA under nuv-light (12 h light, 12 h dark) at 25 °C for 3 wk; drought stress and scratches on media induce sporulation of the asexual morph.

Distribution: Worldwide.

Hosts: Pathogens on a wide range of woody plants.

Disease symptoms: Canker and dieback.

Notes: *Cytospora* was established by Ehrenberg (1818) and subsequently resulted in a confusing taxonomy due to

identifications that were largely based on host affiliation and similar morphological characters. More than 660 species epithets named *Cytospora* have been recorded in Index Fungorum (<http://www.indexfungorum.org/>; 2020) but most of them have no available materials with DNA sequences. Adams *et al.* (2005) described 28 species of *Cytospora* from *Eucalyptus* based on combined morphology and ITS sequence data, of which 11 species were new to science. Adams *et al.* (2006) described 14 additional species from South Africa using the same methodology. Recent studies have subsequently focussed on *Cytospora* species from specific hosts using a polyphasic approach (Fan *et al.* 2014a, b, 2015a, b, Yang *et al.* 2015, Lawrence *et al.* 2017, Norphanphoun *et al.* 2017, 2018, Zhu *et al.* 2018, 2020, Pan *et al.* 2019, 2020). Fan *et al.* (2020) summarised 52 species of *Cytospora* associated with canker and dieback disease in China using a six-gene matrix (ITS, LSU, *act1*, *rpb2*, *tef1* and *tub2*), of which 13 species were new to science. Morphologically, six locule types were widely accepted (Spielman 1983, 1985). Lamyelloid refers to multiple independent locules with multiple ostioles, e.g. *Cy. ceratosperma* (Fig. 18E, I). Cytosporoid refers to a divided locule and shared walls, including most species of *Cytospora*, e.g. *Cy. chrysosperma* (Fig. 18F, J). Torselloid refers to multiple independent locules with one ostiole. Cyclocytosporoid refers to a toruloid locule with a central column. Leucostosporoid refers to divided locule and shared walls surrounded by a black circle (conceptacle), e.g. *Cy. leucostoma* (Fig. 18G, K). Cytophomoid refers to an undivided locule and wing-like ectostroma around the ostiole (sometimes it is inconspicuous), e.g. *Cy. pruinosa* (Fig. 18H, L).

References: Adams *et al.* 2005, Fan *et al.* 2020 (morphology and phylogeny).

Genome sequenced strain: Cytospora chrysosperma. China, Shaanxi Province, poplar tree in temperate region, collection date and collector unknown, strain YSFL. This Whole Genome Shotgun project has been deposited at GenBank under the accession LJZO00000000 (BioProject: PRJNA296468, BioSample: SAMN04099705); CFL2056 v1.0 in MycoCosm (Yin & Huang, unpublished).

Authors: M. Pan & X.L. Fan

Dendrostoma X.L. Fan & C.M. Tian, *Persoonia* 40: 126. 2018. Fig. 20.

Classification: Sordariomycetes, Diaporthomycetidae, Diaporthales, Erythrogloeaceae.

Type species: Dendrostoma mali X.L. Fan & C.M. Tian. Holotype and ex-type strain: CF 2017445, CFCC 52102.

DNA barcode (genus): LSU.

DNA barcodes (species): ITS, *rpb2*, *tef1*. Table 7. Fig. 21.

Pseudostromata small to large, distinct, circular, erumpent, consisting of an inconspicuous ectostromatic disc, semi-immersed to superficial, causing a pustulate bark surface. *Ectostromatic disc* flat or concave, orange, surrounded by bark flaps. *Central column* beneath the disc more or less conical. *Stromatic zones* lacking. *Ascomata* perithecial, conspicuous, umber to fuscous black, embedded in orange to umber pseudostromatic tissue, regularly scattered, surrounding the ectostromatic disc, with small to long ostioles that emerge within the ectostromatic disc. *Ostioles* flat in the disc or sometimes slightly projecting, cylindrical, sometimes obscuring the disc, covered by an orange, umber to fuscous black crust. *Paraphyses* deliquescent. *Asci* fusoid, 8-spored, 2–3-seriate, with an apical ring, becoming detached from the perithecial wall. *Ascospores* hyaline, fusoid to cylindrical, symmetrical to asymmetrical, straight to curved, bicellular, with a median septum, constricted at the septum, smooth, multiguttulate. *Conidiomata* acervular, spherical to conical to pulvinate, occurring separately, immersed to semi-immersed in bark; wall of several layers of yellow *textura angularis*. *Central column* beneath the disc conical or not. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner walls of cavity, hyaline, smooth, subcylindrical to ampulliform. *Conidia* hyaline, aseptate, smooth, multiguttulate or not, thin-walled, ellipsoid to fusoid, straight to curved (adapted from Fan *et al.* 2018, Jaklitsch & Voglmayr 2019, Jiang *et al.* 2019a).

Culture characteristics: Colonies on PDA circular to irregular, reaching 70 mm diam with 5–20 d at 25 °C in darkness, originally flat with white felted aerial mycelium, becoming yellow, grey to black mycelium due to different pigment formation, producing sexual ascomata or not after 1 mo.

Optimal media and cultivation conditions: MEA and PDA at 25 °C under continuous nuv-light to promote sporulation.

Distribution: Australia, China and Europe (Austria, Croatia, France, Greece, Italy, Poland, Spain).

Hosts: Tree genera including *Castanea*, *Quercus* (Fagaceae), *Elaeocarpus* (Elaeocarpaceae), *Malus* (Rosaceae) and *Osmanthus* (Oleaceae).

Disease symptoms: Stem canker.

Notes: *Dendrostoma* is characterised by having multiguttulate and bicellular ascospores that are constricted at the septum and acervular conidiomata, with subcylindrical to ampulliform conidiogenous cells and hyaline to olivaceous, aseptate conidia (Fan *et al.* 2018, Jiang *et al.* 2019a). This genus was initially described by Fan *et al.* (2018) based on the type species, *De. mali* from *Malus spectabilis*, together with two other species, *De. osmanthi* and *De. quercinum*. Subsequently, *De. leiphaemia* on *Quercus* trees in Europe was transferred from *Amphiportha* (Senanayake *et al.* 2018). Another 15 species from *Castanea* and *Quercus* trees were added, which revealed a high diversity of *Dendrostoma* on Fagaceae hosts (Jaklitsch & Voglmayr 2019, Jiang *et al.* 2019a, Zhu *et al.* 2019).

The family *Erythrogloeaceae* comprises four genera, namely *Chrysocrypta*, *Dendrostoma*, *Disculoides* and *Erythrogloeum*. Species of *Dendrostoma* are all known from bark, while those of the other three genera are all foliar pathogens (Jiang *et al.* 2019a). Additionally, the only genus of this family for which sexual morphs are known is *Dendrostoma*. Although all *Dendrostoma* species have been described from symptomatic tissues, no pathogenicity tests have thus far been conducted.

References: Fan *et al.* 2018 (morphology and phylogeny); Jiang *et al.* 2019a (morphology and phylogeny).

Dendrostoma elaeocarpi C.M. Tian & Q. Yang, *sp. nov.* MycoBank MB 829528. Fig. 22.

Etymology: Named after the host genus from which it was collected, *Elaeocarpus*.

Pseudostromata erumpent, consisting of an inconspicuous yellowish to orange ectostromatic disc, semi-immersed to superficial, causing a pustulate bark surface, 540–750 µm diam. *Ectostromatic disc* flat or concave, orange, or brown to black, sometimes concealed by ostioles, surrounded by bark flaps, 395–490 µm diam. *Central column* yellowish to brownish. *Stromatic zones* lacking. *Perithecia* conspicuous, umber to fuscous black, regularly scattered, surrounding the ectostromatic disc, (170–) 205–245(–300) µm diam. *Ostioles* 2–5 per disc, flat in the disc or sometimes slightly projecting, cylindrical, covered by an orange, umber to fuscous black crust, 75–100 µm diam. *Paraphyses* deliquescent. *Asci* fusoid, 8-spored, biseriate or triseriate, with an apical ring, (40.5–)43–44.5(–47) × (8.5–)10.5–12 µm. *Ascospores* hyaline, ellipsoidal to fusoid, smooth, biguttulate, symmetrical to asymmetrical, straight to slightly curved, bicellular, with a median septum distinctly constricted, (10.5–)11–13 × 3–3.5 µm.

Culture characteristics: Colonies on PDA circular to irregular, reaching 70 mm diam after 10 d at 25 °C in darkness, originally flat with white felted aerial mycelium, becoming saffron yellow mycelium due to pigment formation, producing ascomata after 1 mo.

Typus: **China**, Jiangxi Province, Ganzhou, Jinpenshan Forest Farm, 25°14'08.51"N, 115°12'41.21"E, on branches of *Elaeocarpus decipiens* (Elaeocarpaceae), 19 Jul. 2018, Q. Yang, Y. Liu, Y.M. Liang & C.M. Tian (**holotype** BJFC-S1682, culture ex-type CFCC 53113).

Additional material examined: **China**, Jiangxi Province, Ganzhou, Jinpenshan Forest Farm, 25°14'08.51"N, 115°12'41.21"E, on branches of *Elaeocarpus decipiens*, 19 Jul. 2018, Q. Yang, Y. Liu, Y.M. Liang & C.M. Tian, culture CFCC 53114.



Fig. 20. *Dendrostoma* spp. **A–D.** Disease symptoms on host barks. **A.** *Osmanthus fragrans*. **B–D.** *Quercus* spp. **E.** Pseudostroma. **F.** Transverse section through pseudostroma. **G.** Longitudinal section through pseudostroma. **E–G.** *Dendrostoma osmanthi* (CF 2017474) on *Osmanthus fragrans*. **H.** Conidioma of *Dendrostoma dispersum* (BJFC-S1537) on *Quercus* sp. **I.** Transverse section through conidioma of *Dendrostoma aurorae* (BJFC-S1561) on *Castanea mollissima*. **J.** Longitudinal section through conidioma of *Dendrostoma qinlingense* (BJFC-S1539) on *Quercus wutaishanica*. **K, L.** Ascus and ascospores of *Dendrostoma osmanthi* (CF 2017474) on *Osmanthus fragrans*. **M, N.** Conidiogenous cells and conidia of *Dendrostoma dispersum* (BJFC-S1538) on *Quercus* sp. Scale bars: E–H, J = 500 μ m; I = 200 μ m; K–N = 10 μ m.

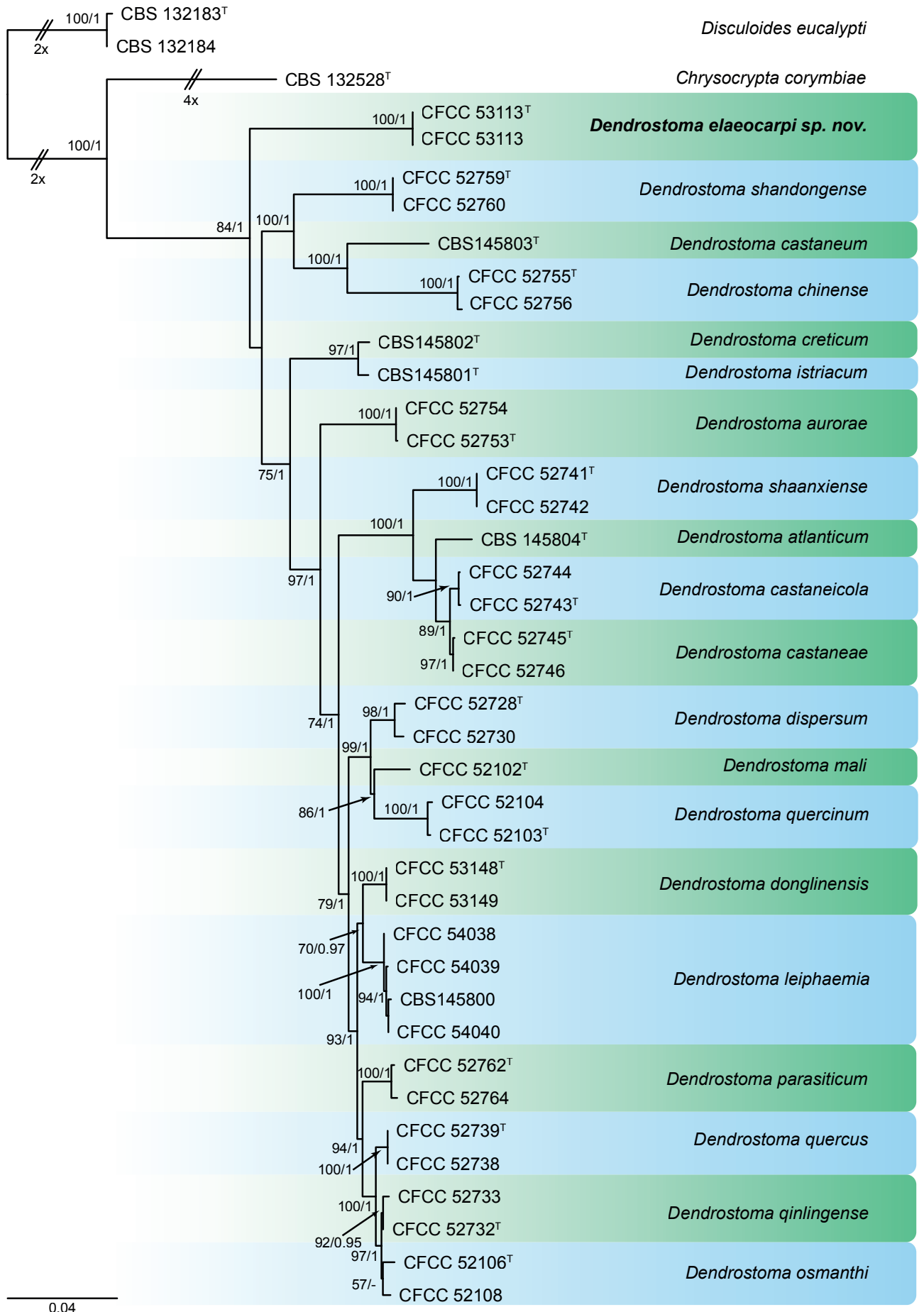


Fig. 21. Maximum Likelihood (ML) phylogram constructed from ITS (495 bp), *rpb2* (1 075 bp) and *tef1* (402 bp) sequences of all accepted species of *Dendrostoma*. Bootstrap support values (> 50%) for ML and Bayesian posterior probabilities (> 0.95) are shown at the nodes. The novel taxon is printed in **bold**. The phylogenetic tree was rooted to *Disculooides eucalypti* CBS 132183 and CBS132184. GenBank accession numbers are indicated in Table 7. ^T indicates ex-type strain. TreeBASE: S26124.

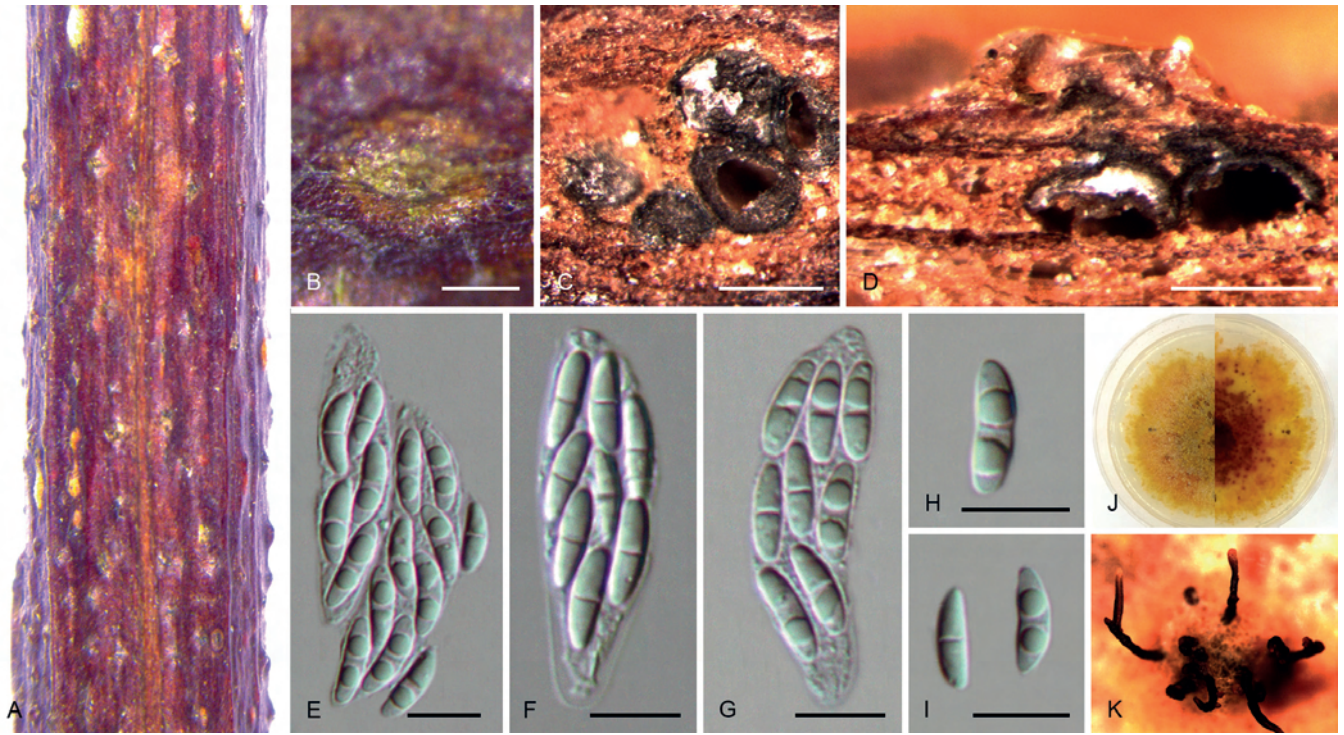


Fig. 22. *Dendrostoma elaeocarpi* (holotype BJFC-S1682). **A, B.** Habit of pseudostromata on twigs. **C.** Transverse section of pseudostromata. **D.** Longitudinal section through pseudostromata. **E–G.** Asci. **H, I.** Ascospores. **J.** The colony on PDA (front and reverse). **K.** Sexual ascomata on PDA. Scale bars: B–D = 200 µm; E–I = 10 µm.

Table 7. DNA barcodes of accepted *Dendrostoma* spp.

Species	Isolates ¹	GenBank accession numbers ²			References
		ITS	<i>tef1</i>	<i>rpb2</i>	
<i>Dendrostoma atlanticum</i>	CBS 145804 ^T	MN447223	MN432167	MN432160	Jaklitsch <i>et al.</i> (2019)
<i>De. aurorae</i>	CFCC 52753 ^T	MH542498	MH545447	MH545405	Jiang <i>et al.</i> (2019a)
	CFCC 52754	MH542499	MH545448	MH545406	Jiang <i>et al.</i> (2019a)
<i>De. castaneae</i>	CFCC 52745 ^T	MH542488	MH545437	MH545395	Jiang <i>et al.</i> (2019a)
	CFCC 52746	MH542489	MH545438	MH545396	Jiang <i>et al.</i> (2019a)
<i>De. castaneicola</i>	CFCC 52743 ^T	MH542496	MH545445	MH545403	Jiang <i>et al.</i> (2019a)
	CFCC 52744	MH542497	MH545446	MH545404	Jiang <i>et al.</i> (2019a)
<i>De. castaneum</i>	CBS 145803 ^T	MN447225	MN432169	MN432162	Jaklitsch <i>et al.</i> (2019)
<i>De. chinense</i>	CFCC 52755 ^T	MH542500	MH545449	MH545407	Jiang <i>et al.</i> (2019a)
	CFCC 52756	MH542501	MH545450	MH545408	Jiang <i>et al.</i> (2019a)
<i>De. creticum</i>	CBS 145802 ^T	MN447228	MN432171	MN432163	Jaklitsch <i>et al.</i> (2019)
<i>De. dispersum</i>	CFCC 52730	MH542467	MH545416	MH545374	Jiang <i>et al.</i> (2019a)
	CFCC 52728 ^T	MH542469	MH545418	MH545376	Jiang <i>et al.</i> (2019a)
<i>De. donglinensis</i>	CFCC 53148 ^T	MN266206	MN315480	MN315491	Zhu <i>et al.</i> (2019)
	CFCC 53149	MN266207	MN315481	MN315492	Zhu <i>et al.</i> (2019)
<i>De. elaeocarpi</i>	CFCC 53113 ^T	MK432638	MK578096	MK578114	Present study
	CFCC 53114	MK432639	MK578097	MK578115	Present study
<i>De. istriacum</i>	CBS 145801 ^T	MN447229	MN432172	MN432164	Jaklitsch <i>et al.</i> (2019)
<i>De. leiphaemia</i>	CFCC 54038	MN545571	MN551288	MN551291	Present study
	CFCC 54039	MN545572	MN551289	MN551292	Present study
	CFCC 54040	MN545573	MN551290	MN551293	Present study
<i>De. mali</i>	CBS 145800	MN447230	MN432173	MN432165	Jaklitsch <i>et al.</i> (2019)
<i>De. osmanthi</i>	CFCC 52102 ^T	MG682072	MG682052	MG682032	Fan <i>et al.</i> (2018)
	CFCC 52106 ^T	MG682073	MG682053	MG682033	Fan <i>et al.</i> (2018)
	CFCC 52108	MG682074	MG682054	MG682034	Fan <i>et al.</i> (2018)

Table 7. (Continued).

Species	Isolates ¹	GenBank accession numbers ²			References
		ITS	<i>tef1</i>	<i>rpb2</i>	
<i>De. parasiticum</i>	CFCC 52762 [†]	MH542482	MH545431	MH545389	Jiang <i>et al.</i> (2019a)
	CFCC 52764	MH542483	MH545432	MH545390	Jiang <i>et al.</i> (2019a)
<i>De. qinlingense</i>	CFCC 52732 [†]	MH542471	MH545420	MH545378	Jiang <i>et al.</i> (2019a)
	CFCC 52733	MH542472	MH545421	MH545379	Jiang <i>et al.</i> (2019a)
<i>De. quercinum</i>	CFCC 52103 [†]	MG682077	MG682057	MG682037	Fan <i>et al.</i> (2018)
	CFCC 52104	MG682078	MG682058	MG682038	Fan <i>et al.</i> (2018)
<i>De. quercus</i>	CFCC 52739 [†]	MH542476	MH545425	MH545383	Jiang <i>et al.</i> (2019a)
	CFCC 52738	MH542477	MH545426	MH545384	Jiang <i>et al.</i> (2019a)
<i>De. shaanxiense</i>	CFCC 52741 [†]	MH542486	MH545435	MH545393	Jiang <i>et al.</i> (2019a)
	CFCC 52742	MH542487	MH545436	MH545394	Jiang <i>et al.</i> (2019a)
<i>De. shandongense</i>	CFCC 52759 [†]	MH542504	MH545453	MH545411	Jiang <i>et al.</i> (2019a)
	CFCC 52760	MH542505	MH545454	MH545412	Jiang <i>et al.</i> (2019a)

¹ CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CFCC: China Forestry Culture Collection Center, Beijing, China. [†] indicates ex-type.

² ITS: internal transcribed spacers and intervening 5.8S nrDNA; *rpb2*: partial RNA polymerase II second largest subunit gene; *tef1*: partial elongation factor 1- α gene.

Notes: *Dendrostoma elaeocarpi* is associated with canker disease of *Elaeocarpus decipiens*, representing a first report from this host. *Dendrostoma elaeocarpi* can be distinguished from other *Dendrostoma* species by host associations and ellipsoidal to fusoid, biguttulate ascospores.

Genome sequenced strain: *Dendrostoma leiphaemia*. **The Netherlands**, on *Quercus* sp., 25 Apr. 2019, N. Jiang, culture ex-type CFCC 54038. This Whole Genome Shotgun project has been deposited at GenBank under the accession JALRMF000000000 (BioProject: PRJNA827019, BioSample: SAMN27594414; present study).

Authors: N. Jiang, Q. Yang & C.M. Tian

Didymella Sacc. ex Sacc. *emend.* Qian Chen & L. Cai, *Stud. Mycol.* 82: 173. 2015. Fig. 23.

Synonym: *Peyronellaea* Goid. ex Togliani, *Ann. Sperim. Agrar.* II 6: 93. 1952.

Classification: Dothideomycetes, Pleosporomycetidae, Pleosporales, Didymellaceae.

Type species: *Didymella exigua* (Niessl) Sacc., basionym: *Didymosphaeria exigua* Niessl, *Oesterr. bot. Z.* 25: 165. 1875. Neotype and ex-neotype strain: CBS H-20123, CBS 183.55.

DNA barcodes (genus): LSU, ITS.

DNA barcodes (species): *rpb2*, *tub2*. Table 8. Fig. 24.

Ascomata pseudothecial, immersed or erumpent, (sub-)globose to flattened, solitary or confluent, ostiolate; *ascomatal wall* multi-layered, composed of pseudoparenchymatous cells. *Asci* cylindrical to clavate or saccate, 8-spored, bitunicate, arising from a broad hymenium among pseudoparaphyses. *Ascospores* mostly hyaline or brownish, ellipsoidal to cymbiform, uniseptate, symmetrical or asymmetrical, constricted at the septum, or multiseptate. *Conidiomata* pycnidial,

(sub-)globose to ellipsoidal, flask-shaped, or obpyriform, becoming irregular, superficial on or immersed into the agar, solitary or confluent, ostiolate or poroid, sometimes with elongated necks; micropycnidia occur in some species; *conidiomatal wall* pseudoparenchymatous, multi-layered. *Conidiogenous cells* phialidic, hyaline, smooth, flask-shaped, subglobose, lageniform, ampulliform or doliiform. *Conidia* generally aseptate, variable in shape, smooth and thin-walled, *i.e.* ellipsoidal to (sub-)globose, cylindrical, oblong, ovoid, sometimes allantoid, hyaline, but in older cultures conidia may become pigmented, larger or septate conidia may occur in at least one species, mostly guttulate. *Unicellular chlamydospores* often abundantly formed in and on the agar and in the aerial mycelium, globose, intercalary, brown or (pale) olivaceous pigmented; *multicellular chlamydospores* mainly alternarioid, muriformly septate, terminal or intercalary, often in chains, brown or (pale) olivaceous (de Gruyter *et al.* 2009, Aveskamp *et al.* 2010, Zhang *et al.* 2012, Crous *et al.* 2014, Chen *et al.* 2015b, 2017, Hou *et al.* 2020a).

Cultural characteristics: Colonies on OA covered by flat, felted, or floccose, white to pale olivaceous grey, pale luteous to buff, or yellow olivaceous to dull green aerial mycelium, margin mostly regular, white to smoke/mouse/iron/yellowish grey, buff, amber to brown, pale olivaceous to dark olivaceous, yellowish green to dull green, fuscous-black, sometimes with saffron, salmon, red to dark vinaceous colour.

Optimal media and cultivation conditions: OA or sterile pine needles placed on OA under nuv-light (12 h light, 12 h dark) to promote sporulation at 25 °C.

Distribution: Worldwide.

Hosts: Mainly found as saprobes on dead stems or bark, and (opportunistic) parasites of herbaceous and woody plants on a wide range of plant families, *i.e.* *Aceraceae*, *Actinidiaceae*, *Amaryllidaceae*, *Anacardiaceae*, *Aquifoliaceae*, *Araceae*, *Araliaceae*, *Asphodelaceae*, *Asteraceae*, *Berberidaceae*, *Bromeliaceae*, *Cactaceae*, *Caprifoliaceae*, *Chenopodiaceae*, *Combretaceae*, *Cucurbitaceae*, *Elaeagnaceae*, *Ericaceae*, *Fabaceae*, *Gentianaceae*,

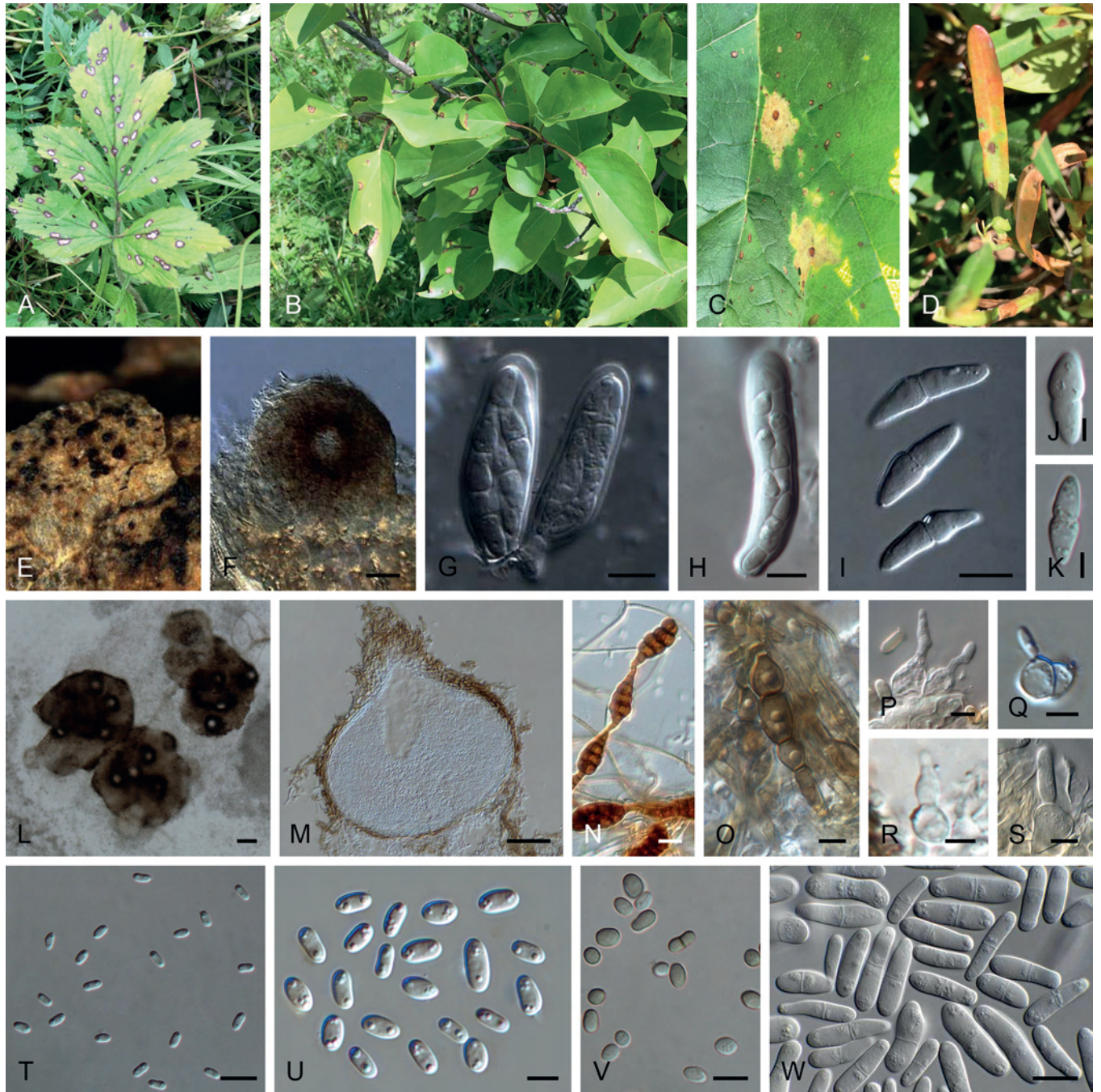


Fig. 23. *Didymella* spp. **A–D.** Disease symptoms. **A.** Symptoms caused by *Didymella gei* (ex-type CGMCC 3.20068) on *Geum* sp. **B.** Symptoms caused by *Didymella uniseptata* (ex-type CGMCC 3.20069) on *Syringa vulgaris*. **C.** Symptoms caused by *Didymella qilianensis* (ex-type CGMCC 3.20071) on *Rheum officinale*. **D.** Symptoms caused by *Didymella chlamydospora* (LC13589) on *Polygonum sibiricum*. **E–K.** Sexual morph. **E.** Ascomata on host of *Didymella exigua* (ex-neotype CBS 183.55). **F.** Ascoma of *Didymella exigua* (ex-neotype CBS 183.55). **G, H.** Asci. **G.** *Didymella exigua* (ex-neotype CBS 183.55). **H.** *Didymella pinodes* (holotype K 56275). **I–K.** Ascospores. **I.** *Didymella exigua* (ex-neotype CBS 183.55). **J.** *Didymella pinodes* (holotype K 56275). **K.** *Didymella sinensis* (ex-type CGMCC 3.18348). **L–W.** Asexual morph. **L.** Conidiomata of *Didymella aquatica* (ex-type CGMCC 3.18349). **M.** Section through the conidioma of *Didymella degraaiffae* (ex-type CBS 144956). **N, O.** Chlamydospores. **N.** Alternaroid chlamydospores of *Didymella glomerata* (UTHSCD 116-205). **O.** *Didymella degraaiffae* (ex-type CBS 144956). **P–S.** Conidiogenous cells. **P.** *Didymella brunneospora* (ex-type CBS 115.58). **Q.** *Didymella degraaiffae* (ex-type CBS 144956). **R.** *Didymella illicicola* (ex-type CGMCC 3.18355). **S.** *Didymella cari* (ex-type CBS 144497). **T–W.** Conidia. **T.** *Didymella aquatica* (ex-type CGMCC 3.18349). **U.** *Didymella degraaiffae* (ex-type CBS 144956). **V.** *Didymella infuscatispora* (CGMCC 3.18356). **W.** *Didymella cari* (ex-type CBS 144497). Scale bars: L = 50 µm; F–I, M, N, S, T, V, W = 10 µm; J, K, O–R, U = 5 µm. Pictures E–J taken from Chen et al. (2015b); K, L, R, T, V from Chen et al. (2017); M, O, Q, U from Hou et al. (2020b); N, P from Valenzuela-Lopez et al. (2018); S, W from Crous et al. (2018c).

Geraniaceae, Hamamelidaceae, Lamiaceae, Liliaceae, Lythraceae, Myrtaceae, Oleaceae, Orchidaceae, Pinaceae, Poaceae, Polygonaceae, Pteridaceae, Rosaceae, Rubiaceae, Saxifragaceae, Scrophulariaceae, Simaroubaceae, Solanaceae, Theaceae, Umbelliferae, Urticaceae and Vitaceae, and also from different human and environment samples.

Disease symptoms: Blossom blight, flower-stalk diseases, leaf spots, leaf scorch, neck rot, stem lesions, seed-borne diseases, wood discolouration, damping-off of seedlings, red spot disease, and black root rot.

Table 8. DNA barcodes of accepted *Didymella* spp.

Species	Isolates ¹	GenBank accession numbers ²				References
		LSU	ITS	<i>rpb2</i>	<i>tub2</i>	
<i>Didymella acetosellae</i>	CBS 631.76 ^{ET}	MN943749	MN973542	MT018176	MT005645	Hou <i>et al.</i> (2020a)
<i>Di. aeria</i>	CGMCC 3.18353 ^T	KY742205	KY742051	KY742137	KY742293	Chen <i>et al.</i> (2017)
<i>Di. aliena</i>	CBS 379.93	GU238037	GU237851	KP330416	GU237578	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015c)
<i>Di. aloaicola</i>	CBS 562.88 ^T	MN943742	MN973535	MT018164	MT005638	Hou <i>et al.</i> (2020a)
<i>Di. americana</i>	CBS 185.85	GU237990	FJ426972	KT38 9594	FJ427088	Aveskamp <i>et al.</i> (2009, 2010), Chen <i>et al.</i> (2015b)
<i>Di. anserina</i>	CBS 360.84	GU237993	GU237839	KT389596	GU237551	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015b)
<i>Di. aquatica</i>	CGMCC 3.18349 ^T	KY742209	KY742055	KY742140	KY742297	Chen <i>et al.</i> (2017)
<i>Di. arachidicola</i>	CBS 333.75 ^{ISO} ^T	GU237996	GU237833	KT389598	GU237554	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015b)
<i>Di. aurea</i>	CBS 269.93 ^T	GU237996	GU237833	KT389598	GU237554	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015b)
<i>Di. bellidis</i>	CBS 714.85	GU238046	GU237904	KP330417	GU237586	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015c)
<i>Di. boeremae</i>	CBS 109942 ^{NT}	GU238048	FJ426982	KT389600	FJ427097	Aveskamp <i>et al.</i> (2009, 2010), Chen <i>et al.</i> (2015b)
<i>Di. brunneospora</i>	CBS 115.58 ^T	KT389723	KT389505	KT389625	KT389802	Chen <i>et al.</i> (2015b), Valenzuela-Lopez <i>et al.</i> (2018)
<i>Di. calidophila</i>	CBS 448.83 ^{NT}	GU238052	FJ427059	MT018170	FJ427168	Aveskamp <i>et al.</i> (2009, 2010), Hou <i>et al.</i> (2020a)
<i>Di. cari</i>	CBS 144497 ^T	MH327861	MH327825	—	MH327899	Crous <i>et al.</i> (2018c)
<i>Di. chenopodii</i>	CBS 128.93	GU238055	GU237775	KT389602	GU237591	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015b)
<i>Di. chlamydospora</i>	LC 13586	MT229671	MT229694	MT239091	MT249262	Present study
	CGMCC 3.20072 = LC 13587 ^T	MT229672	MT229695	MT239092	MT249263	Present study
	LC 13588	MT229673	MT229696	MT239093	MT249264	Present study
	LC 13589	MT229674	MT229697	MT239094	MT249265	Present study
<i>Di. chloroguttulata</i>	CGMCC 3.18351 ^T	KY742211	KY742057	KY742142	KY742299	Chen <i>et al.</i> (2017)
<i>Di. coffeae-arabicae</i>	CBS 123380 ^T	GU238005	FJ426993	KT389603	FJ427104	Aveskamp <i>et al.</i> (2009, 2010), Chen <i>et al.</i> (2015b)
<i>Di. combreti</i>	CBS 137982 ^T	KJ869191	KJ869134	MT018139	MT005626	Crous <i>et al.</i> (2014), Hou <i>et al.</i> (2020a)
<i>Di. curtisii</i>	CBS 251.92	GU238013	FJ427038	MT018131	FJ427148	Aveskamp <i>et al.</i> (2009, 2010), Hou <i>et al.</i> (2020a)
<i>Di. dactylidis</i>	CBS 124513 ^T	GU238061	GU237766	MT018173	GU237599	Aveskamp <i>et al.</i> (2010), Hou <i>et al.</i> (2020a)
<i>Di. degraaffiae</i>	CBS 144956 ^T	MN823295	MN823444	MN824470	MN824618	Hou <i>et al.</i> (2020b)
<i>Di. dimorpha</i>	CBS 346.82 ^T	GU238068	GU237835	MT018158	GU237606	Aveskamp <i>et al.</i> (2010), Hou <i>et al.</i> (2020a)
<i>Di. ellipsoidea</i>	CGMCC 3.18350 ^T	KY742214	KY742060	KY742145	KY742302	Chen <i>et al.</i> (2017)
<i>Di. eucalyptica</i>	CBS 377.91	GU238007	GU237846	KT389605	GU237562	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015b)
<i>Di. exigua</i>	CBS 183.55 ^T	EU754155	GU237794	EU874850	GU237525	Chilvers <i>et al.</i> (2009), de Gruyter <i>et al.</i> (2009), Aveskamp <i>et al.</i> (2010)
<i>Di. finnmarkica</i>	CBS 145572 ^T	MK876429	MK876388	MK876484	—	Crous <i>et al.</i> (2019a)
<i>Di. gardeniae</i>	CBS 626.68 ^{IT}	GQ387595	FJ427003	KT389606	FJ427114	Aveskamp <i>et al.</i> (2009), de Gruyter <i>et al.</i> (2010), Chen <i>et al.</i> (2015b)
<i>Di. gei</i>	CGMCC 3.20068 = LC 13581 ^T	MT229675	MT229698	MT239095	MT249266	Present study
<i>Di. glomerata</i>	CBS 528.66	EU754184	FJ427013	GU371781	FJ427124	Aveskamp <i>et al.</i> (2009), de Gruyter <i>et al.</i> (2009), Schoch <i>et al.</i> (2009)
<i>Di. guttulata</i>	CBS 127976 ^T	MN943730	MN973524	MT018138	MT005625	Hou <i>et al.</i> (2020a)
<i>Di. heteroderae</i>	CBS 109.92 ^T	GU238002	FJ426983	KT389601	FJ427098	Aveskamp <i>et al.</i> (2009, 2010), Chen <i>et al.</i> (2015b)
<i>Di. ilicicola</i>	CGMCC 3.18355 ^T	KY742219	KY742065	KY742150	KY742307	Chen <i>et al.</i> (2017)
<i>Di. indica</i>	CBS 653.77 ^T	MN943741	MN973534	MT018159	MT005637	Hou <i>et al.</i> (2020a)
<i>Di. infuscatisspora</i>	CGMCC 3.18356 ^T	KY742221	KY742067	KY742152	KY742309	Chen <i>et al.</i> (2017)
<i>Di. keratinophila</i>	CBS 143032 ^T	LN907343	LT592901	LT593039	LT592970	Valenzuela-Lopez <i>et al.</i> (2018)
<i>Di. kooimaniorum</i>	CBS 144951 ^T	MN823299	MN823448	MN824474	MN824622	Hou <i>et al.</i> (2020b)
<i>Di. lethalis</i>	CBS 103.25	GU238010	GU237729	KT389607	GU237564	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015b)
<i>Di. ligulariae</i>	CGMCC 3.20070 = LC 13583 ^T	MT229676	MT229699	MT239096	MT249267	Present study
<i>Di. longicolla</i>	CBS 124514 ^T	GU238095	GU237767	MT018161	GU237622	Aveskamp <i>et al.</i> (2010), Hou <i>et al.</i> (2020a)
<i>Di. macrophylla</i>	CGMCC 3.18357 ^T	KY742224	KY742070	KY742154	KY742312	Chen <i>et al.</i> (2017)

Table 8. DNA barcodes of accepted *Didymella* spp.

Species	Isolates ¹	GenBank accession numbers ²				References
		LSU	ITS	<i>rpb2</i>	<i>tub2</i>	
<i>Di. macrostoma</i>	CBS 223.69	GU238096	GU237801	KT389608	GU237623	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015b)
<i>Di. maydis</i>	CBS 588.69 ^T	EU754192	FJ427086	GU371782	FJ427190	Aveskamp <i>et al.</i> (2009), de Gruyter <i>et al.</i> (2009), Schoch <i>et al.</i> (2009)
<i>Di. microchlamydospora</i>	CBS 105.95 ^T	GU238104	FJ427028	KP330424	FJ427138	Aveskamp <i>et al.</i> (2009, 2010), Chen <i>et al.</i> (2015c)
<i>Di. mitis</i>	CBS 443.72 ^T	MN943729	MN973523	MT018137	MT005624	Hou <i>et al.</i> (2020a)
<i>Di. molleriana</i>	CBS 229.79	GU238067	GU237802	KP330418	GU237605	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015c)
<i>Di. musae</i>	CBS 463.69	GU238011	FJ427026	MT018148	FJ427136	Aveskamp <i>et al.</i> (2009, 2010), Hou <i>et al.</i> (2020a)
<i>Di. negriana</i>	CBS 358.71	GU238116	GU237838	KT389610	GU237635	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015b)
<i>Di. nigricans</i>	CBS 444.81 ^{isoT}	GU238000	GU237867	MT018146	GU237558	Aveskamp <i>et al.</i> (2010), Hou <i>et al.</i> (2020a)
<i>Di. ocimicola</i>	CGMCC 3.18358 ^T	KY742232	KY742078	MT018181	KY742320	Chen <i>et al.</i> (2017), Hou <i>et al.</i> (2020a)
<i>Di. pedeiaae</i>	CBS 124517 ^T	GU238127	GU237770	KT389612	GU237642	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015b)
<i>Di. pinodella</i>	CBS 531.66	GU238017	FJ427052	KT389613	FJ427162	Aveskamp <i>et al.</i> (2009, 2010), Chen <i>et al.</i> (2015b)
<i>Di. pinodes</i>	CBS 525.77 ^{ET}	GU238023	GU237883	KT389614	GU237572	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015b)
<i>Di. pomorum</i>	CBS 539.66	GU238028	FJ427056	KT389618	FJ427166	Aveskamp <i>et al.</i> (2009, 2010), Chen <i>et al.</i> (2015b)
<i>Di. prolaticolla</i>	CBS 126182 ^T	MN943740	MN973533	MT018157	MT005636	Hou <i>et al.</i> (2020a)
<i>Di. prosopidis</i>	CBS 136414 ^T	KF777232	KF777180	MT018149	MT005631	Crous <i>et al.</i> (2013b)
<i>Di. protuberans</i>	CBS 381.96 ^{NT}	GU238029	GU237853	KT389620	GU237574	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015b)
<i>Di. pteridis</i>	CBS 379.96 ^T	KT389722	KT389504	KT389624	KT389801	Chen <i>et al.</i> (2015b), Chen <i>et al.</i> (2017)
<i>Di. qilianensis</i>	LC 13584	MT229677	MT229700	MT239097	MT249268	Present study
	CGMCC 3.20071 = LC 13585 ^T	MT229678	MT229701	MT239098	MT249269	Present study
<i>Di. rhei</i>	CBS 109177	GU238139	GU237743	KP330428	GU237653	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015c)
<i>Di. rumicicola</i>	CBS 683.79 ^{isoT}	KT389721	KT389503	KT389622	KT389800	Chen <i>et al.</i> (2015b)
<i>Di. sancta</i>	CBS 281.83 ^T	GU238030	FJ427063	KT389623	FJ427170	Aveskamp <i>et al.</i> (2009, 2010), Chen <i>et al.</i> (2015b)
<i>Di. segeticola</i>	CGMCC 3.17489 ^T	KP330455	KP330443	KP330414	KP330399	Chen <i>et al.</i> (2015c), Chen <i>et al.</i> (2017)
<i>Di. senecionicola</i>	CBS 160.78	GU238143	GU237787	MT018177	GU237657	Aveskamp <i>et al.</i> (2010), Hou <i>et al.</i> (2020a)
<i>Di. sinensis</i>	CGMCC 3.18348 ^T	KY742239	KY742085	MT018127	KY742327	Chen <i>et al.</i> (2017), Hou <i>et al.</i> (2020a)
<i>Di. subglobispora</i>	CBS 364.91 ^T	MN943737	MN973531	MT018153	MT005634	Hou <i>et al.</i> (2020a)
<i>Di. subglomerata</i>	CBS 110.92	GU238032	FJ427080	KT389626	FJ427186	Aveskamp <i>et al.</i> (2009, 2010), Chen <i>et al.</i> (2015b)
<i>Di. subherbarum</i>	CBS 250.92 ^T	GU238145	GU237809	MT018162	GU237659	Aveskamp <i>et al.</i> (2010), Hou <i>et al.</i> (2020a)
<i>Di. subrosea</i>	CBS 733.79 ^T	MN943747	MN973540	MT018174	MT005643	Hou <i>et al.</i> (2020a)
<i>Di. suiyangensis</i>	CGMCC 3.18352 ^T	KY742243	KY742089	KY742168	KY742330	Chen <i>et al.</i> (2017)
<i>Di. uniseptata</i>	CGMCC 3.20069 = LC 13582 ^T	MT229679	MT229702	MT239099	MT249270	Present study
<i>Di. variabilis</i>	CBS 254.79 ^T	MN943751	MN973544	MT018182	MT005647	Hou <i>et al.</i> (2020a)
<i>Di. viburnicola</i>	CBS 523.73	GU238155	GU237879	KP330430	GU237667	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015c)

¹ CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CGMCC: Chinese General Microbiological Culture Collection Center, Beijing, China; LC: Dr Lei Cai's personal collection deposited in laboratory, housed at Chinese Academy of Sciences, China. ^T, ^{ET}, ^{isoT} and ^{NT} indicate ex-type, ex-epitype, ex-isotype and ex-neotype strains, respectively.

²ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial 28S large subunit nrDNA gene; *rpb2*: partial RNA polymerase II second largest subunit gene; *tub2*: partial β -tubulin gene.

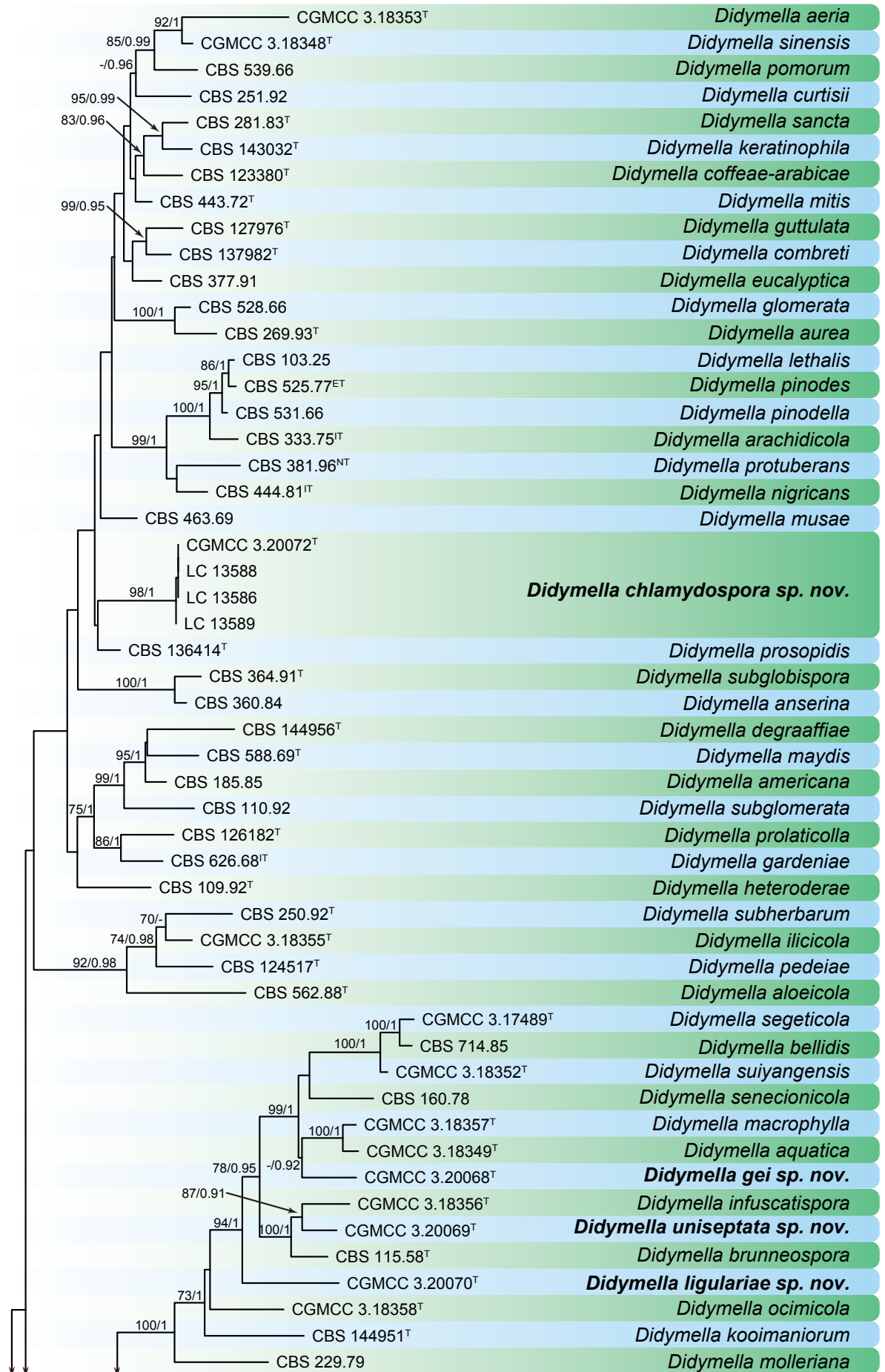


Fig. 24. Maximum Likelihood (ML) phylogram constructed from LSU (962 bp), ITS (462 bp), *tub2* (346 bp) and *rpb2* (596 bp) sequences of all accepted species of *Didymella*. RAxML bootstrap support values (> 70 %) and Bayesian posterior probability scores (> 0.90) are shown at the nodes. Novel taxa are printed in bold. The phylogenetic tree was rooted to *Neoascochyta exitialis* CBS 389.86. GenBank accession numbers are indicated in Table 8. ^T, ^{ET}, ^{ISO} and ^{NT} indicate ex-type, ex-epitype, ex-isotype and ex-neotype strains, respectively. TreeBASE: S26040.

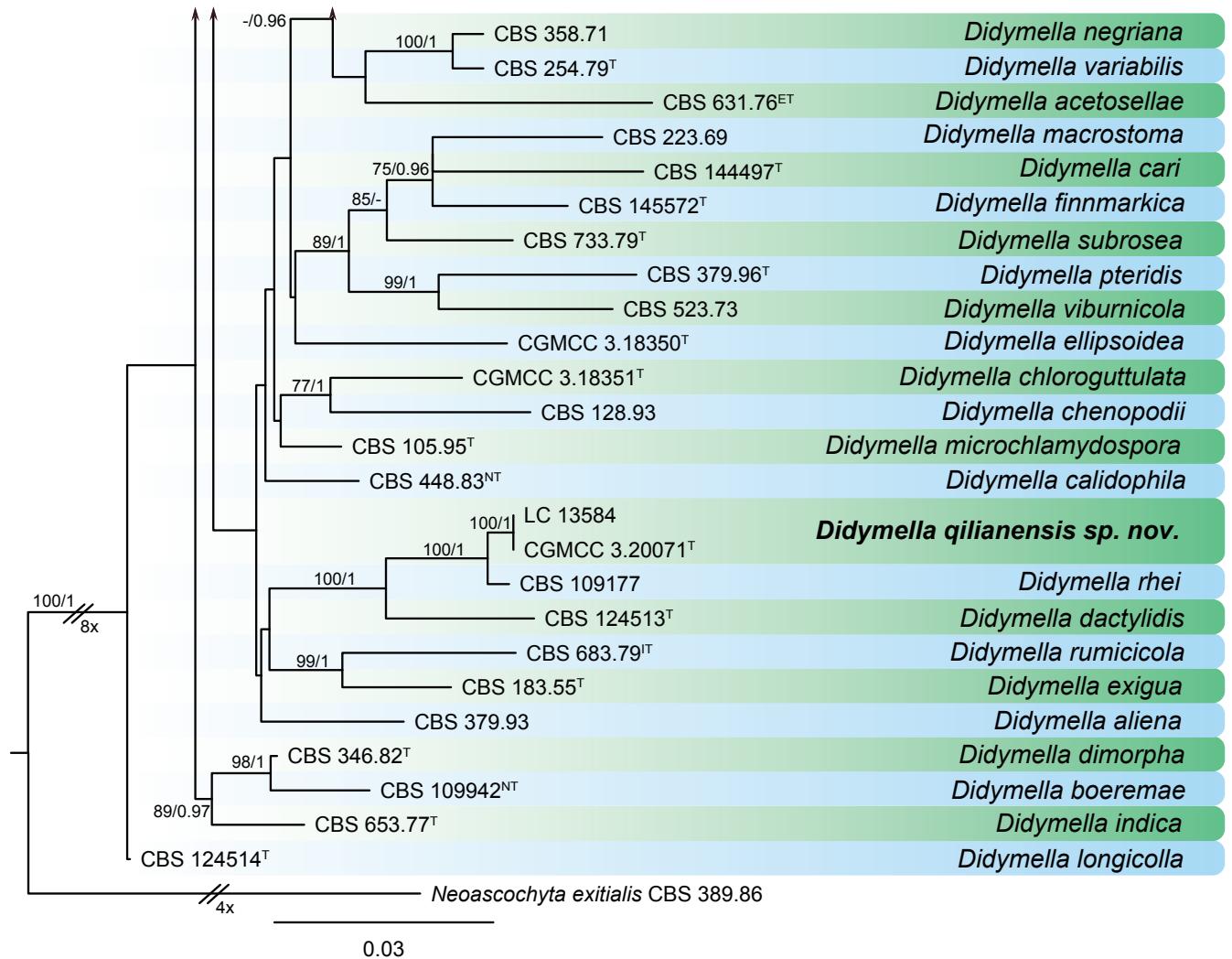


Fig. 24. (Continued).

Notes: *Didymella* was introduced as genus name in 1880, with the description of the type species *Di. exigua*, and later validated when a Latin diagnosis was provided (Saccardo 1880, 1882, de Gruyter *et al.* 2009). It was introduced in the *Mycosphaerellaceae* at first, and subsequently accommodated in several different families, such as *Pleosporaceae*, *Phaeosphaeriaceae*, *Venturiaceae*, and in the *Pleosporales* as *incertae sedis* (de Gruyter *et al.* 2009). The family *Didymellaceae* was established with *Didymella* as type genus, comprising species mostly from two related asexually typified genera *Ascochyta* and *Phoma*. The taxonomy of *Didymellaceae* has been recently revised by Aveskamp *et al.* (2010) and Chen *et al.* (2015b), in which *Ascochyta*, *Didymella* and *Phoma* were resolved based on their phylogenetic relationships, each restricted to a monophyletic group. *Didymella* species are variable in morphology and DNA sequences are necessary for accurate species identification. Among the four DNA barcodes studied, *rpb2* performed best at both generic and species level (Chen *et al.* 2015b, 2017, Valenzuela-Lopez *et al.* 2018, Hou *et al.* 2020a). Currently circumscribed *Didymella* includes phytopathogenic and saprobic fungi associated with more than 40 plants families, and those from clinical samples, such as human lesion, skin, toenails and sputum, and also environmental origin, such as air, soil and lake water (Corlett 1981, Aveskamp *et al.* 2010, Chen *et al.* 2015b, 2017, Valenzuela-Lopez *et al.* 2018, Hou *et al.* 2020a).

References: Boerema *et al.* 2004 (morphology and pathogenicity); Aveskamp *et al.* 2009, 2010, Chen *et al.* 2015b, c, 2017, Valenzuela-

Lopez *et al.* 2018, Hou *et al.* 2020a, b (morphology, phylogeny and pathogenicity).

Didymella chlamydospora Qian Chen & L. Cai, **sp. nov.** MycoBank MB 834961. Fig. 25.

Etymology: Name reflects its production of chlamydospores.

Conidiomata pycnidial, aggregated, globose to subglobose, later merging into a large irregular one, glabrous, mostly produced on the surface, 130–230 × 90–290 μm; *ostiole* single, elongated to a short wide neck with age; *conidiomatal wall* pseudoparenchymatous 2–4-layered, 11–30 μm thick, composed of isodiametric cells, the outer layer slightly pigmented. *Conidiogenous cells* phialidic, hyaline, smooth, lageniform to ampulliform, doliiform, 4–8.5 × 4–6 μm. *Conidia* variable in shape, ellipsoidal, ovoid or oblong, incidentally slightly curved, smooth- and thin-walled, hyaline, aseptate, 3.5–6.5(–8) × 2.5–3.5 μm, with several polar guttules. *Conidial exudates* pale pink. *Chlamydospores* unicellular, occasionally 1-septate, hyaline or pale brown to brown, thin-walled, intercalary, globose to subglobose, solitary or in short chains, eguttulate, 8–18 μm diam.

Culture characteristics: Colonies on OA, 60–65 mm diam after 1 wk, margin regular, floccose, white, pale olivaceous brown near the centre; reverse cream-white, pale olivaceous to dark olivaceous

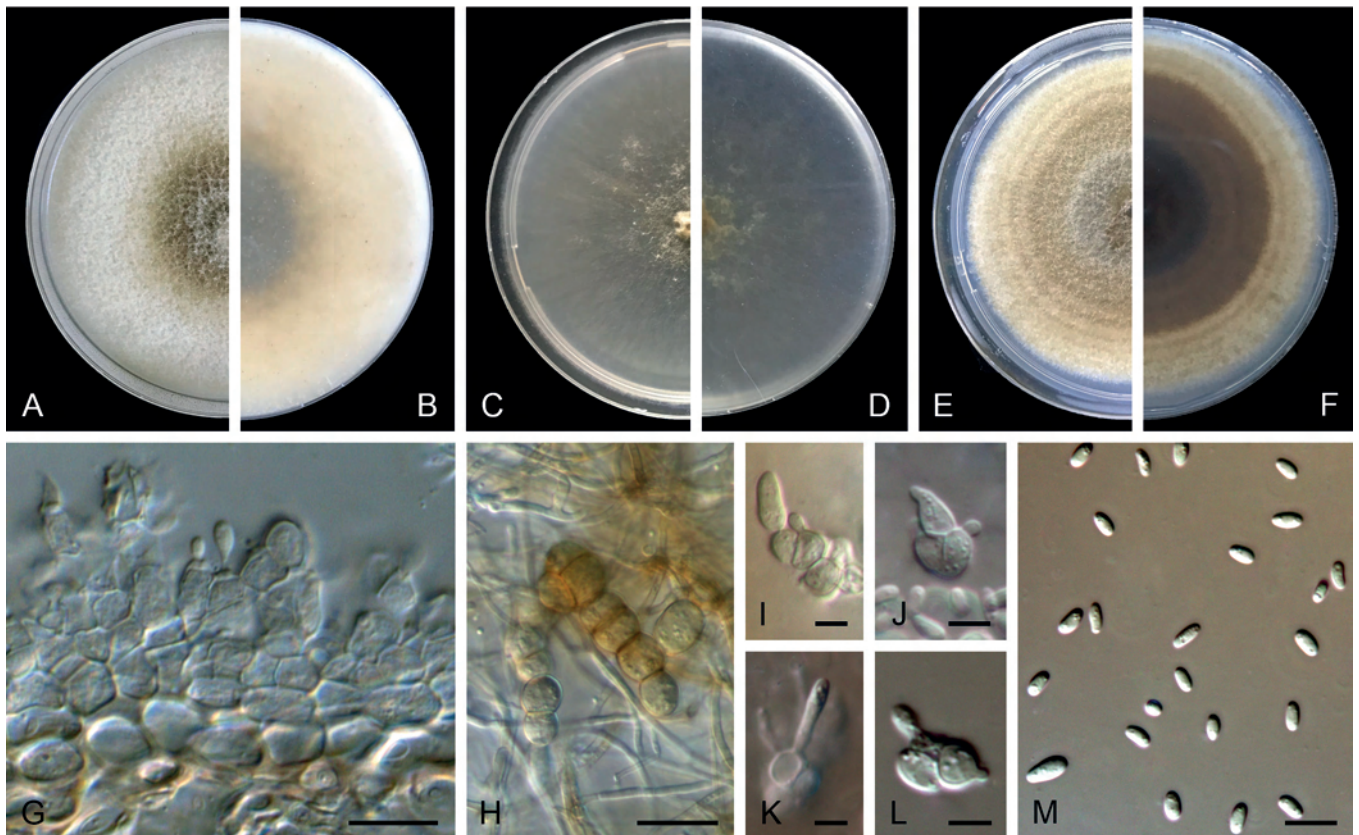


Fig. 25. *Didymella chlamydospora* (ex-type CGMCC 3.20072). **A, B.** Colony on OA (front and reverse). **C, D.** Colony on MEA (front and reverse). **E, F.** Colony on PDA (front and reverse). **G.** Section of conidiomatal wall. **H.** Chlamydospores. **I–L.** Conidiogenous cells. **M.** Conidia. Scale bars: H = 20 µm; G, M = 10 µm; I–L = 5 µm.

towards the centre. Colonies on MEA 55–65 mm diam after 1 wk, margin regular, aerial mycelium sparsely floccose, pale yellowish olivaceous; reverse concolourous. Colonies on PDA, 55–65 mm diam after 1 wk, margin regular, floccose to woolly, hazel to pale brown, grey near the centre, cream-white near the margin, with pale brown concentric rings; reverse brown, leaden grey to dark brown near the centre, hazel near the margin, with pale brown concentric rings. Application of NaOH results in a pale yellowish green discolouration of the agar.

Typus: **China**, Qinghai Province, Menyuan County, Gangshika snow-capped Mountain, from diseased leaves of *Elymus glaucus* (*Poaceae*), 9 Aug. 2019, L.W. Hou (**holotype** HMAS 248355, dried culture, culture ex-type CGMCC 3.20072 = LC 13587).

Additional materials examined: **China**, Qinghai Province, Menyuan County, Gangshika snow-capped Mountain, from diseased leaves of *Elymus glaucus* (*Poaceae*), 9 Aug. 2019, L.W. Hou, culture LC 13586; Qinghai, Qilian County, Ladong, from diseased leaves of *Polygonum viviparum* (*Polygonaceae*), 9 Aug. 2019, L.W. Hou, culture LC 13588; from diseased leaves of *Polygonum sibiricum* (*Polygonaceae*), 9 Aug. 2019, L.W. Hou, culture LC 13589.

Notes: *Didymella chlamydospora* is phylogenetically closely related to *Didymella prosopidis* (Fig. 24; 5 bp difference in ITS, 2 in LSU, 19 in *rpb2* and 17 in *tub2*), but differs in the size of chlamydospores (8–18 µm diam) from the latter (5–9 µm diam; Crous *et al.* 2013b).

Didymella gei Qian Chen & L. Cai, **sp. nov.** MycoBank MB 834956. Fig. 26.

Etymology: Named after the host genus from which the holotype was collected, *Geum*.

Conidiomata pycnidial, aggregated and confluent, globose to subglobose, brown, glabrous or with few hyphal outgrowths, superficial on the agar, 105–260 × 85–225 µm; **ostiole** inconspicuous; **conidiomatal wall** pseudoparenchymatous 2–3-layered, 10–27 µm thick, composed of oblong or isodiametric cells. **Conidiogenous cells** phialidic, hyaline, smooth, ampulliform to doliiform, 5–8.5 × 4–7 µm. **Conidia** oval to oblong, smooth- and thin-walled, hyaline, aseptate, 4–6.5 × 2–2.5 µm, with 1–2 guttules. Conidial exudates not recorded.

Culture characteristics: Colonies on OA, 60–65 mm diam after 1 wk, margin regular, woolly, white near the centre, hazel, abundant brown pycnidia visible; reverse hazel, white to pale saffron near the centre. Colonies on MEA 50–60 mm diam after 1 wk, margin regular, aerial mycelium pale olivaceous grey, floccose to woolly, olivaceous; reverse brownish olivaceous, greyish hazel. Colonies on PDA, 50–60 mm diam after 1 wk, margin regular, floccose to woolly, pale grey to hazel; reverse hazel to pale salmon, dark brown dots forming by pycnidia. Application of NaOH results in a pale brownish green discolouration of the agar.

Typus: **China**, Qinghai Province, Menyuan County, Xianmi National Forest Park, from leaf spots on *Geum* sp. (*Rosaceae*), 8 Aug. 2019, L.W. Hou (**holotype** HMAS 248351, dried culture, culture ex-type CGMCC 3.20068 = LC13581).

Notes: *Didymella gei* formed a distinct lineage sister to *Di. aquaticae* and *Di. macrophylla* (Fig. 24). Morphologically, the conidiogenous

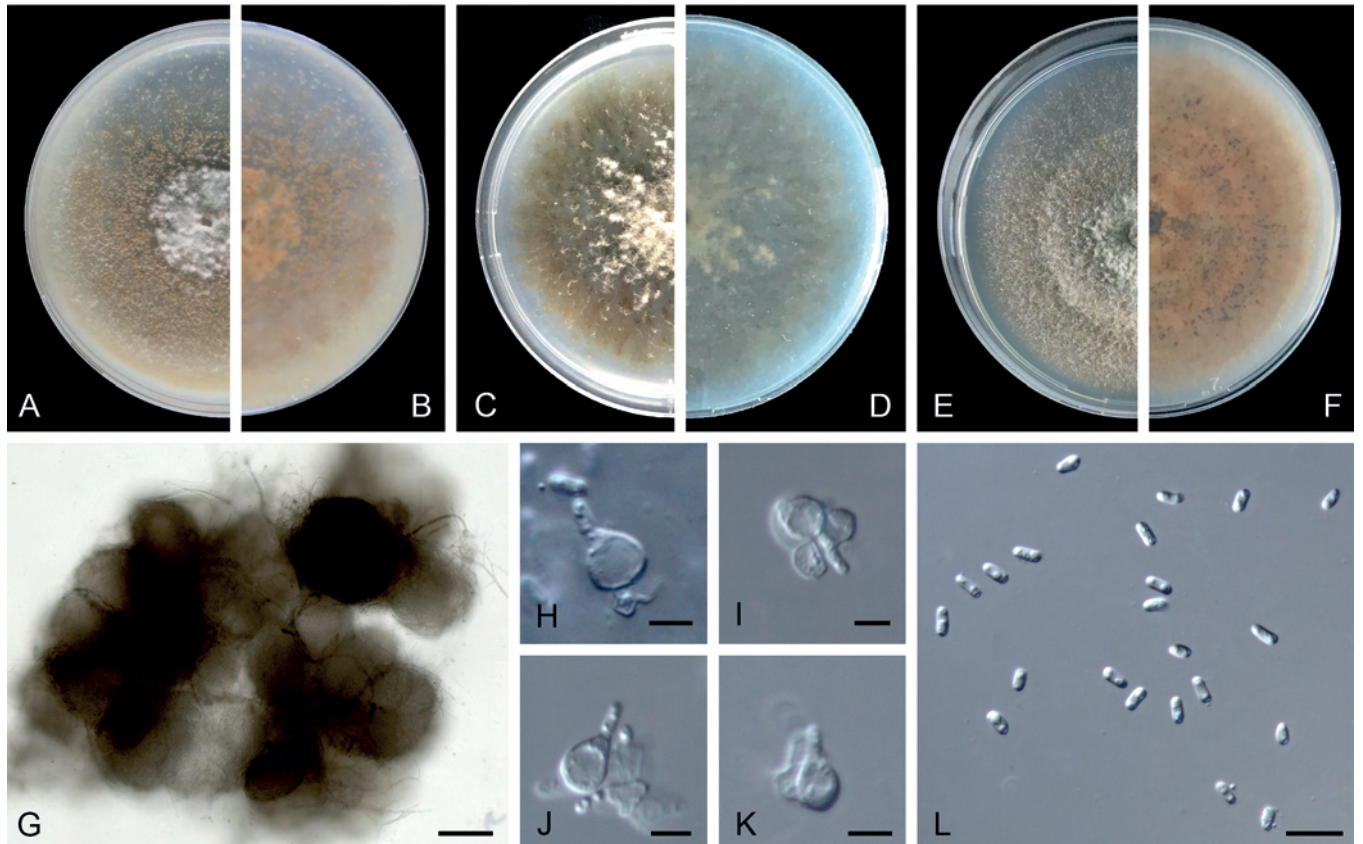


Fig. 26. *Didymella gei* (ex-type CGMCC 3.20068). **A, B.** Colony on OA (front and reverse). **C, D.** Colony on MEA (front and reverse). **E, F.** Colony on PDA (front and reverse). **G.** Conidiomata. **H–K.** Conidiogenous cells. **L.** Conidia. Scale bars: G = 100 μ m; L = 10 μ m; H–K = 5 μ m.

cells of *Di. gei* (5–8.5 \times 4–7 μ m) are larger than those of *Di. aquatica* (4–5 \times 3.5–5 μ m). In addition, the ostiole of *Di. gei* is inconspicuous, while the latter have 2–13 ostioles on pycnidia (Chen *et al.* 2017). *Didymella gei* also differs from *Di. macrophylla* in the NaOH test (a pale brownish green discolouration vs. negative).

Didymella ligulariae Qian Chen & L. Cai, **sp. nov.** MycoBank MB 834957. Fig. 27.

Etymology: Named after the host genus *Ligularia*, from which the holotype of the species was isolated.

Conidiomata pycnidial, mostly solitary, sometimes 2–3 aggregated, globose to subglobose, dark brown, glabrous or with few hyphal outgrowths, superficial or (semi-)immersed, 95–260 \times 75–190 μ m; **ostiole** single, papillate, sometimes elongated to a wide short neck, pale brown; **conidiomatal wall** pseudoparenchymatous, 3–5-layered, 15.5–30 μ m thick, composed of oblong or isodiametric cells, outer two layers slightly pigmented. **Conidiogenous cells** phialidic, hyaline, smooth, ampulliform to doliiform, 5.5–8.5 \times 4–7.5 μ m. **Conidia** oblong to cylindrical, ovoid, incidentally slightly curved, smooth- and thin-walled, hyaline, aseptate, 6–10 \times 2.5–4 μ m, with large guttules. **Conidial exudates** not recorded. **Chlamydozoospores** unicellular, pale brown, intercalary, in chains, globose to subglobose, 8.5–23 μ m diam, thick-walled.

Culture characteristics: Colonies on OA, 40–50 mm diam after 1 wk, margin regular, floccose, white aerial mycelium, smoky grey near the centre, buff to pale brown near the margin; reverse buff to pale salmon, olivaceous brown near the centre. Colonies on MEA

45–50 mm diam after 1 wk, margin regular, with scant floccose aerial mycelium, buff; reverse white to buff, with olivaceous shade. Colonies on PDA, 15–40 mm diam after 1 wk, margin regular, covered by woolly, flat, pale grey aerial mycelium, grey near the centre, with several concentric rings forming by aerial mycelium; reverse hazel to brown, with some concentric rings, buff towards the margin. Application of NaOH results in a pale yellowish green discolouration on OA.

Typus: **China**, Qinghai Province, Menyuan County, Xianmi National Forest Park, on diseased leaves of *Ligularia sibirica* (Asteraceae), 8 Aug. 2019, M. Li (**holotype** HMAS 248353, dried culture, culture ex-type CGMCC 3.20070 = LC 13583).

Notes: *Didymella ligulariae* clustered in a well-supported clade (MLBS = 94 %; BPP = 1) containing *Di. aquatica*, *Di. bellidis*, *Di. brunneospora*, *Di. gei*, *Di. infuscatispora*, *Di. macrophylla*, *Di. segeticola*, *Di. senecionicola*, *Di. suiyangensis* and *Di. uniseptata* (Fig. 24). *Didymella ligulariae* can be differentiated from all these species by the production of chlamydozoospores, and differs from *Di. aquatica*, *Di. segeticola* and *Di. suiyangensis* in producing larger conidiogenous cells (5.5–8.5 \times 4–7.5 μ m vs 4–5 \times 3.5–5 μ m, 5–6.5 \times 4–5.5 μ m and 4–4.5 \times 3–4 μ m), from *Di. bellidis*, *Di. brunneospora*, *Di. gei*, *Di. macrophylla* and *Di. senecionicola* in producing larger conidia (6–10 \times 2.5–4 μ m vs 3.8–6.4 \times 1.8–2.6 μ m, 4.5–7 \times 3–3.5 μ m, 4–6.5 \times 2–2.5 μ m, 3.5–5.5 \times 1.5–2.5 μ m and 4–6.4 \times 1.6–2.4 μ m), and from *Di. infuscatispora* and *Di. uniseptata* in the colour of conidia (hyaline vs hyaline to brown) (de Gruyter *et al.* 1993, Chen *et al.* 2015c, 2017, Valenzuela-Lopez *et al.* 2018). *Didymella ligulariae* is the first species of *Didymella* described from the plant genus *Ligularia*.

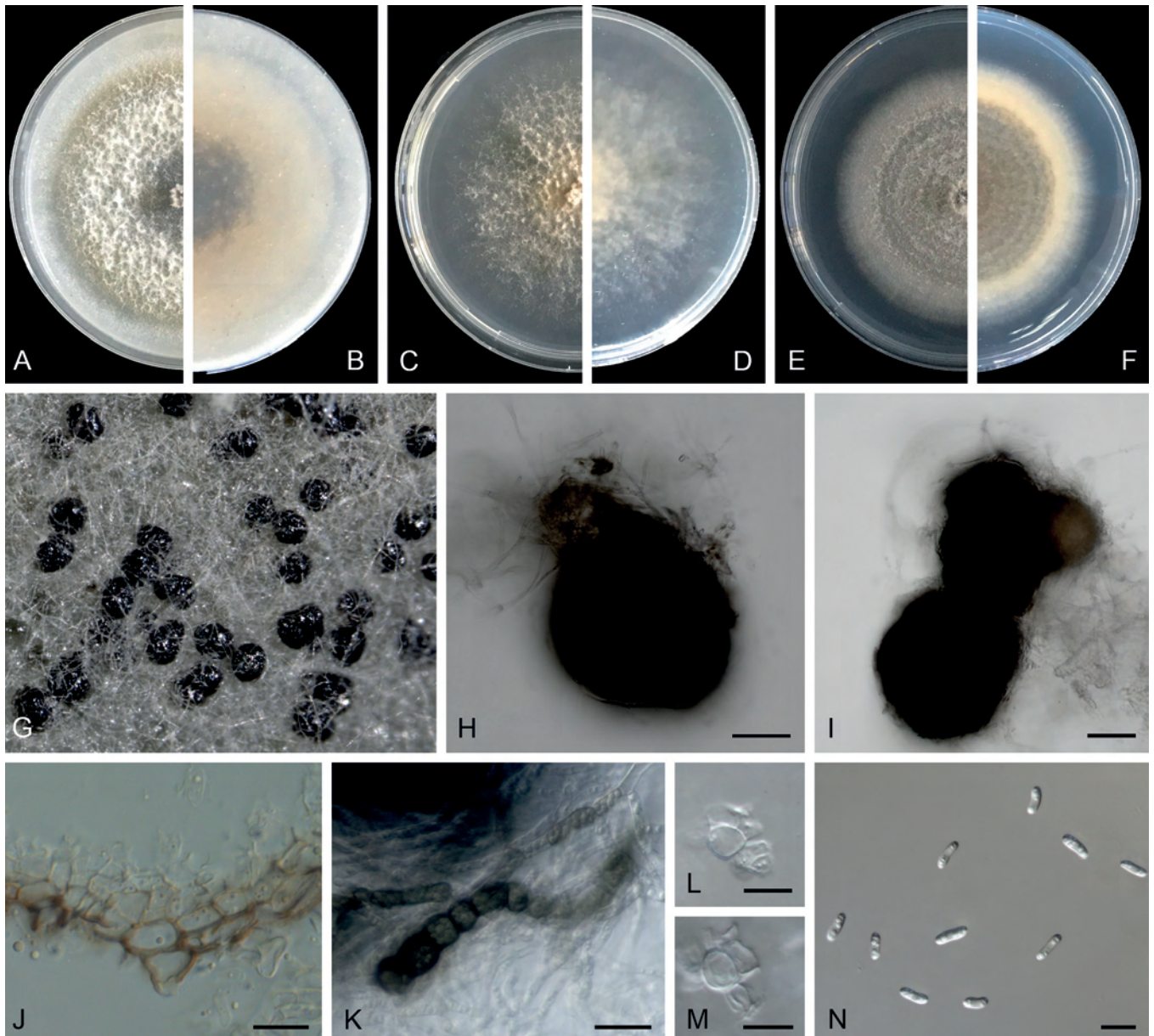


Fig. 27. *Didymella ligulariae* (ex-type CGMCC 3.20070). **A, B.** Colony on OA (front and reverse). **C, D.** Colony on MEA (front and reverse). **E, F.** Colony on PDA (front and reverse). **G.** Conidiomata sporulating on OA. **H, I.** Conidiomata. **J.** Section of conidiomatal wall. **K.** Chlamydospores. **L, M.** Conidiogenous cells. **N.** Conidia. Scale bars: H, I = 50 µm; K = 20 µm; J, L–N = 10 µm.

Didymella qilianensis Qian Chen & L. Cai, **sp. nov.** MycoBank MB 834958. Fig. 28.

Etymology: Epithet derived from the location of origin, Qilian County, Qinghai Province in China.

Conidiomata pycnidial, solitary or aggregated, globose to subglobose, pale brown, glabrous, superficial on the agar or semi-immersed, 75–310 × 65–225 µm; **ostiole** single, slightly papillate; **conidiomatal wall** pseudoparenchymatous 2–4-layered, 15.5–28 µm thick, composed of isodiametric cells. **Conidiogenous cells** phialidic, hyaline, smooth, flask-shaped, ampulliform to doliiform, 4.5–8 × 3–6.5 µm. **Conidia** oval, oblong, ovoid, smooth- and thin-walled, hyaline, aseptate, 3.5–7.5(–13.5) × 2–3.5 µm, with several polar guttules. **Conidial matrix** whitish cream.

Culture characteristics: Colonies on OA, 50–55 mm diam after 1 wk, margin regular, floccose to woolly, white aerial mycelium,

smoky grey, with buff to pale salmon concentric rings forming by the conidial exudate; reverse smoky grey to leaden dark, buff near the centre, white to pale purple near the margin. Colonies on MEA 40–45 mm diam after 1 wk, margin regular, floccose aerial mycelium, olivaceous; reverse concolourous. Colonies on PDA, 45–50 mm diam after 1 wk, margin regular, floccose to woolly, pale greyish olivaceous to olivaceous, pale salmon near the centre forming by the conidial exudate, pale brown near the margin; reverse dull green. Application of NaOH results in a pale yellowish green discolouration of the agar.

Typus: **China**, Qinghai Province, Qilian County, Ladong, from leaf spots on *Rheum officinale* (*Polygonaceae*), 9 Aug. 2019, L.W. Hou (**holotype** HMAS 248354, dried culture, culture ex-type CGMCC 3.20071 = LC 13585).

Additional material examined: **China**, Qinghai Province, Qilian County, Ladong, from leaf spots on *Rheum officinale* (*Polygonaceae*), 9 Aug. 2019, L.W. Hou, culture LC 13584.

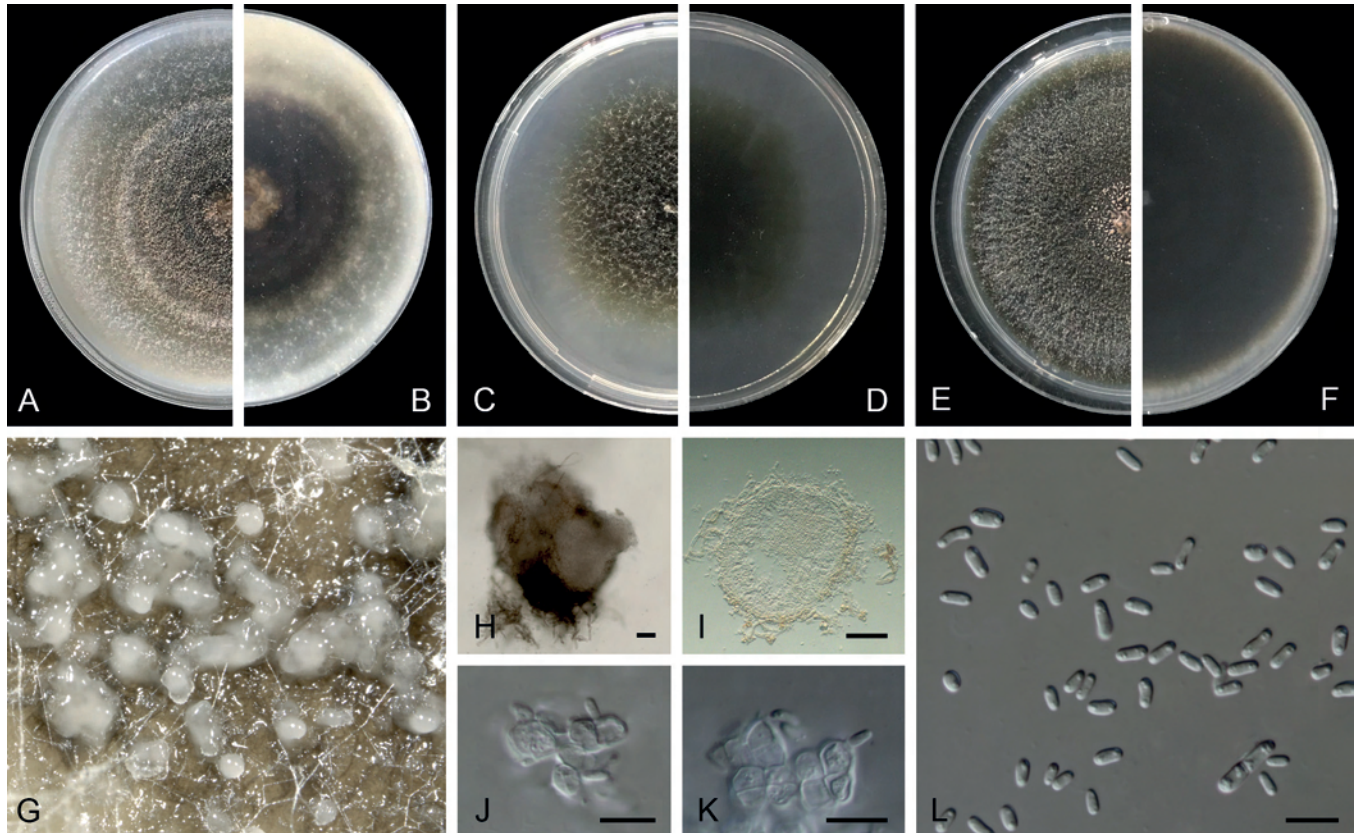


Fig. 28. *Didymella qilianensis* (ex-type CGMCC 3.20071). **A, B.** Colony on OA (front and reverse). **C, D.** Colony on MEA (front and reverse). **E, F.** Colony on PDA (front and reverse). **G.** Conidiomata sporulating on OA. **H.** Conidiomata. **I.** Section through conidiomata. **J, K.** Conidiogenous cells. **L.** Conidia. Scale bars: H, I = 50 μ m; J–L = 10 μ m.

Notes: *Didymella qilianensis* is closely related to *Di. rhei* (Fig. 24) but differs from the latter species mainly in DNA sequences of *rpb2* and *tub2*. Moreover, *Di. qilianensis* produces narrower conidiogenous cells (4.5–8 \times 3–6.5 μ m) than those of *Di. rhei* (3–8 \times 5–8.5 μ m). The NaOH spot test on OA showed a pale yellowish green discolouration of *Di. qilianensis*, while it proved negative for *Di. rhei* (de Gruyter *et al.* 2002).

Didymella uniseptata Qian Chen & L. Cai, **sp. nov.** MycoBank MB 834959. Fig. 29.

Etymology: Name reflects the fact that conidia are 1-septate.

Conidiomata pycnidial, mostly solitary, sometimes several aggregated, globose to subglobose, dark brown, glabrous or with few hyphal outgrowths, abundant, scattered, mostly produced on the surface, but sometimes partly in the agar, 215–525 \times 210–445 μ m; **ostiole** inconspicuous; **conidiomatal wall** pseudoparenchymatous 2–6-layered, 16.5–36 μ m thick, composed of isodiametric cells, outer 2–3 cell layers slightly pigmented. **Conidiogenous cells** phialidic, hyaline, smooth, ampulliform to doliiform, 8.5–16.5 \times 6–11.5 μ m. **Conidia** ellipsoidal, ovoid, smooth- and thin-walled, hyaline, later becoming pale brown to brown, 0–1-septate, 8–13 \times 4.5–6.5 μ m, with numerous minute guttules. Conidial exudates not recorded.

Culture characteristics: Colonies on OA, 40–50 mm diam after 1 wk, margin irregular, aerial mycelium sparse, hazel to pale olivaceous, with an irregular black zone near the centre forming by abundant black pycnidia; reverse concolourous. Colonies on MEA 25–30 mm diam after 1 wk, margin regular, aerial mycelium sparse, woolly, white

to pale olivaceous; reverse concolourous. Colonies on PDA, 25–35 mm diam after 1 wk, margin regular, woolly, compact, buff, abundant black pycnidia visible, forming a concentric ring near the centre, white near the margin; reverse buff, black dots and a concentric ring forming by pycnidia. NaOH spot test negative on OA.

Typus: **China**, Qinghai Province, Datong County, Yaozigou National Forest Park, from leaf spots on *Syringa vulgaris* (*Oleaceae*), 6 Aug. 2019, L.W. Hou (**holotype** HMAS 248352, dried culture, culture ex-type CGMCC 3.20069 = LC 13582).

Notes: *Didymella uniseptata* and *Di. infuscatispora* clustered in a well-supported clade (Fig. 24). Morphologically, *Di. uniseptata* can be easily differentiated from the latter by producing larger conidiogenous cells (8.5–16.5 \times 6–11.5 μ m vs 6–8.5 \times 5.5–8 μ m) and conidia (8–13 \times 4.5–6.5 μ m vs 5–8.5 \times 3.5–5.5 μ m; Chen *et al.* 2017).

Genome sequenced strain: *Didymella exigua*. **France**, Menise sur Tholon, from *Rumex alpestris* (= *Rumex arifolius*), deposited in CBS May 1955, E. Müller, culture ex-neotype CBS 183.55. This Whole Genome Shotgun project has been deposited at GenBank under the accession JALRMG000000000 (BioProject: PRJNA827019, BioSample: SAMN27594415; present study).

Authors: Q. Chen & L. Cai

Endothia Fr., Sum. Veg. Scand: 385. 1849. Fig. 30.

Classification: Sordariomycetes, Sordariomycetidae, Diaporthales, Cryphonectriaceae.

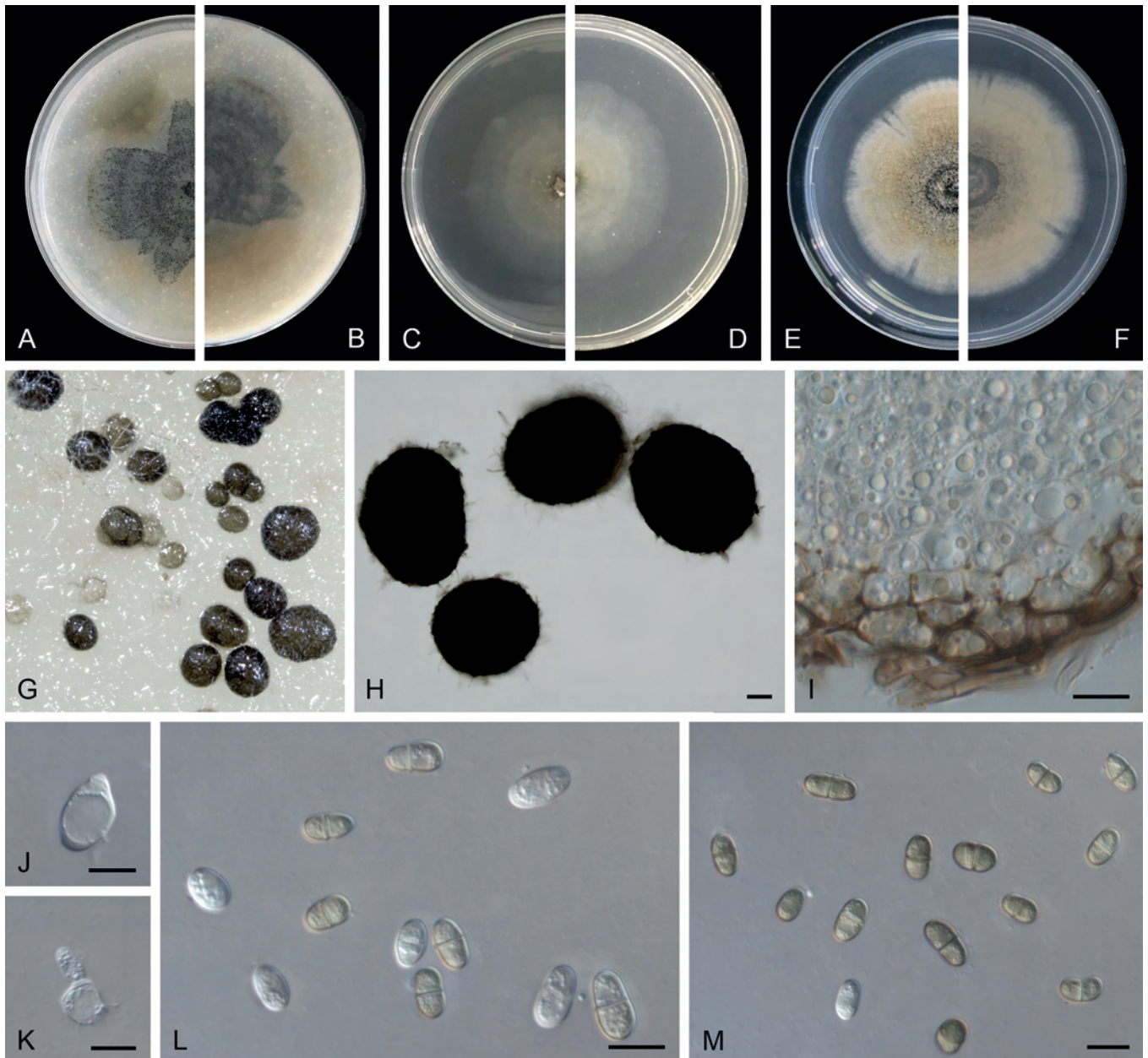


Fig. 29. *Didymella uniseptata* (ex-type CGMCC 3.20069). **A, B.** Colony on OA (front and reverse). **C, D.** Colony on MEA (front and reverse). **E, F.** Colony on PDA (front and reverse). **G.** Conidiomata sporulating on OA. **H.** Conidiomata. **I.** Section of conidiomatal wall. **J, K.** Conidiogenous cells. **L, M.** Conidia. Scale bars: H = 50 µm; I-M = 10 µm.

Type species: *Endothia gyrosa* (Schwein.: Fr.) Fr., basionym: *Sphaeria gyrosa* Schwein.; *Melogramma gyrosum* (Schwein.: Fr.) Tul. & C. Tul.; *Endothia gyrosum* (Schwein.: Fr.) Fuckel. Holotype could not be located, and a neotype from USA is required. Representative strains: CBS 112915 = CMW 2091, CBS 118850 = CMW 10442.

DNA barcodes (genus): LSU, ITS.

DNA barcodes (species): ITS, *tef1*, *tub1*, *tub2*. Table 9. Fig. 31.

Ascostromata large, erumpent, pulvinate to clavate, superficial to semi-immersed to immersed in bark, orange, upper region eustromatic, lower region pseudostromatic. **Stromatic tissues** pseudoparenchymatous on edge of stroma, prosenchymatous in centre. **Perithecia** usually diatrypoid, embedded in stromata at irregular levels, fuscous black. **Perithecial necks** emerge at

stromatal surface as black ostioles covered with orange stromatal tissue to form papillae. **Asci** 8-spored, fusiform. **Ascospores** hyaline, cylindrical to fusoid, aseptate. **Conidiomata** part of ascostromata as conidial locules or as separate structures, large, pulvinate, superficial to semi-immersed, orange, multiloculate, non-ostiolate. **Conidiophores** cylindrical or flask-shaped, occasionally with separating septa and branching. **Conidiogenous cells** phialidic. **Paraphyses** or **cylindrical sterile cells** absent. **Conidia** minute, hyaline, cylindrical, aseptate, exuded as orange to sienna droplets.

Culture characteristics: Colonies grown on MEA and PDA showing abundant floccose aerial mycelia, white, yellow white, buff to cinnamon when immature, margins smooth or crenate.

Optimal media and cultivation conditions: *Endothia cerciana*, *E. chinensis*, *E. gyrosa*, *E. singularis*, all display optimal growth on 2% MEA or 1.8% PDA at 25 °C.

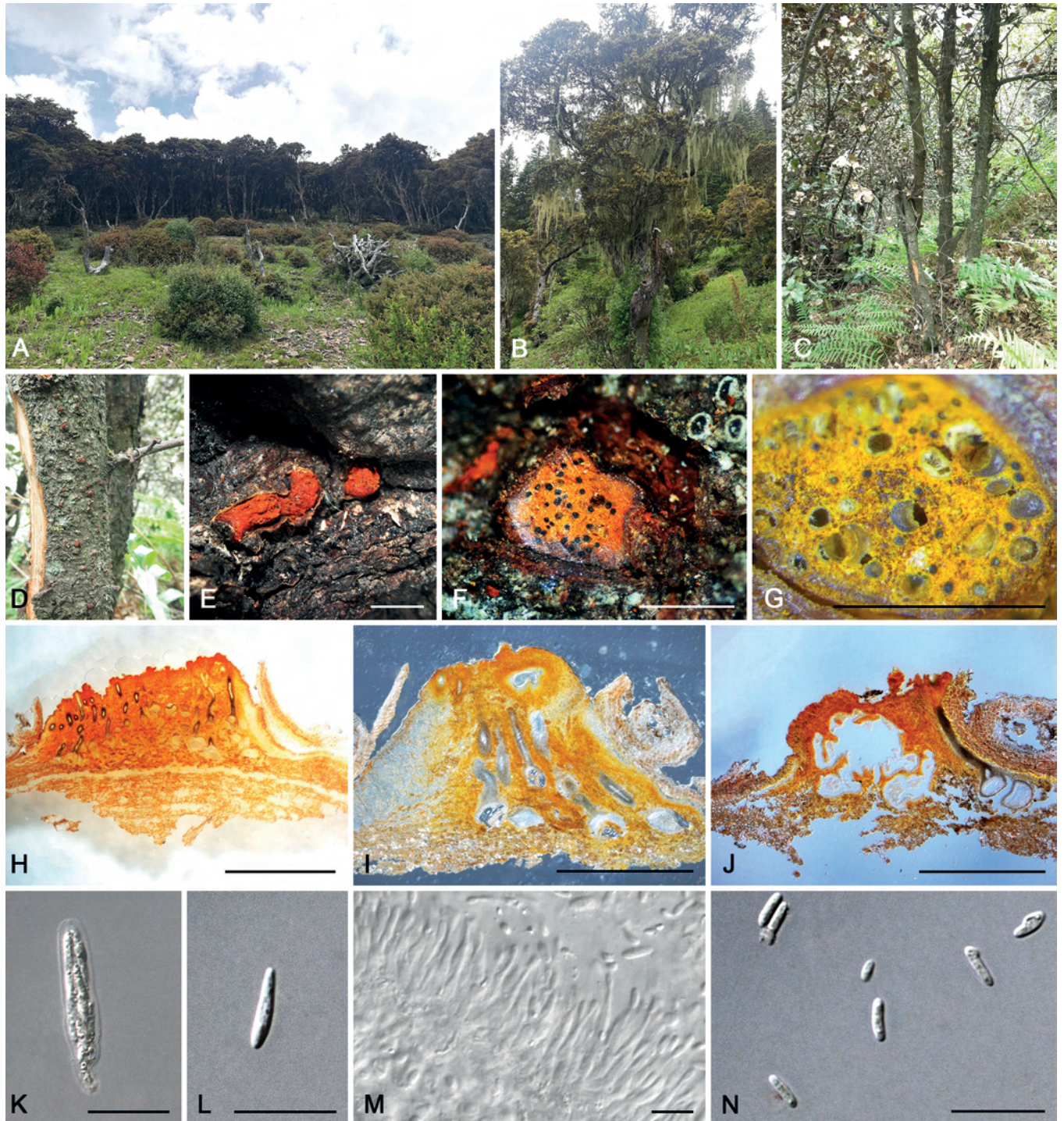


Fig. 30. *Endothia* spp. **A–C.** Host of *Endothia cerciana*. **A, B.** *Quercus aquifolioides*. **C.** *Quercus semecarpifolia*. **D.** Disease symptoms of *Endothia cerciana* on *Quercus semecarpifolia*, showing fruiting structures on bark. **E.** Orange fruiting structures of *Endothia cerciana* on *Quercus semecarpifolia*. **F, G.** Transverse section through ascostromata. **F.** *Endothia cerciana* (HMAS 255732). **G.** *Endothia chinensis* (BJFC-S1432). **H, I.** Longitudinal section through ascostromata of *Endothia cerciana* (HMAS 255732). **J.** Longitudinal section through conidiomata and ascostromata of *Endothia cerciana* (HMAS 255732). **K.** Ascus of *Endothia cerciana* (HMAS 255732). **L.** Ascospore of *Endothia cerciana* (HMAS 255732). **M.** Conidiophores of *Endothia gyrosa* (not available). **N.** Conidia of *Endothia cerciana* (HMAS 255732). Scale bars: E–J = 1 mm; K–N = 10 µm. Picture G taken from Jiang *et al.* (2019b); M from Gryzenhout *et al.* (2009).

Distribution: China, USA.

Hosts: *Acer* (*Aceraceae*), *Castanea*, *Fagus*, *Quercus* (*Fagaceae*), *Corylus* (*Corylaceae*), *Ilex* (*Aquifoliaceae*), *Liquidambar* (*Hamamelidaceae*), *Prunus* (*Rosaceae*), *Ulmus* (*Ulmaceae*) and *Vitis* (*Vitaceae*).

Disease symptoms: Cankers on branches, stems or roots, die-back and defoliation.

Notes: *Endothia* presents the oldest generic name in the *Cryphonectriaceae* (Fries 1849). Previously, *Cryphonectria* was treated as a synonym of *Endothia* (Shear *et al.* 1917, Kobayashi 1970, Roane 1986), and the genus *Endothia* has accommodated most of the known species of *Cryphonectria* and *Endothia* (Micales & Stipes 1987). Currently, *Endothia* and *Holocryphia* are the only genera in *Cryphonectriaceae* with aseptate ascospores. These two genera can be distinguished by their stromatal structures: the stromata of *Endothia* are large, erumpent, and no paraphyses

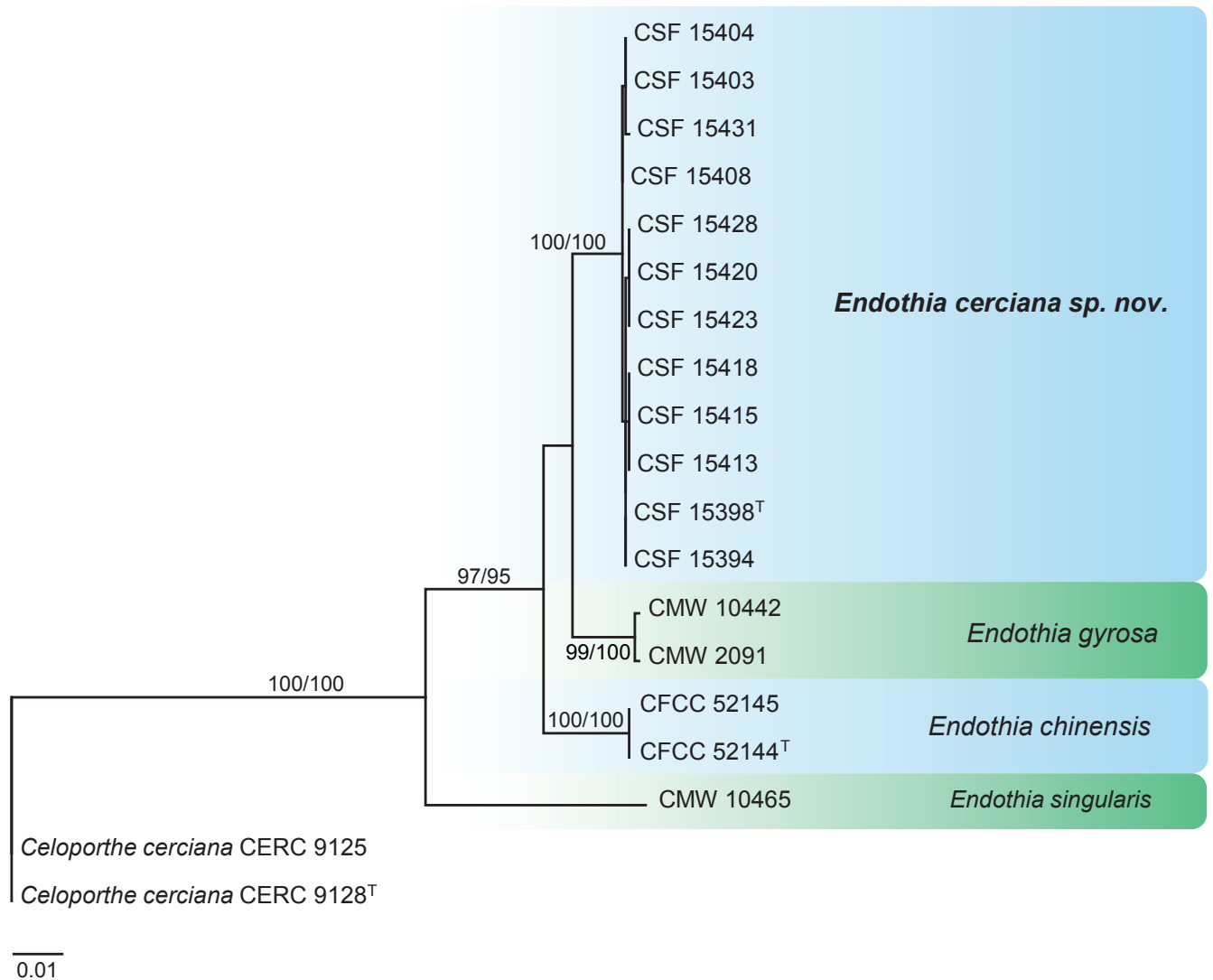


Fig. 31. Maximum Likelihood (ML) phylogram constructed from ITS (480 bp), *tub2* (360 bp), *tub1* (410 bp) and *tef1* (185 bp) sequences of all accepted species of *Endothia*. Bootstrap support values (> 70 %) for ML and maximum parsimony (MP) analyses are presented at the nodes (ML/MP). The novel taxon is printed in **bold**. The phylogenetic tree was rooted to *Celoportha cerciana* CERC 9125 and CERC 9128^T. GenBank accession numbers are indicated in Table 9. ^T indicates ex-type strains. TreeBASE: S26038.

are produced among conidiophores (Barr 1978, Myburg *et al.* 2004, Gryzenhout *et al.* 2009, Jiang *et al.* 2019b), while stromata of *Holocryphia* are smaller, and prominent paraphyses are present among conidiophores (Venter *et al.* 2002, Gryzenhout *et al.* 2009). Four species reside in *Endothia*, i.e. *E. cerciana*, *E. chinensis*, *E. gyrosa* and *E. singularis* (Fries 1849, Shear *et al.* 1917, Gryzenhout *et al.* 2009, Jiang *et al.* 2019b). Although some morphological differences exist among these species, such as sizes of ascospores and conidia, DNA sequence data are essential to species identifications (Venter *et al.* 2002, Myburg *et al.* 2004, Gryzenhout *et al.* 2009, Jiang *et al.* 2019b). The ITS and *tub* (*tub1* and *tub2*) regions provide accurate species resolution when used alone, and the combination of these regions provide stronger support (Venter *et al.* 2002, Myburg *et al.* 2004, Gryzenhout *et al.* 2009, Jiang *et al.* 2019b). *Endothia gyrosa* was the first species described from what now represents the *Cryphonectriaceae* (Fries 1849). This species has been reported from many different woody plant hosts, including species of *Acer*, *Castanea*, *Corylus*, *Fagus*, *Ilex*, *Liquidambar*, *Prunus*, *Quercus*, *Ulmus* and *Vitis* (Shear *et al.* 1917, Snow *et al.* 1974, Roane 1986) and it has an extensive distribution in North America (Shear *et al.* 1917). *Endothia singularis* was reported from several species of *Quercus* in the USA

(Gryzenhout *et al.* 2009). *Endothia cerciana* and *E. chinensis* were both only reported in China, *E. cerciana* from *Quercus aquifolioides* and *Q. semecarpifolia*, and *E. chinensis* from *Castanea mollissima* (Jiang *et al.* 2019b). *Endothia gyrosa* caused cankers on branches, stems or roots that results in die-back, defoliation and decline of trees (Stipes & Phipps 1971, Roane *et al.* 1974), and *E. chinensis* is pathogenic to detached *C. mollissima* branches (Jiang *et al.* 2019b), but whether *E. cerciana* is pathogenic to its original hosts is unknown.

References: Venter *et al.* 2002, Myburg *et al.* 2004, Gryzenhout *et al.* 2009, Jiang *et al.* 2019b (morphology, nomenclature, phylogeny and pathogenicity); Gryzenhout *et al.* 2006, 2009, Wang *et al.* 2020b, Jiang *et al.* 2020 (higher classification).

Endothia cerciana W. Wang & S.F. Chen, **sp. nov.** MycoBank MB 842889. Fig. 32.

Etymology: The name refers to CERC, a research institute that is pioneering the study of tree diseases caused by *Cryphonectriaceae* in China.

Table 9. DNA barcodes of accepted *Endothia* spp.

Species	Isolates ¹	GenBank accession numbers ²				References
		ITS	<i>tub2</i>	<i>tub1</i>	<i>tef1</i>	
<i>Endothia cerciana</i>	CSF 15394	OM801200	OM685025	OM685037	OM685049	Present study
	CSF 15398 = CGMCC 3.20105 [†]	OM801201	OM685026	OM685038	OM685050	Present study
	CSF 15403	OM801202	OM685027	OM685039	OM685051	Present study
	CSF 15404	OM801203	OM685028	OM685040	OM685052	Present study
	CSF 15408	OM801204	OM685029	OM685041	OM685053	Present study
	CSF 15413	OM801205	OM685030	OM685042	OM685054	Present study
	CSF 15415	OM801206	OM685031	OM685043	OM685055	Present study
	CSF 15418	OM801207	OM685032	OM685044	OM685056	Present study
	CSF 15420 = CGMCC 3.20106	OM801208	OM685033	OM685045	OM685057	Present study
	CSF 15423	OM801209	OM685034	OM685046	OM685058	Present study
	CSF 15428	OM801210	OM685035	OM685047	OM685059	Present study
	CSF 15431	OM801211	OM685036	OM685048	OM685060	Present study
	<i>E. chinensis</i>	CFCC 52144 [†]	MH514027	MH539690	MH539680	MN271860
CFCC 52145		MH514028	MH539691	MH539681	—	Jiang <i>et al.</i> (2019b, 2020)
<i>E. gyrosa</i>	CMW 2091 = CBS 112915	AF368325	AH011601	AH011601	—	Venter <i>et al.</i> (2002), Gryzenhout <i>et al.</i> (2006)
	CMW 10442 = CBS 118850	AF368326	AH011602	AH011602	—	Venter <i>et al.</i> (2002), Gryzenhout <i>et al.</i> (2006)
<i>E. singularis</i>	CMW 10465 = CBS 112921	AF368323	AH011599	AH011599	—	Venter <i>et al.</i> (2002), Myburg <i>et al.</i> (2004)

¹ CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, Netherlands; CSF: Collections at China Eucalypt Research Centre, Chinese Academy of Forestry, Zhanjiang, Guangdong, China; CFCC: China Forestry Culture Collection Center, Beijing, China; CGMCC: Chinese General Microbiological Culture Collection Center, Beijing, China; CMW: Tree Protection Co-operative Program, Forestry and Agricultural Biotechnology Institute, University of Pretoria, South Africa. [†] indicates ex-type strain.

² ITS: internal transcribed spacers and intervening 5.8S nrDNA; *tef1*: partial translation elongation factor 1- α gene; *tub1*, *tub2*: partial β -tubulin gene.

Ascstromata on host single, pulvinate, large, semi-immersed to immersed in bark, orange, 850–1500 μ m high, 800–4250 μ m diam, upper region eustromatic, lower region pseudostromatic. *Stromatic tissues* pseudoparenchymatous on edge of stroma, prosenchymatous in centre. *Perithecia* usually diatrypod, embedded in stromata at irregular levels, fuscous black. *Perithecial necks* emerge at stromatal surface as black ostioles covered with orange stromatal tissue to form papillae extending up to 200 μ m above stromatal surface. *Asci* (21–)24.5–35(–39) \times (4.5–)5–7(–8.5) μ m (av. 30 \times 6 μ m), oblong ellipsoidal to sub-clavate, 8-spored. *Ascospores* (7–)8.5–10.5(–12) \times (1–)1.5–2 μ m (av. 9.5 \times 1.6 μ m), hyaline, ellipsoidal to fusoid, ends round, aseptate. *Conidiomata* part of ascostromata as conidial locules or separate structures, large, pulvinate, semi-immersed to immersed in bark, orange, multiloculate structures with the same tissue morphology, stromatic structure and size to the ascostromata, locules numerous in labyrinthine pattern, non-ostiolate. *Conidiophores* (6–)8–10(–14) μ m long, occasionally with separating septa and branching, hyaline. *Conidiogenous cells* 1–1.5 μ m wide, cylindrical or flask-shaped with attenuated apices. *Paraphyses* or *cylindrical sterile cells* absent. *Conidia* (3.5–)4.5–5.5(–6) \times 1–1.5 μ m (av. 5 \times 1.3 μ m), hyaline, cylindrical, aseptate.

Culture characteristics: Colonies grown on 2 % MEA showing abundant floccose aerial mycelia, white when young, turning buff to cinnamon after 2 wk, margins smooth or crenate; reverse white

to buff, often makes growth medium perilla purple. Optimal growth temperature 25 °C, grow slowly at 5 °C and 35 °C. After 1 wk, the colonies at 5 °C, 10 °C, 15 °C, 20 °C, 25 °C, 30 °C, and 35 °C reached 8.5, 18, 31, 65, 82, 17, and 8 mm, respectively.

Typus: **China**, Sichuan Province, Ganzi Region, Batang County, Moduo Town, Moduo Village, 30°14'0.1032"N, 99°15'19.8252"E, from the stem bark of *Quercus semecarpifolia* (*Fabaceae*), 28 Jun. 2018, S.F. Chen, W. Wang & Q.C. Wang (**holotype** HMAS 255732, culture ex-type CSF 15398 = CGMCC 3.20105).

Additional materials examined: **China**, Sichuan Province, Ganzi Region, Yajiang County, Bajiao Town, Rimu Village, 30°4'22.44"N, 101°9'58.6164"E, from the stem bark of *Quercus aquifolioides* (*Fagaceae*), 30 Jun. 2018, S.F. Chen, W. Wang & Q.C. Wang, HMAS 255733, culture CSF 15420 = CGMCC 3.20106; *ibid.* cultures CSF 15394, CSF 15403, CSF 15404, CSF 15408, CSF 15413, CSF 15415, CSF 15418, CSF 15423, CSF 15428, CSF 15431.

Notes: *Endothia cerciana* isolated from *Quercus* species in China represents a fourth species in this genus (Table 9). It is closely related to *E. gyrosa* in the phylogenetic analysis (Fig. 31). *Endothia cerciana*, *E. chinensis*, *E. gyrosa* and *E. singularis* all produce perithecia embedded in stromata at irregular levels, with paraphyses or cylindrical sterile cells absent (asexual morph is unknown for *E. chinensis*) (Gryzenhout *et al.* 2009, Jiang *et al.* 2019b). Some differences have been observed among the four species in ascospore and conidial dimensions. The ascospores of



Fig. 32. *Endothia cerciana* (ex-type CGMCC 3.20105). **A, B.** Fruiting structures on canker. **C, D.** Transverse section through ascostromata. **E–G.** Longitudinal section through ascostromata. **H, I.** Longitudinal section through conidiomata. **J.** Ascus. **K.** Ascospore. **L.** Conidiophores. **M.** Conidia. **N–Q.** Colonies on 2 % MEA in 1 wk (N: front, O: reverse) and 30 d (P: front, Q: reverse) in dark. Scale bars: A–I = 1 mm; J–M = 10 μ m.

E. gyrosa (av. $10 \times 2 \mu\text{m}$) are longer than *E. cerciana* (av. $9.5 \times 1.6 \mu\text{m}$), *E. chinensis* (av. $8.5 \times 1.5 \mu\text{m}$) and *E. singularis* (av. $9 \times 2.5 \mu\text{m}$), and the ascospores of *E. chinensis* are the smallest, while *E. singularis* are the widest. The conidia of *E. cerciana* (av. $5 \times 1.3 \mu\text{m}$) are narrower than those of *E. gyrosa* (av. $3.75 \times 1.5 \mu\text{m}$) and *E. singularis* (av. $3.5 \times 1.5 \mu\text{m}$) (Gryzenhout *et al.* 2009, Jiang *et al.* 2019b).

Genome sequenced strain: *Endothia cerciana*. China, from the stem bark of *Quercus semecarpifolia*, 28 Jun. 2018, S.F. Chen,

W. Wang & Q.C. Wang, culture ex-type CSF 15398 = CGMCC 3.20105. This Whole Genome Shotgun project has been deposited at GenBank under the accession JALRMH000000000 (BioProject: PRJNA827019, BioSample: SAMN27594416; present study).

Authors: W. Wang & S.F. Chen

Leptosphaerulina McAlpine, Fungus Diseases of stone-fruit trees in Australia: 103. 1902. Fig. 33.



Fig. 33. *Leptosphaerulina* spp. **A–C.** Disease symptoms. **A.** Symptoms caused by *Leptosphaerulina miscanthi* (ex-type CGMCC 3.20073) on *Miscanthus floridulus*. **B.** Symptoms caused by *Leptosphaerulina miscanthi* (LC 13590) on *Swertia tetraptera*. **C.** Symptoms caused by *Leptosphaerulina miscanthi* (LC 13591) on *Sonchus asper*. **D–R.** Sexual morph. **D.** Ascoma with asci of *Leptosphaerulina conyzicola* (ex-type VIC 31627). **E.** Ascoma of *Leptosphaerulina sisyrynchiicola* (ex-type CBS 121688). **F, G.** Sections through ascoma. **F.** *Leptosphaerulina longiflori* (holotype MFLU18-2527). **G.** *Leptosphaerulina obtusispora* (ex-type CBS 569.94). **H–L.** Asci. **H.** *Leptosphaerulina conyzicola* (ex-type VIC 31627). **I.** *Leptosphaerulina saccharicola* (holotype MFLU11-0205). **J.** *Leptosphaerulina longiflori* (holotype MFLU18-2527). **K.** *Leptosphaerulina obtusispora* (ex-type CBS 569.94). **L.** *Leptosphaerulina sisyrynchiicola* (ex-type CBS 121688). **M–R.** Ascospores. **M.** *Leptosphaerulina conyzicola* (ex-type VIC 31627). **N.** *Leptosphaerulina saccharicola* (holotype MFLU11-0205). **O.** *Leptosphaerulina longiflori* (holotype MFLU18-2527). **P.** *Leptosphaerulina obtusispora* (ex-type CBS 569.94). **Q.** *Leptosphaerulina sisyrynchiicola* (ex-type CBS 121688). **R.** *Leptosphaerulina australis* (CBS 116307). Scale bars: E = 50 μm ; D, G, K, L = 20 μm ; F, H, I, P–R = 10 μm ; J, M–O = 5 μm . Pictures D, H, M taken from Duarte *et al.* (2016); E, G, K, L, P, Q from Hou *et al.* (2020a); F, J, O from Tennakoon *et al.* (2019); I, N from Phookamsak *et al.* (2013); R from Crous *et al.* (2011c).

Classification: *Dothideomycetes*, *Pleosporomycetidae*, *Pleosporales*, *Didymellaceae*.

Type species: *Leptosphaerulina australis* McAlpine. Reference strain: CBS 317.83.

DNA barcodes (genus): LSU, ITS.

DNA barcodes (species): *rpb2*, *tub2*. Table 10. Fig. 34.

Ascomata pseudothecial, immersed or erumpent, solitary or clustered, obpyriform to subglobose, globose, membranous, ostiolate; **ascomatal wall** multi-layers, composed of cells in *textura*

angularis. **Asci** clavate to ovoid, or obovoid, subglobose, obpyriform, saccate, oblong, bitunicate, 8-spored. **Ascospores** muriform or phragmosporous, oblong to cylindrical, ellipsoidal to obovoid, subfusoid, hyaline to brown, smooth, 1(–9)-septate (including transverse and longitudinal), sometimes slightly constricted at the septum, biseriate or triseriate, sometimes surrounded by a thin mucilaginous sheath (Saccardo 1905, Graham & Luttrell 1961, Roux 1986, Inderbitzin *et al.* 2000, Abler 2003, Crous *et al.* 2011c, Hou *et al.* 2020a). **Conidiophores** mononematous, solitary, with one apical pore, mostly unbranched, septate, hyaline to pale brown, smooth-walled. **Conidiogenous cells** holoblastic, integrated, terminal, cylindrical, hyaline to brown. **Conidia** solitary thalloconidia, oblong to cylindrical or ellipsoidal, muriform or phragmosporous,

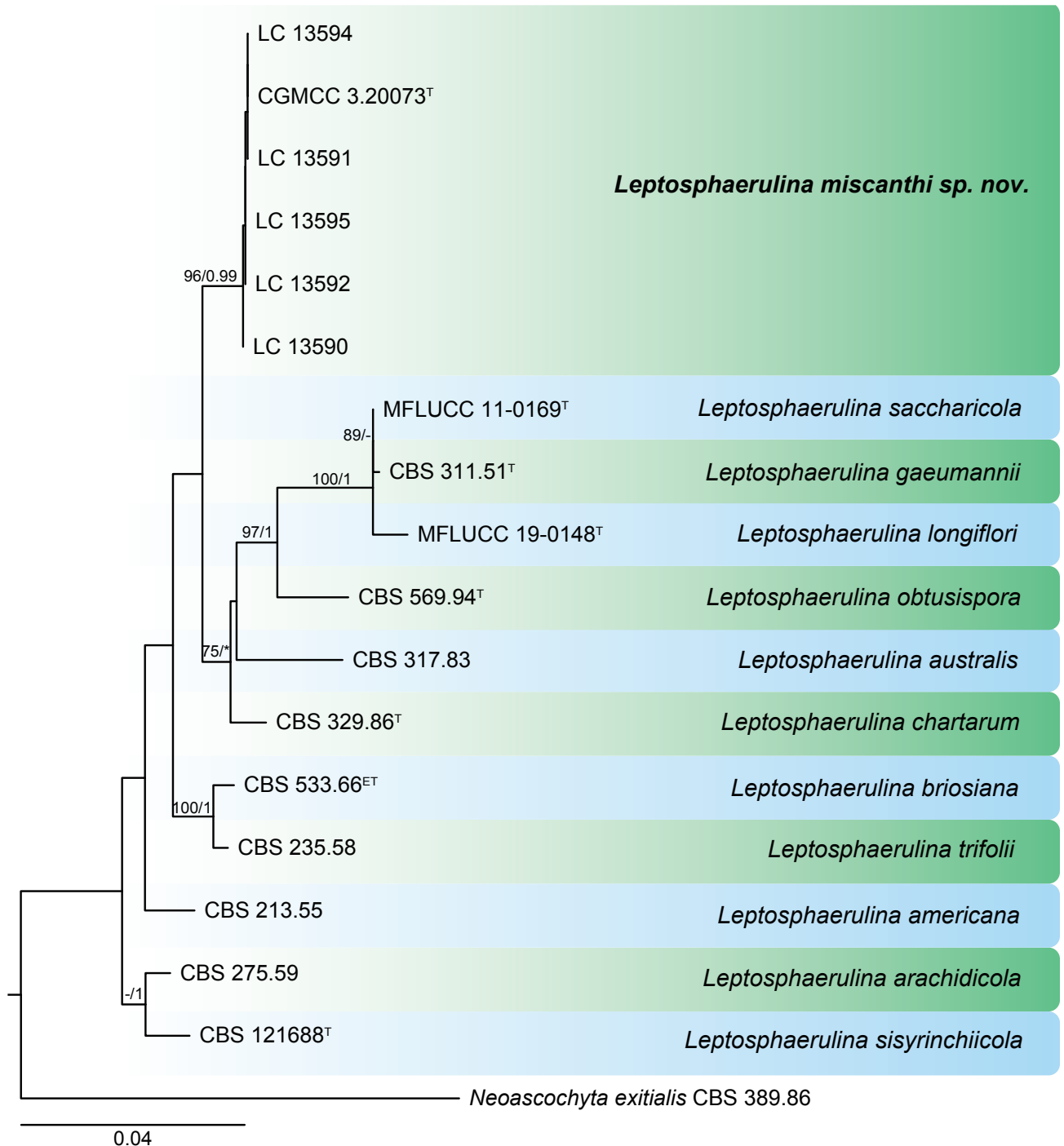


Fig. 34. Maximum Likelihood (ML) phylogram constructed from LSU (960 bp), ITS (453 bp), *tub2* (333 bp) and *rpb2* (596 bp) sequences of all accepted species of *Leptosphaerulina*. RAxML bootstrap support values (> 70 %) and Bayesian posterior probability scores (> 0.90) are shown at the nodes. The novel taxon is printed in **bold**. The phylogenetic tree was rooted to *Neoascochyta exitialis* CBS 389.86. GenBank accession numbers are indicated in Table 10. ^T and ^{ET} indicate ex-type and ex-epitype strains, respectively. TreeBASE: S26039.

Table 10. DNA barcodes of accepted *Leptosphaerulina* spp.

Species	Isolates ¹	GenBank accession numbers ²				References
		LSU	ITS	<i>rpb2</i>	<i>tub2</i>	
<i>Leptosphaerulina americana</i>	CBS 213.55	GU237981	GU237799	KT389641	GU237539	Aveskamp <i>et al.</i> (2010), Chen <i>et al.</i> (2015b)
<i>L. arachidicola</i>	CBS 275.59	GU237983	GU237820	MT018278	GU237543	Aveskamp <i>et al.</i> (2010), Hou <i>et al.</i> (2020a)
<i>L. australis</i>	CBS 317.83	EU754166	GU237829	GU371790	GU237540	de Gruyter <i>et al.</i> (2009), Aveskamp <i>et al.</i> (2010)
<i>L. briosiana</i>	CBS 533.66 ^{ET}	MN943804	EU167575	MT018266	MT005704	Simon <i>et al.</i> (2009), Hou <i>et al.</i> (2020a)
<i>L. chartarum</i>	CBS 329.86 ^T	MN943813	MN973604	MT018277	MT005714	Hou <i>et al.</i> (2020a)
<i>L. gaemannii</i>	CBS 311.51 ^T	MN943810	MN973601	MT018274	MT005711	Hou <i>et al.</i> (2020a)
<i>L. longiflori</i>	MFLUCC 19-0148 ^T	MK503811	MK503800	MK503805	—	Tennakoon <i>et al.</i> (2019)
<i>L. miscanthi</i>	LC 13590	MT229680	MT229703	MT239100	MT249271	Present study
	LC 13591	MT229681	MT229704	MT239101	MT249272	Present study
	LC 13592	MT229682	MT229705	MT239102	MT249273	Present study
	CGMCC 3.20073 = LC 13593 ^T	MT229683	MT229706	MT239103	MT249274	Present study
	LC 13594	MT229684	MT229707	MT239104	MT249275	Present study
<i>L. obtusispora</i>	LC 13595	MT229685	MT229708	MT23910	MT249276	Present study
	CBS 569.94 ^T	MN943811	MN973602	MT018275	MT005712	Hou <i>et al.</i> (2020a)
<i>L. saccharicola</i>	MFLUCC 11-0169 ^T	KF670716	KF670717	KF670714	—	Phookamsak <i>et al.</i> (2013)
<i>L. sisyrinchicola</i>	CBS 121688 ^T	MN943814	MN973605	MT018279	MT005715	Hou <i>et al.</i> (2020a)
<i>L. trifolii</i>	CBS 235.58	GU237982	GU237806	MT018271	GU237542	Aveskamp <i>et al.</i> (2010), Hou <i>et al.</i> (2020a)

¹ CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CGMCC: Chinese General Microbiological Culture Collection Center, Beijing, China; LC: Dr Lei Cai's personal collection deposited in laboratory, housed at Chinese Academy of Sciences, China; MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand. ^T and ^{ET} indicate ex-type and ex-epitype strains, respectively.

² ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial 28S large subunit nrRNA gene; *rpb2*: partial RNA polymerase II second largest subunit gene; *tub2*: partial β -tubulin gene.

initially hyaline, becoming brown to dark brown, mostly with 3–4 transverse septa and 0–1 longitudinal septa (Phookamsak *et al.* 2013).

Cultural characteristics: Colonies on OA covered by flat aerial mycelium, pale olivaceous to olivaceous black, sometimes dirty white near the centre, olivaceous grey to iron-grey near the margin, margin regular.

Optimal media and cultivation conditions: OA or sterile pine needles placed on OA under nuv-light (12 h light, 12 h dark) to promote sporulation at 20 to 25 °C.

Distribution: Worldwide.

Hosts: Occurring on forage plants as saprobes and pathogens, mainly found in members of *Fabaceae*, and also on other plants of *Aizoaceae*, *Asteraceae*, *Caprifoliaceae*, *Gentianaceae*, *Iridaceae*, *Liliaceae*, *Myrtaceae*, *Poaceae*, *Rhizophoraceae*, *Rosaceae* and *Vitaceae*.

Disease symptoms: Leaf blight, leaf scorch, leaf spot, pepper spot, stem spots.

Notes: *Leptosphaerulina* comprises plant pathogenic species that cause leaf spot and pepper spot mainly on legumes and turfgrasses, and saprophytes on decaying or dead branches, stems or leaves (Graham & Luttrell 1961, Inderbitzin *et al.* 2000, Abler 2003, Phookamsak *et al.* 2013, Chen *et al.* 2015b, Tennakoon *et al.* 2019). This genus is well characterised by small, immersed-erumpent ascomata, bitunicate, saccate, obpyriform or oblong asci, and muriform, hyaline or pigmented ascospores (Graham & Luttrell 1961, Barr 1972, Chen *et al.* 2015b, Tennakoon *et al.* 2019). *Leptosphaerulina chartarum* was reported to be the sexual morph of *Pithomyces chartarum* (Roux 1986), but this has been refuted by molecular evidence. Recent phylogenetic studies showed that the genus *Pithomyces* resided in the family *Astrosphaeriellaceae*, clearly distant from *Didymellaceae* (Pratibha & Prabhugaonkar 2015, Wanasinghe *et al.* 2019). To date, the asexual morph of *Leptosphaerulina* was only recorded for *L. saccharicola* by Phookamsak *et al.* (2013), which produced hyaline to brown, muriform or phragmosporous conidia from mononematous conidiophores on hyphae. Among the names under *Leptosphaerulina*, 13 have been recognised based on both morphology and molecular data. Nevertheless, *L. conyzicola* from the weed *Conyza canadensis* was not included in the phylogenetic tree, because only LSU sequence data are available (Duarte *et al.* 2016).

References: Graham & Luttrell 1961, Roux 1986, Inderbitzin *et al.* 2000, Abler 2003, Crous *et al.* 2011c, Phookamsak *et al.* 2013, Tennakoon *et al.* 2019, Hou *et al.* 2020a (morphology and pathogenicity); de Gruyter *et al.* 2009, Aveskamp *et al.* 2010, Chen *et al.* 2015b (phylogeny).

Leptosphaerulina miscanthi Qian Chen & L. Cai, *sp. nov.*
Mycobank MB 834960. Fig. 35.

Etymology: Name after *Miscanthus*, the grass genus from which it was collected.

Ascomata pseudothecial, superficial or semi-immersed, solitary or aggregated, uniloculate, globose to subglobose, membranous, brown, 165–330 × 125–210 µm; *ostioles* circular, central, papillate; *pseudothecial wall pseudoparenchymatous*, of *textura angularis*, 2–4 layers, outer wall 2–3-layered, brown, 17–48 µm thick. *Pseudoparaphyses* not observed. *Asci* hyaline, subclavate, saccate, obpyriform or ovoid, 8-spored, bitunicate, fissionate, 72–173 × 23.5–58.5 µm. *Ascospores* 32–42.5 × 13.5–18 µm, irregularly biserial or overlapping, crowned in the ascus, fusoid, muriform, hyaline to pale brown, with 4–5 transverse septa, and 2–4 longitudinal septa, apex obtuse, base broadly obtuse to subobtuse, usually widest in the second cell, slightly constricted at the septum, smooth-walled.

Culture characteristics: Colonies on OA, 30–35 mm diam after 1 wk, margin entire, regular, covered by flat aerial mycelium, buff to pale olivaceous, buff near the margin; reverse buff to olivaceous, black pseudothecia visible. Colonies on MEA, 30–35 mm diam after 1 wk, margin regular, aerial mycelium sparse, dark green; reverse concolourous, with a greenish brown concentric ring near the centre. Colonies on PDA, 30 mm diam after 1 wk, margin regular, covered by flat aerial mycelium, buff to hazel, greyish olivaceous toward the periphery, some irregular radially furrowed zones near the margin; reverse buff to pale salmon, brownish olivaceous near the centre, some irregular radially furrowed zones near the margin. Application of NaOH results in a pale yellowish green discolouration of the agar.

Typus: **China**, Qinghai Province, Qilian County, Arou, on leaves of *Miscanthus floridulus* (*Poaceae*), 10 Aug. 2019, M. Li (**holotype** HMAS 248356, culture ex-type CGMCC 3.20073 = LC 13593).

Additional materials examined: **China**, Qinghai Province, Qilian County, Ladong, on leaves of *Elymus dahuricus* (*Poaceae*), 9 Aug. 2019, M. Li, culture LC 13592; Menyuan County, Haomen, on leaves of *Swertia tetraptera* (*Gentianaceae*), 7 Aug. 2019, M. Li, culture LC 13590; Menyuan County, Xianmi National Forest Park, on leaves of *Sonchus asper* (*Asteraceae*), 8 Aug. 2019, M. Li, culture LC 13591; on leaves of *Iris lacteal* (*Iridaceae*), 8 Aug. 2019, L.W. Hou, culture LC 13594; on leaves of *Spiraea* sp. (*Rosaceae*), 8 Aug. 2019, L.W. Hou, culture LC 13595.

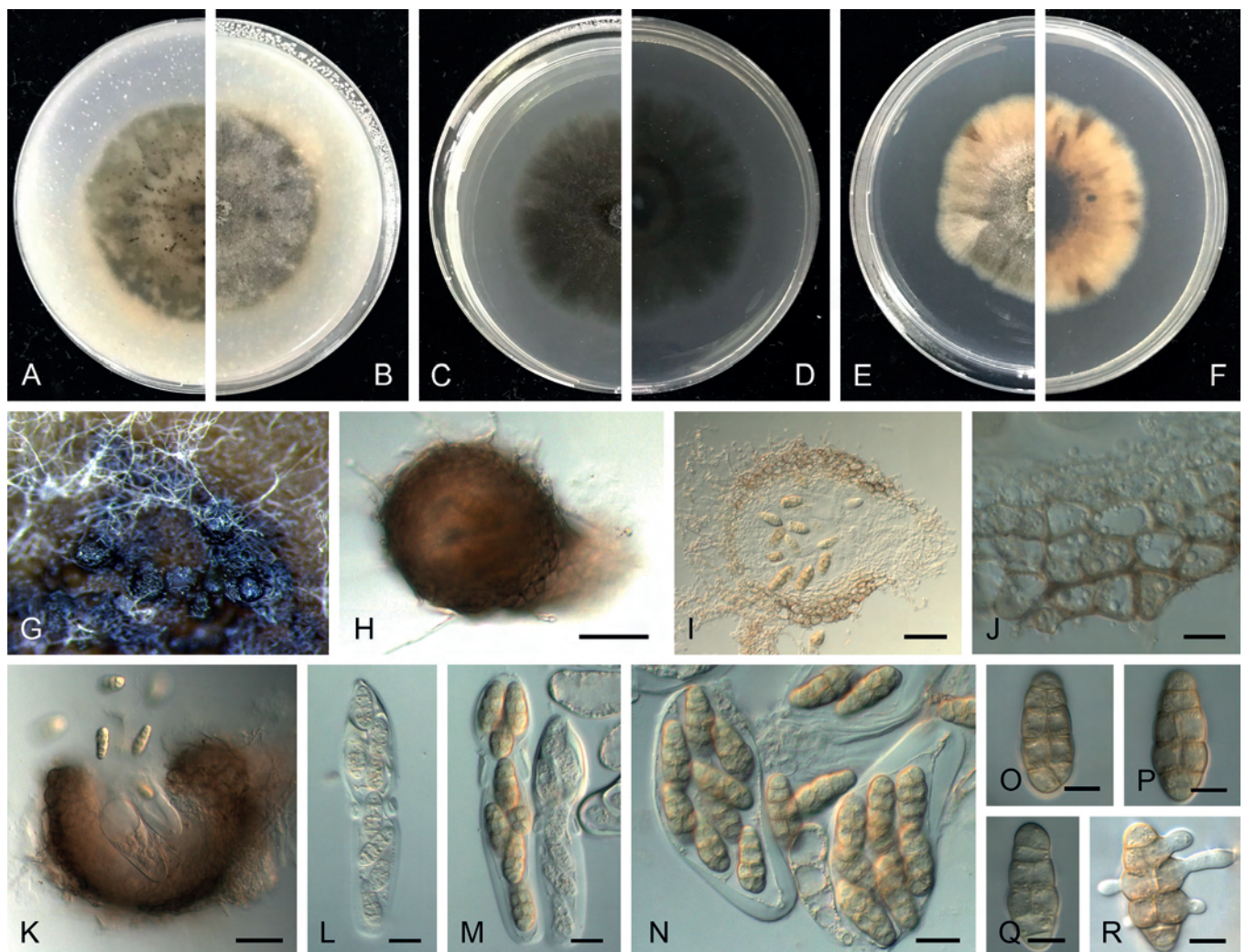


Fig. 35. *Leptosphaerulina miscanthi* (ex-type CGMCC 3.20073). **A, B.** Colony on OA (front and reverse). **C, D.** Colony on MEA (front and reverse). **E, F.** Colony on PDA (front and reverse). **G.** Pseudothecia sporulating on OA. **H.** Pseudothecium. **I.** Section of pseudothecium. **J.** Section of pseudothecial wall. **K.** Pseudothecium with asci. **L–N.** Asci. **O–Q.** Ascospores. **R.** Germinating ascospore. Scale bars: H, I, K = 50 µm; L–N = 20 µm; J, O–R = 10 µm.

Notes: *Leptosphaerulina miscanthi* formed a sister clade to *L. briosiana* and *L. trifolii* in the phylogenetic analysis based on four loci (Fig. 34; LSU, ITS, *rpb2* and *tub2*), but differs from *L. briosiana* in producing slightly longer asci ($72\text{--}173 \times 23.5\text{--}58.5 \mu\text{m}$ vs $109\text{--}122 \times 55\text{--}59 \mu\text{m}$), and from *L. trifolii* in its narrower asci ($72\text{--}173 \times 23.5\text{--}58.5 \mu\text{m}$ vs $91\text{--}137 \times 65\text{--}71 \mu\text{m}$) and smaller ascospores ($32\text{--}42.5 \times 13.5\text{--}18 \mu\text{m}$ vs $38\text{--}62 \times 17\text{--}26 \mu\text{m}$) (Graham & Luttrell 1961).

Genome sequenced strain: *Leptosphaerulina australis*. **Indonesia**, Lampung, from *Syzygium aromaticum* (= *Eugenia aromatica*), Dec. 1982, H. Vermeulen, reference culture CBS 317.83. This Whole Genome Shotgun project has been deposited at GenBank under the accession JALRMI000000000 (BioProject: PRJNA827019, BioSample: SAMN27594417; present study).

Authors: Q. Chen & L. Cai

Melampsora Castagne, Observ. Uréd. 2: 18. 1843. Fig. 36.

Classification: Basidiomycota, Pucciniomycotina, Pucciniomycetes, Pucciniales, Melampsoraceae, *Melampsora*.

Type species: *Melampsora euphorbiae* (Ficinus & C. Schub.) Castagne on *Euphorbia exigua*, basionym: *Xyloma euphorbiae* Ficinus & C. Schub., Fl. Geg. Dresd. 2: 310. 1823. Reference specimen: BPI 871135.

DNA barcodes (genus): ITS, LSU.

DNA barcodes (species): CO1, ITS, LSU, MS208, MS277 and *Nad6*. Table 11. Fig. 37.

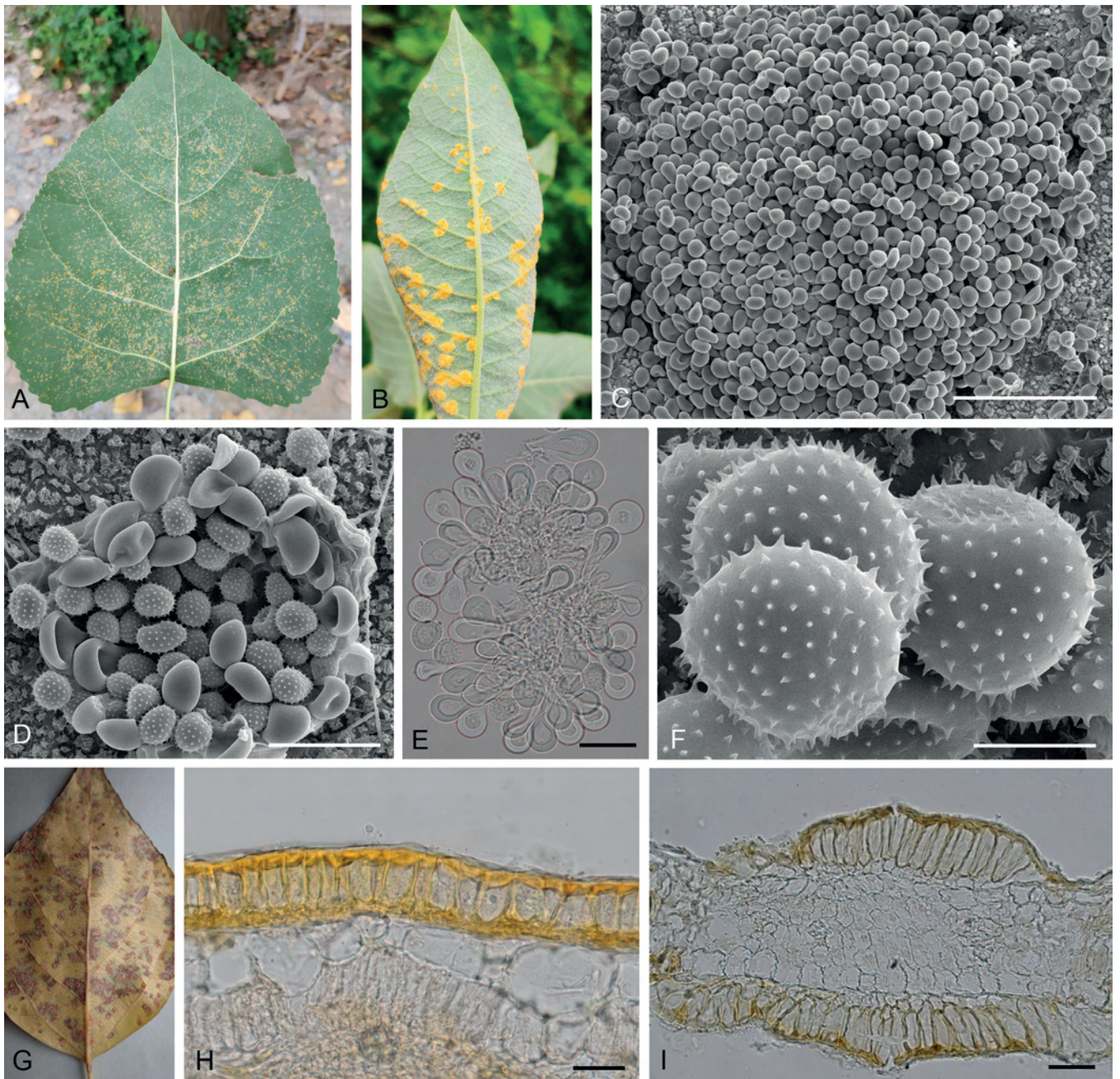


Fig. 36. *Melampsora* spp. **A–F.** Uredinial stage. **A, B.** Disease symptoms. **A.** *Melampsora medusae* on poplar leaf. **B.** *Melampsora salicis-albae* on willow leaf. **C, D.** Scanning electron micrographs of uredinia. **C.** *Melampsora epitea* (epitype TNS-F-121034). **D.** *Melampsora salicis-futurae* (holotype TSH-R9620). **E.** Capitulate paraphyses of *Melampsora epitea* (epitype TNS-F-121034). **F.** Scanning electron micrographs of urediniospores of *Melampsora epitea* (epitype TNS-F-121034). **G–I.** Telial stage. **G.** Disease symptoms of *Melampsora medusae* on the poplar leaf. **H, I.** Teliospores. **H.** *Melampsora salicis-bakko* (epitype TSH-R3879). **I.** *Melampsora ribesii-purpureae* (TSH-R7549). Scale bars: C = 100 μm ; D, E = 50 μm ; H, I = 20 μm ; F = 10 μm .

Table 11. DNA barcodes of accepted *Melampsora* spp.

Species	Specimen ¹	GenBank accession numbers ²						References
		CO1	ITS	LSU	MS208	MS277	Nad6	
<i>Melampsora abietis-canadensis</i>	1399MEA-POG-USA	JQ011188	JN881733	JN934918	JQ011098	JQ011008	JN985832	Vialle <i>et al.</i> (2013)
<i>M. abietis-caprearum</i>	KR-M-0048700	—	MK697300	—	—	—	—	Scholler <i>et al.</i> (2020)
<i>M. abietis-populi</i>	HMAS 55410	—	AB116870	AB116799	—	—	—	Tian <i>et al.</i> (2004)
<i>M. aecidioides</i>	380ME-PO-BC7	EU702405	EU808041	JN934930	JQ011114	JQ011021	JN985844	Vialle <i>et al.</i> (2013)
<i>M. albertensis</i>	BPI 0021209	—	JX416848	JX416843	—	—	—	Vialle <i>et al.</i> (unpublished)
<i>M. allii-populina</i>	1260MEAP-POC-HU	JQ011172	JN881728	JN934902	JQ011082	JQ010992	JN985816	Vialle <i>et al.</i> (2013)
<i>M. amygdalinae</i>	HMAAC4082	—	MK372149	MK372182	—	—	—	Wang <i>et al.</i> (2020a)
<i>M. apocyni</i>	LYR3	—	KR296802	KR296803	—	—	—	Gao <i>et al.</i> (unpublished)
<i>M. arctica</i>	HMAS 8629	—	KX386084	KX386113	—	—	—	Zhao <i>et al.</i> (2017)
<i>M. bigelowii</i>	1268MEB-SAN-SKA	—	GQ479205	—	—	—	—	Vialle <i>et al.</i> (unpublished)
<i>M. capraearum</i>	NYS-F-003819 ^T	—	KU550034	KU550033	—	—	—	Zhao <i>et al.</i> (2016)
<i>M. chelidonii-pierotii</i>	TSH-R7713	—	AB646769	—	—	—	—	Shinyama & Yamaoka (2012)
<i>M. coleosporioides</i>	HNMAP3114	—	KF780755	KF780638	—	—	—	Zhao <i>et al.</i> (2015)
<i>M. epiphylla</i>	TSH-R12280 ^{ET}	—	KF780789	KF780672	—	—	—	Zhao <i>et al.</i> (2017)
<i>M. epitea</i>	TNS-F-121034 ^{ET}	—	KX386070	KX386097	—	—	—	Zhao <i>et al.</i> (2017)
<i>M. euonymi-capraearum</i>	Iran 13124 F	—	FJ455132	—	—	—	—	Eslami <i>et al.</i> (unpublished)
<i>M. euphorbiae</i>	BPI 871135	—	DQ351722	—	—	—	—	Deadman <i>et al.</i> (2006)
<i>M. euphorbiae-gerardianae</i>	BRIP 39560	—	EF192199	—	—	—	—	Aime <i>et al.</i> (unpublished)
<i>M. ferrinii</i>	SAG 21943	—	KY053852	KY053853	—	—	—	Zapata (2016)
<i>M. gelmii</i>	PUR N6744	—	KJ136571	KJ136569	—	—	—	Tomme & Aime (2015)
<i>M. helioscopiae</i>	WM 1029	—	—	AF426197	—	—	—	Maier <i>et al.</i> (2003)
<i>M. humilis</i>	TSH-R7650 ^{ET}	—	KF780812	KF780695	—	—	—	Zhao <i>et al.</i> (2017)
<i>M. hypericorum</i>	PDD 97325	—	KJ716353	—	—	—	—	Padamsee & McKenzie (2014)
<i>M. idesiae</i>	KUS-F29304	—	KX944285	—	—	—	—	Lee <i>et al.</i> (2017)
<i>M. iranica</i>	HMAAC4055	—	MK372158	MK372191	—	—	—	Wang <i>et al.</i> (2020a)
<i>M. kamikotica</i>	HNMAP3186	—	KF780760	KF780643	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. kupreviczii</i>	TSH-R6016	—	KX386080	KX386109	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. kiusiana</i>	HH-77887 ^T	—	KF780808	KF780691	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. laricis</i>	HMAS 46905	—	AB116867	AB116809	—	—	—	Tian <i>et al.</i> (2004)
<i>M. laricis-miyabeana</i>	TSH-R950826	—	KX386072	KX386099	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. laricis-pentandrae</i>	HNMAP3201	—	KF780801	KF780684	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. laricis-populina</i>	880MLP-LAD-QC	JQ011213	GQ479844	JN934946	JQ011130	JQ011040	JN985860	Vialle <i>et al.</i> (2013)
<i>M. laricis-tremulae</i>	PFH-99-1	JQ011224	JN881745	JN934957	JQ011142	JQ011052	JN985871	Vialle <i>et al.</i> (2013)
<i>M. laricis-urbanianae</i>	TSH-R7420 ^{ET}	—	KF780778	KF780661	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. lini</i>	5261	—	—	L20283	—	—	—	Berres <i>et al.</i> (1995)
<i>M. magnusiana</i>	1426MEG-CJ-DSD	JQ011196	GQ479845	JN934927	JQ011108	JQ011018	JN985841	Vialle <i>et al.</i> (2013)
<i>M. medusae</i>	97CN5	JQ011228	GQ479302	JN934961	JQ011146	JQ011056	JN985875	Vialle <i>et al.</i> (2013)
<i>M. medusae-populina</i>	97G13	—	AY375276	—	—	—	—	Vialle <i>et al.</i> (2013)
<i>M. microsora</i>	HH-53150 ^T	—	KF780834	KF780717	—	—	—	Zhao <i>et al.</i> (2015c)

Table 11. (Continued).

Species	Specimen ¹	GenBank accession numbers ²						References
		CO1	ITS	LSU	MS208	MS277	Nad6	
<i>M. microspora</i>	1407MEMI-PON-IRQ	JQ011199	JN881737	JN934931	JQ011115	JQ011025	JN985845	Vialle <i>et al.</i> (2013)
<i>M. nujiangensis</i>	1423MEN-POY-CHI ^T	JQ011201	JN881739	JN934933	JQ011117	JQ011027	JN985847	Vialle <i>et al.</i> (2013)
<i>M. occidentalis</i>	411MEO-PO-BC13	JQ011205	GQ479885	JN934937	JQ011121	JQ011031	JN985851	Vialle <i>et al.</i> (2013)
<i>M. pakistanica</i>	BAQAU13 ^T	—	KU097001	KU847978	—	—	—	Ali <i>et al.</i> (2016)
<i>M. paradoxa</i>	649ME-LAL-ZM45.1	—	GQ479269	—	—	—	—	Vialle <i>et al.</i> (unpublished)
<i>M. pinitorqua</i>	1367MPI-PNI-FI	JQ011238	GQ479897	JN934973	JQ011158	JQ011068	JN985887	Vialle <i>et al.</i> (2013)
<i>M. populnea</i>	AAH00-1	—	AY444772	AY444786	—	—	—	Pei <i>et al.</i> (2005)
<i>M. pruinosa</i>	1366MEPR-POPRURT	JQ011207	GQ479898	JN934939	JQ011122	JQ011034	JN985853	Vialle <i>et al.</i> (2013)
<i>M. pulcherrima</i>	O8ZK4	JQ011209	GQ479320	JN934941	JQ011125	JQ011035	JN985855	Vialle <i>et al.</i> (2013)
<i>M. reticulatae</i>	TNS-F-107037	—	KF780844	KF780727	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. ribesii-purpureae</i>	NWC-06843	—	KF780830	KF780713	—	—	—	Zhao <i>et al.</i> (2015b)
<i>M. ribesii-viminalis</i>	HNMAP3218	—	KF780796	KF780679	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. ricini</i>	PDD 98363	—	KJ716352	—	—	—	—	Padamsee & McKenzie (2014)
<i>M. rostrupii</i>	PFH-08-3	JQ011246	JN881752	JN934981	JQ011169	JQ011079	JN985895	Vialle <i>et al.</i> (2013)
<i>M. salicis-albae</i>	NWC-09234	—	KF780774	KF780657	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. salicis-argyraceae</i>	HMAS52984 ^T	—	KF780733	KF780616	—	—	—	Zhao <i>et al.</i> (2015a)
<i>M. salicis-bakko</i>	TSH-R3879 ^{ET}	—	KC631854	KC685611	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. salicis-cavaleriei</i>	HMAAC4043	—	MK277296	MK277301	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. salicis-cupularis</i>	HMAS 76122 ^{ET}	—	KF780752	KF780635	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. salicis-futurae</i>	TSH-R9620 ^T	—	KC631860	KC685617	—	—	—	Zhao <i>et al.</i> (2017)
<i>M. salicis-purpureae</i>	HMAS 62584 ^T	—	KF780766	KF780649	—	—	—	Zhao <i>et al.</i> (2015a)
<i>M. salicis-reinii</i>	TSH-R10306 ^T	—	KF780777	KF780660	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. salicis-sinicae</i>	HNMAP1710 ^T	—	KC631839	KC685596	—	—	—	Zhao <i>et al.</i> (2014)
<i>M. salicis-triandrae</i>	HNMAP3181 ^T	—	KF780829	KF780712	—	—	—	Zhao <i>et al.</i> (2015b)
<i>M. salicis-viminalis</i>	HMAS 38658 ^T	—	KF780732	KF780615	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. salicis-warburgii</i>	HH-53135 ^T	—	KF780837	KF780720	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. tsinlingensis</i>	HNMAP3185	—	KF780748	KF780631	—	—	—	Zhao <i>et al.</i> (2015c)
<i>M. yezoensis</i>	HH-99463 ^T	—	KF780833	KF780730	—	—	—	Zhao <i>et al.</i> (2015c)
<i>Melampsora cf. yezoensis</i>	PUR N6744	—	KJ13657	KJ136569	—	—	—	Tomme & Aime (2015)
<i>Melampsora x columbiana</i>	SN-35	—	JQ042235	—	—	—	—	Busby <i>et al.</i> (2012)

¹ BPI: Systematic Mycology and Microbiology Laboratory, Agricultural Research Service, USDA, USA; BRIP: Queensland Plant Pathology Herbarium, Queensland, Australia; HH: Hiratsuka Herbarium, Tokyo, Japan; HMAAC: Mycological Herbarium of Xinjiang Agricultural University, Xinjiang, China; HMAS: Mycological Herbarium of Institute of Microbiology, Chinese Academy of Sciences, China; HMNWFC: Mycological Herbarium of College of Forestry, Northwest A & F University, China; HNMAP: Mycological Herbarium of Inner Mongolia Agricultural University, Inner Mongolia, China; PDD: New Zealand Fungarium, Lincoln, New Zealand; PUR: Arthur Fungarium, Purdue University, West Lafayette, IN, USA; TNS: National Museum of Nature and Science, Tsukuba, Japan; TSH: Mycological Herbarium of the Graduate School of Life and Environmental Sciences, University of Tsukuba, Tsukuba, Japan. ^T and ^{ET} indicate type and epitype, respectively.

² CO1: partial cytochrome oxidase subunit 1 gene; ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial 28S large subunit nrDNA gene; MS208: gene for DNA replication-licensing factor required for DNA replication initiation and cell proliferation; MS277: gene required for rRNA accumulation during biogenesis of the ribosome; Nad6: partial dehydrogenase subunit 6 gene.

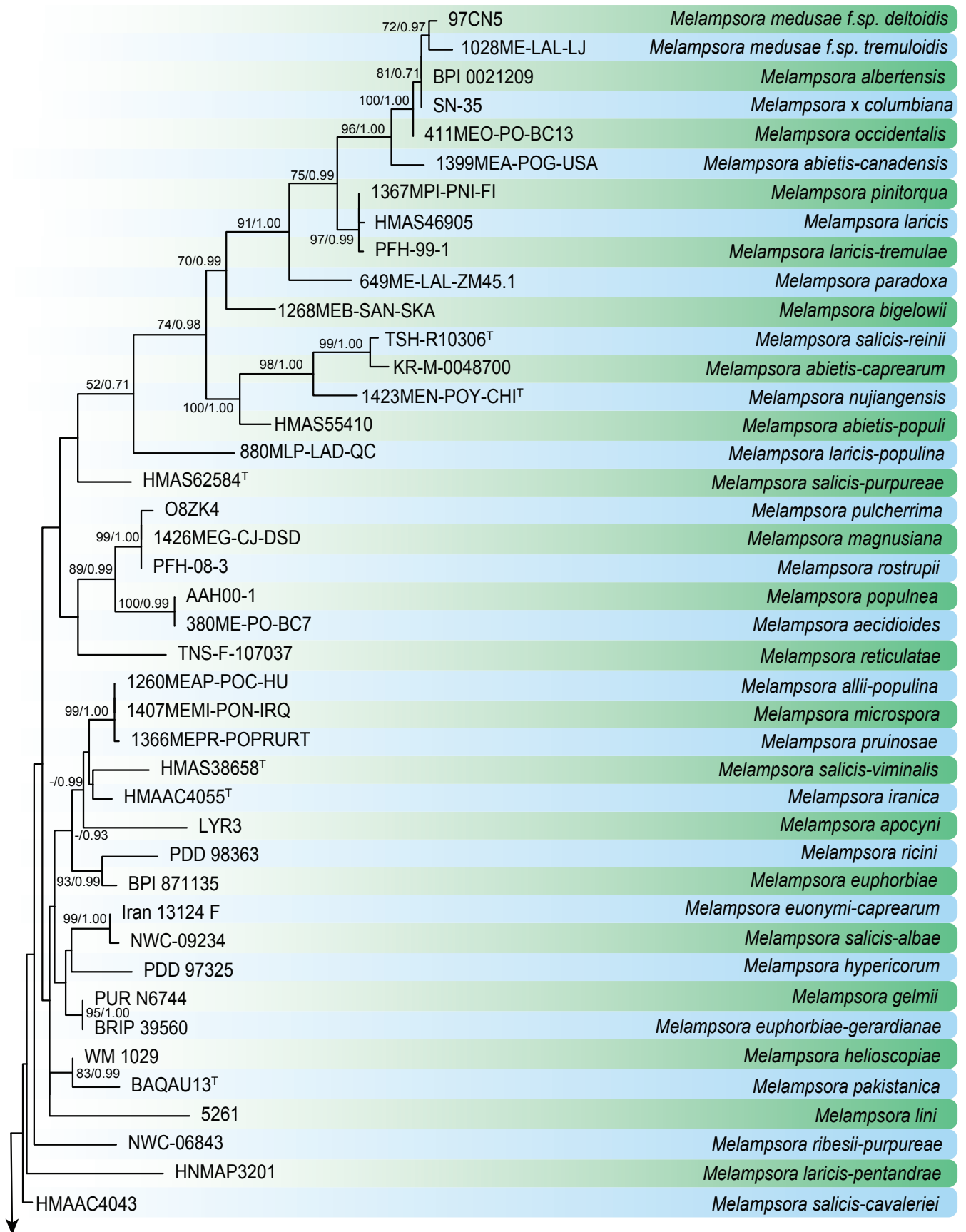


Fig. 37. Phylogenetic tree constructed based on ITS (550 bp) and LSU (700 bp) sequences of all accepted species of *Melampsora*. RAxML bootstrap support values (> 50 %) and Bayesian posterior probability scores (> 0.70) are shown at the nodes. The phylogenetic tree was rooted to *Chrysomyxa monesis* 1361CHM-PCS-BC and *C. empetri* 287CHE-EMN-SA1. GenBank accession numbers are indicated in Table 11. ^T and ^{ET} indicate type and epitype, respectively. TreeBASE: S26038.

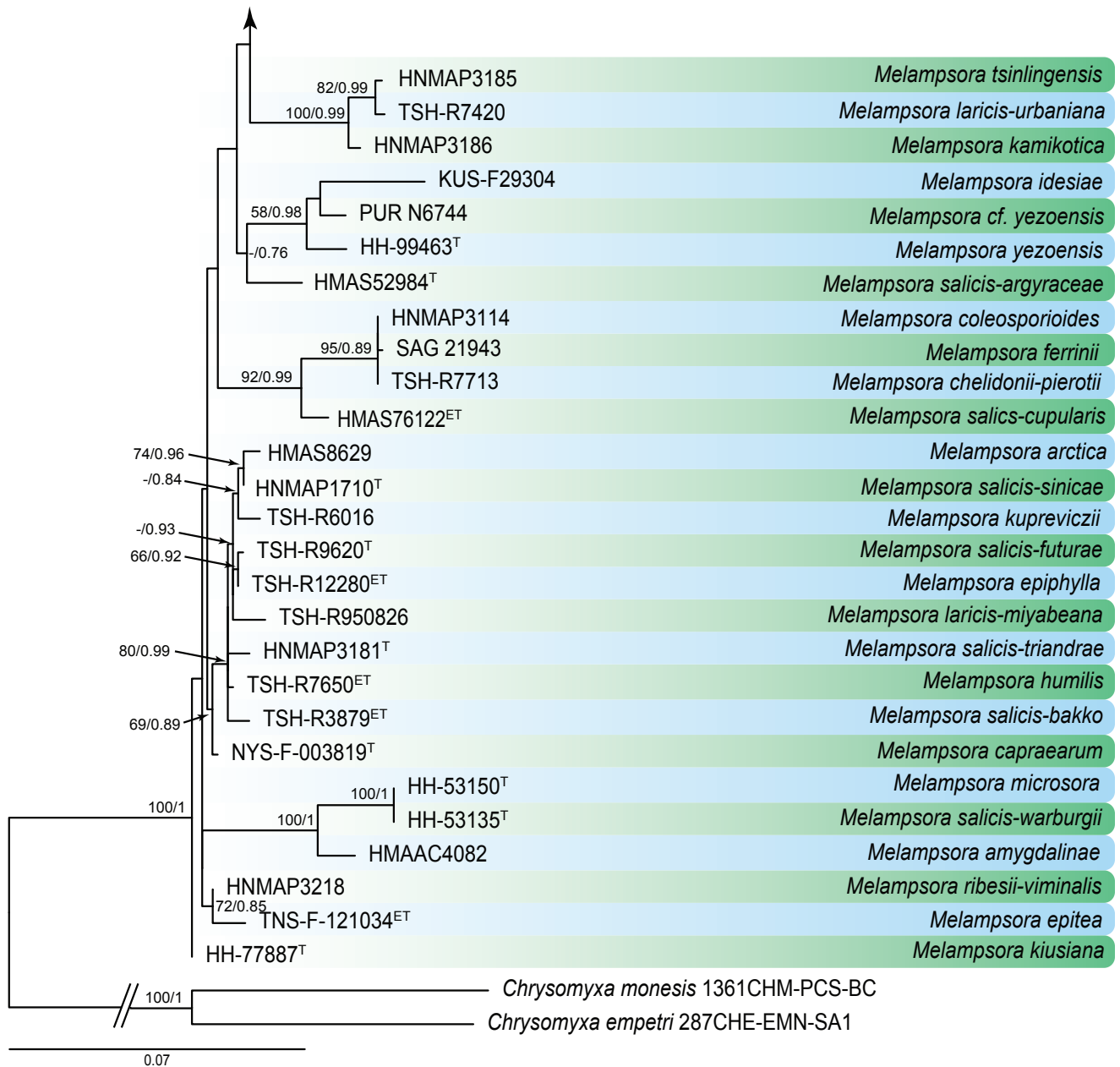


Fig. 37. (Continued).

Spermogonia Group I (type 2 or type 3), subepidermal or subcuticular, determinate, with flat hymenia, bounding structures lacking. *Aecia* *Caecoma*-type, subepidermal, with rudimentary or no peridia, occasionally some species have peridial cells adherent to host epidermis. *Aeciospore* catenulate, with intercalary cells, verrucose with rodlike columns or blocks. *Uredinia* *Uredo*-type, subepidermal, erumpent, brightly yellow or orange when fresh, fading to nearly hyaline, with abundant capitate paraphyses, occasionally with a partial peridium. *Urediniospores* borne singly, echinulate, germ pores scattered or bizonate. *Telia* subepidermal or subcuticular, not erumpent, consisting of laterally adherent teliospores in crusts one spore deep or some species also with subjacent spore-like cells. *Teliospores* aseptate, sessile, pigmented. *Basidia* external.

Distribution: Worldwide.

Life cycle: This genus includes either heteroecious or autoecious life cycles, and most species are recorded as macrocyclic, with five different spore stages, *i.e.* spermogonium, aecium, uredinium, telium

and basidium. Heteroecious species have their uredinia and telia on willows (*Salix*) and poplars (*Populus*) belonging to *Salicaceae*, and spermogonia and aecia of these species occur on coniferous trees of *Pinaceae* such as *Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga* and *Tsuga*, or on various herbaceous plants such as *Allium* (*Alliaceae*), *Chelidonium*, *Corydalis* (*Papaveraceae*), *Ribes* (*Grossulariaceae*), *Saxifraga* (*Saxifragaceae*), and several orchidaceous genera. Most autoecious species of *Melampsora* occur on dicotyledonous plants, including *Euphorbiaceae* and *Linaceae*.

Disease symptoms: Yellow aecia are sometimes visible on cones or needles of coniferous trees and other aecial hosts, infected needles shrivel and die soon after sporulation; yellow to brownish uredinia in small orange-yellow pustules on one or both leaf surfaces on telial hosts, commonly with yellow spots on leaves, eventually become necrotic; the whole trees have a golden appearance in severe infection; heavily infected leaves turn brown, wither, and curl at the margin before falling.

Notes: The family *Melampsoraceae* contains only one genus, *Melampsora*, which possesses Group I spermatogonia and unicellular teliospores embedded under the host epidermis or cuticular layers (Sydow & Sydow 1915, Kuprevich & Tranzschel 1957, Cummins & Hiratsuka 2003). Since *Melampsora* was established in 1843 with *M. euphorbiae* on *Euphorbia exigua* as type species, there have been approximately 212 species described (Farr & Rossman 2022). *Melampsora lini* was listed as one of the *Top 10* most important fungal plant pathogens based on its scientific/economic importance as the cause of rust on cultivated flax (Dean *et al.* 2012). Species recognition in *Melampsora* has been based on the ecological species concept that focused on aecial or telial host ranges, together with a few morphological characters in uredinial and telial stages. More recently, molecular data has revealed interspecific relationships in *Melampsora*, and taxonomic identities have been resolved via rDNA phylogenies (Zhao *et al.* 2020). There have been several systematic studies at the species level in *Melampsora* (Tian *et al.* 2004, Pei *et al.* 2005, Feau *et al.* 2009, Zhao *et al.* 2015c, 2017). Molecular barcodes for identification at both generic and species level are available. At generic level, LSU is used, while for species, CO1, ITS, LSU, MS208, MS277 and Nad6, are useful

barcodes. Among the 212 reported species, nucleotide sequences from 71 species of *Melampsora* are presently available.

References: Hiratsuka & Kaneko 1982 (morphology and host range); Bagyanarayana 2005 (morphology, host range and key of *Melampsora* species on willows); Pei 2005 (morphology and host range); Vialle *et al.* 2011 (morphology, host range and key of *Melampsora* species on poplar); Tian *et al.* 2004, Feau *et al.* 2009, Zhao *et al.* 2015c, Zhao *et al.* 2017, Zhao *et al.* 2020 (phylogeny).

Melampsora laricis-urbaniana Tak. Matsumoto, Ann. Missouri Bot. Gard. 6: 311. 1920. Fig. 38.

Spermatogonia amphigenous, subcuticular. *Aecia* caeomata type, hypophyllous; aeciospores globose or broadly ellipsoid, 15–25 × 13–21 μm, finely and densely verrucose, walls 1.5–2 μm thick, germ pores scattered. *Uredinia* hypophyllous, 0.2–0.6 mm; *urediniospores* obovoid or ellipsoid, 16–30 × 9–21 μm, walls 2–2.5 μm thick at sides, 4–6.9 μm thick at apex, echinulate, germ pores 2–4, tending to bizonate. *Paraphyses* intermixed 30–79 × 11–24 μm, walls slightly thickened at apex up to 12 μm. *Telia* hypophyllous,

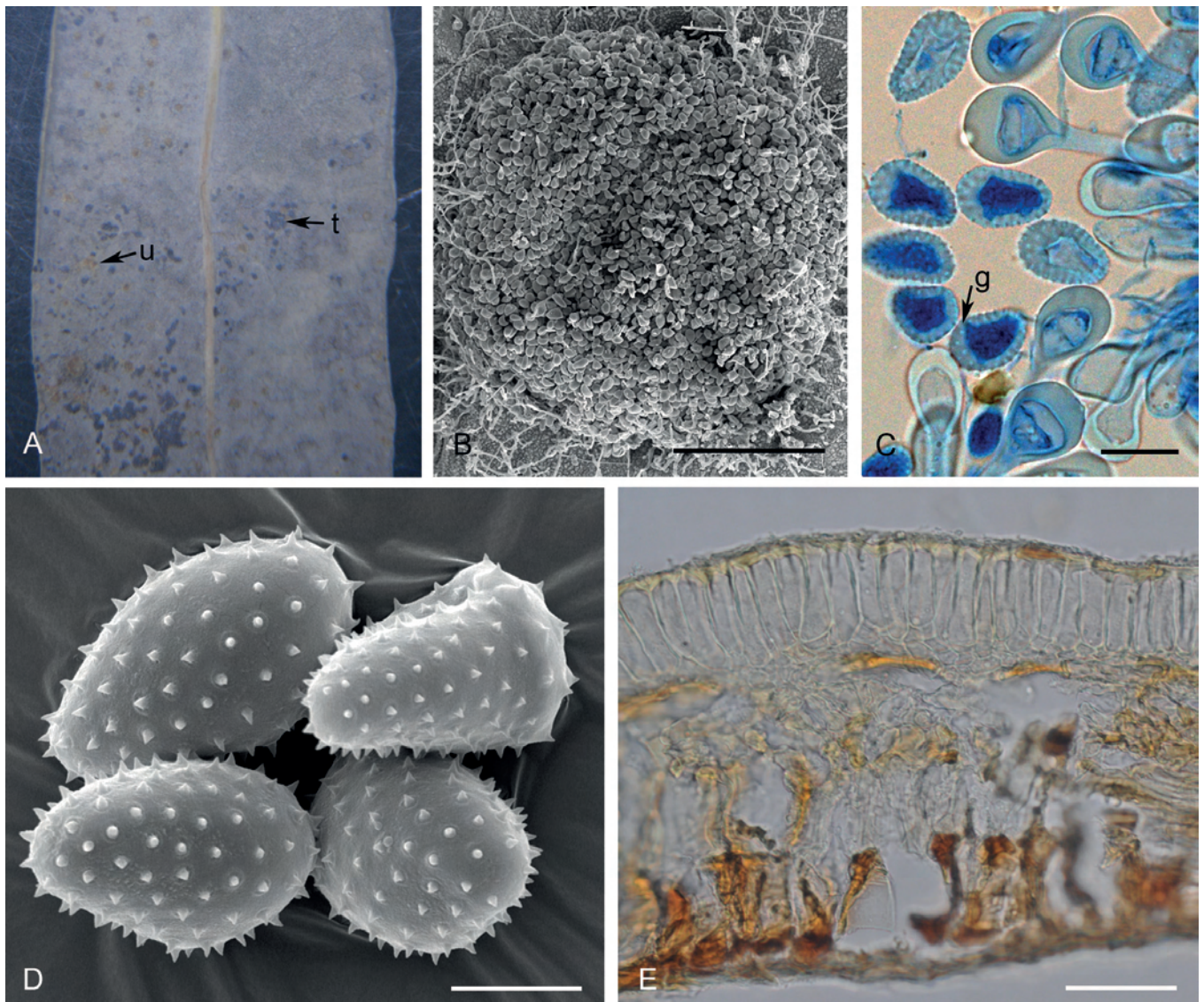


Fig. 38. *Melampsora laricis-urbaniana* (epitype TSH-R7420). **A.** Uredinia (u) and telia (t) on leaves of epitype specimen. **B.** Scanning electron micrographs of uredinia with intermixed paraphyse. **C.** Urediniospores with bizonate germ pores (g), urediniospores and paraphyses with apparently thickened apical wall. **D.** Scanning electron micrographs of urediniospores with echinulate spines. **E.** Section of telia and teliospores. Scale bars: B = 150 μm; E = 30 μm; C = 20 μm; D = 10 μm.

subepidermal, 0.2–0.6 mm; *teliospores* 20–49 × 6–16 µm, walls 1–2.5 µm thick at sides, up to 4.7 µm thick at apex, an apical germ pore sometimes visible.

Host range: Spermogonia and aecia on *Larix leptolepis*, and uredinia and telia on *Toisusu urbaniana*.

Typus: **Japan**, Hokkaido, Sapporo-shi, on *Toisusu urbaniana* (*Salicaceae*), Tak. Matsumoto (Ann. Missouri Bot. Gard. 6: 311. 1920, figs 1–3, **lectotype** designated here, MBT 10005755); Hokkaido, Sapporo-shi, on *T. urbaniana*, data unknown, Y. Yamaoka (**epitype** designated here TSH-R7420, MBT 10005047).

Additional materials examined: **Japan**, Hokkaido, Sapporo-shi, Toyohira, on *T. urbaniana*, 18 Nov. 1925, N. Hiratsuka, HH-53303; Hokkaido, Sapporo-shi, on *Toisusu urbaniana*, 4 Oct. 1901, J. Hanzawa, HH-78307; *ibid.* HH-53302; Hokkaido, Sapporo-shi, on *T. urbaniana*, 21 Aug. 1905, K. Miyabe, HH-53305; Hokkaido, Sapporo-shi, on *T. urbaniana*, date unknown, Y. Yamaoka, TSH-R7419; Nagano, on *T. urbaniana*, date unknown, Y. Yamaoka, TSH-R9834.

Notes: *Melampsora laricis-urbaniana* was first reported on *T. urbaniana* in Sapporo-shi of Hokkaido in Japan and Matsumoto (1920) validly described this species with description and line drawings. Matsumoto (1920) did not cite the materials examined by him, thus, Hiratsuka & Kaneko (1982) designated a neotype and isoneotype during their systematic studies of *Melampsora* species on willows in Japan. However, the neotypification of Hiratsuka & Kaneko (1982) is not Code compliant as original material is available for lectotypification. For this reason, we have designated illustrations of Matsumoto (1920) as lectotype. We also designated an epitype specimen, which was collected by Y. Yamaoka in the Sapporo-shi of Hokkaido in Japan, from which we derived ITS and LSU sequences: TSH-R7420 (ITS: KF780778; LSU: KF780661), TSH-R9834 (ITS: KF164453; LSU: KF164446) and TSH-R9835 (ITS: KF164454; LSU: KF164447). This species was only found in Japan with its aecial stage on *Larix* species and telial stage on *Toisusu*.

Melampsora salicis-cupularis Wang, Contr. Inst. Bot. Natl. Acad. Peiping 6: 225. 1949. Fig. 39.

Spermogonia and *aecia* not found. *Uredinia* hypophyllous, 0.2–0.6 mm; *Urediniospores* globoid or ellipsoid, echinulate, 14–30 × 12–27 µm, wall 1.5–3 µm thick, mean distance between spines 1.01–1.12 µm, germ pores 3–5, scattered. *Paraphyses* mainly capitate, 41–93 × 16–37 µm, with evenly thickened or slightly thickened apex, up to 8 µm. *Telia* amphigenous, mainly hypophyllous, 0.2–0.8 mm; *Teliospores* subepidermal, 20–40 × 5–14 µm, wall 1 µm thick, not thickened at apex.

Host range: Uredinia and telia on *Salix cupularis*.

Typus: **China**, Shaanxi Province, Taibai Mountains, on *Salix cupularis* (*Salicaceae*), 14 Aug. 1942, Y.C. Wang (**holotype** HMAS 957); *ibid.*, 26 Aug. 1996, Z.M. Cao (**epitype** designated here HMAS 76122, MBT 10005048).

Additional materials examined: **China**, Shaanxi Province, Taibai Mountains, on *S. cupularis*, 26 Aug. 1996, Z.M. Cao, HMNWFC-T8540; Inner Mongolia, Alxa, He Lan Mountains on *S. cupularis*, 16 Aug. 1963, Y.Z. Shang, HNMAP3152.

Notes: *Melampsora salicis-cupularis* was first detected on *Salix cupularis* from the Taibai Mountains in China, and it was characterised by relatively large urediniospores, capitate paraphyses in uredinia,

amphigenous telia and subepidermal teliospores with evenly thickened apical wall (Wang 1949). This species resembles *M. epiphylla* in amphigenous telia and subepidermal teliospores, but the two species differ in urediniospores dimensions and teliospore shape (Hiratsuka & Kaneko 1982, Zhao *et al.* 2017). We failed to generate molecular data from the holotype material, and therefore a specimen collected from the host and location in the Taibai Mountains of China was designated as epitype. We successfully characterised its morphological features, as well as phylogenetic placement based on the epitype material. This species is hitherto only known from China (Shaanxi and Inner Mongolia).

Genome sequenced strain: *Melampsora lini*. **Unknown**, collection information unknown, culture CH5 (a hybrid strain obtained from crossing self-fertilised New Zealand “race” 5 and a North American “race” 228 strain). This Whole Genome Shotgun project has been deposited at GenBank under the BioProject: PRJNA239538; Melli1 in MycoCosm (Nemri *et al.* 2014).

Authors: P. Zhao & L. Cai

Nigrospora Zimm., Zentralbl. Bakteriol. Parasitenk., Abt. I, 8: 220. 1902. Fig. 40.

Classification: Sodiariomycetes, Xylariomycetidae, Xylariales, Apiosporaceae.

Type species: *Nigrospora panici* Zimm. Type or reference material not available.

DNA barcode (genus): LSU.

DNA barcodes (species): ITS, *tef1*, *tub2*. Table 12. Fig 41.

Ascomata perithecial, black, aggregated, subepidermal, erumpent, spherical or ovoid, with papillate ostioles. *Asci* short pedicellate, rounded at the apex, unitunicate-operculate, clavate, 8-spored. *Paraphyses* septate, longer than asci, thin-walled. *Ascospores* granular, hyaline, curved, inequilateral, biseriate, initially unicellular, usually unequally two-celled with a transverse septum. *Conidiophores* smooth, branched, micronematous or semi-macronematous, flexuous, hyaline to brown, usually reduced to conidiogenous cells. *Conidiogenous cells* hyaline, discrete, solitary, monoblastic, subspherical, determinate, ampulliform, doliiform, sub-cylindrical to clavate. *Conidia* solitary, sparse, acrogenous, aseptate, globose or sub-globose or ellipsoidal or pyriform, shiny, smooth, simple, pale brown to black, rarely with violent discharge mechanism. *Setae* straight to irregular, curved, subcylindrical, smooth, black, tapering at apex, obtuse or subobtuse, base truncate (adapted from Hudson 1963, Wang *et al.* 2017, Raza *et al.* 2019).

Cultural characteristics: Colonies on PDA filamentous with shiny, small, black conidia, white or pale yellow when are young, floccose, cottony, brown or black when mature with abundant sporulation. Colonies on SNA flat, mycelia immersed, white to greyish surface, greyish reverse with or without patches.

Optimal media and cultivation conditions: Fast growth on PDA and slow growth on SNA media. On SNA at 25 °C to induce sporulation of the asexual morph.

Distribution: Worldwide.

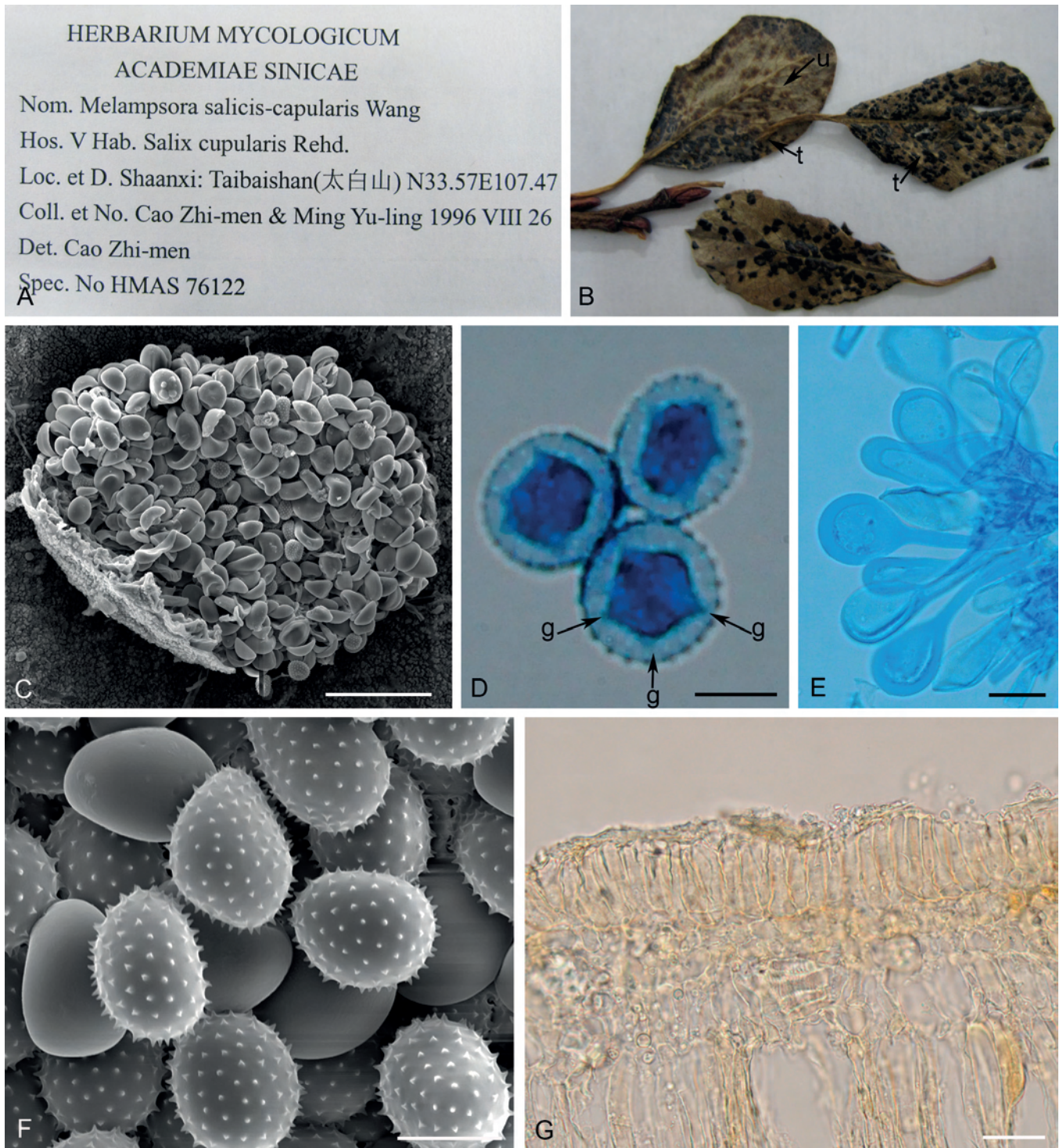


Fig. 39. *Melampsora salicis-cupularis* (epitype HMAS 76122). **A.** Label of epitype specimen. **B.** Uredinia (u) and telia (t) on leaves of *Salix cupularis*. **C.** Scanning electron micrographs of uredinia with intermixed paraphyses. **D.** Urediniospores with scattered germ pores (g). **E.** Capitulate paraphyses. **F.** Scanning electron micrographs of urediniospores with echinulate spines and paraphyses with smooth wall. **G.** Section of telia and teliospores. Scale bars: C = 100 μ m; D, E = 50 μ m; G = 20 μ m; E, F = 10 μ m.

Hosts: *Nigrospora* species are cosmopolitan with wide host ranges and occur as saprobes, endophytes, plant and human pathogens. *Nigrospora sphaerica* (reported from 40 different host genera), *N. oryzae* (reported from 20 different host genera) and *N. chinensis* (reported from 10 different host genera) are the three most ubiquitous species. Overall, *Nigrospora* species lacks host specificity.

Disease symptoms: Leaf spots, twig and shoot or leaf blights, rots.

Notes: *Nigrospora* as recently redefined is a monophyletic genus, and phylogenetic studies employing ITS, *tef1* and *tub2* sequence

data were performed for species identification and delimitation (Wang *et al.* 2017, Raza *et al.* 2019). The type of the genus was reported from *Panicum amphibium* from Java and its holotype has been lost. Unfortunately, to date attempts to locate a suitable specimen to neotypify this species have been unsuccessful. The sexual morph of *Nigrospora* species is rarely observed. *Arthrinium* and *Apiospora* are similar in producing deeply pigmented conidia with or without germ slit and the presence of setae. The distinction among these genera is obscure, but the most characteristic difference is the production of a single conidium produced on each conidiogenous cell in *Nigrospora*, while conidia are produced in clusters in

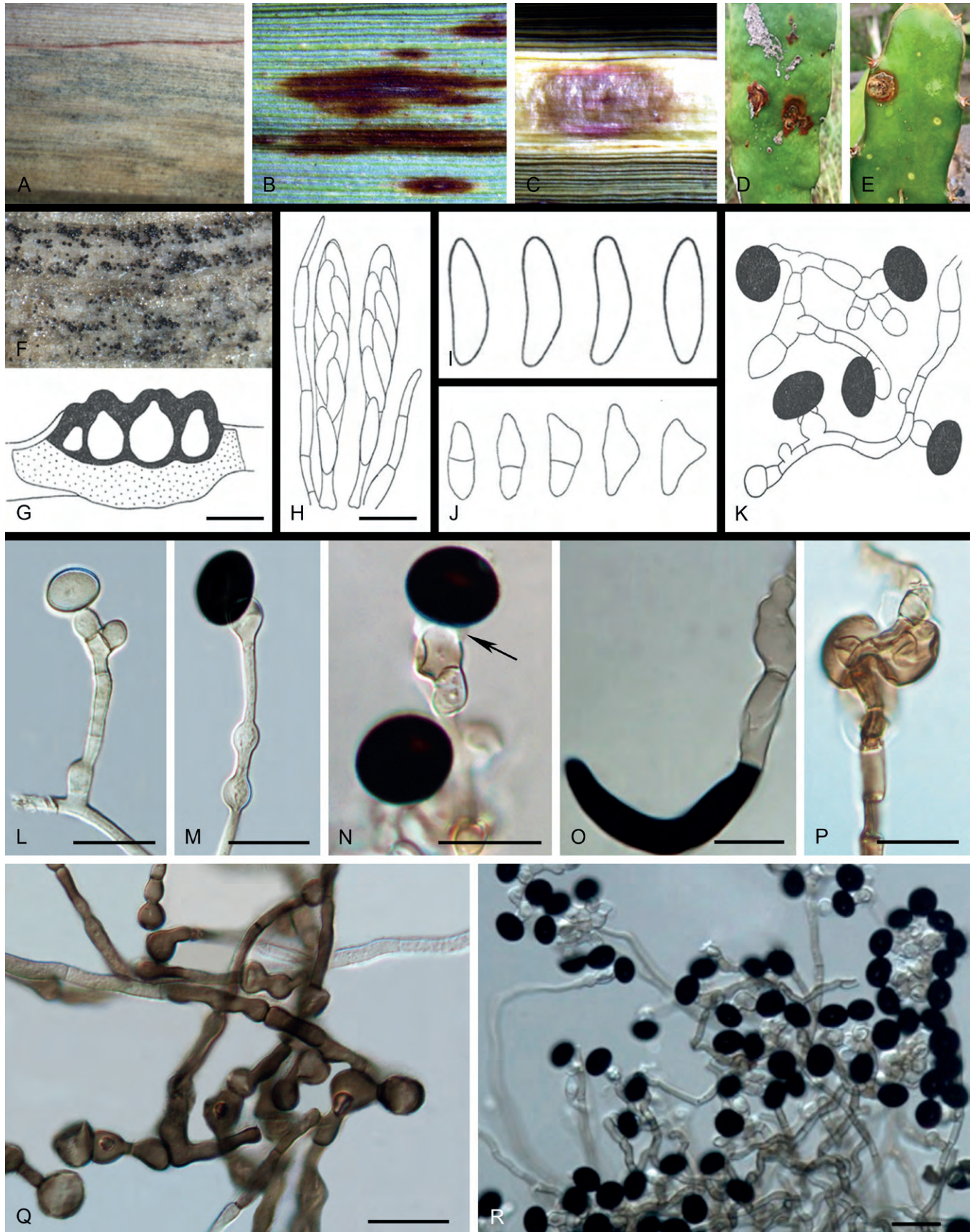


Fig. 40. *Nigrospora* spp. **A–F.** Disease symptoms. **A, F.** *Nigrospora hainanensis* on *Saccharum officinarum*. **B.** *Nigrospora aurantiaca* on *Saccharum officinarum*. **C.** *Nigrospora camelliae-sinensis* on *Saccharum officinarum*. **D.** *Nigrospora lacticolonia* on *Selenicereus undatus*. **E.** *Nigrospora sphaerica* on *Selenicereus undatus*. **G–K.** Sexual morph of *Nigrospora oryzae* (Herb. IMI 79239). **G.** Perithecia. **H.** Asci and paraphyses. **I.** Ascospores, all from *Saccharum officinarum*. **J.** Discharged ascospores. **K.** Germinating ascospores producing conidia. **L–R.** Asexual morph. **L, M.** Conidiophores with conidia of *Nigrospora falsivesicularis* (ex-type CGMCC 3.19678). **N.** Conidiogenous cells giving rise to conidia (arrow indicates the vesicles surrounding the septum) of *Nigrospora sacchari-officinarum* (ex-type CGMCC 3.19335). **O.** Seta of *Nigrospora hainanensis* (ex-type CGMCC 3.18129). **P, Q.** Sterile conidia of *Nigrospora saccharicola* (ex-type CGMCC 3.19362). **R.** Conidia of *Nigrospora guilainensis* (ex-type CGMCC 3.18124). Scale bars: G = 200 µm; H, J–M, P–R = 20 µm; I, N, O = 10 µm. Pictures A–C, F, L–N, P, Q taken from Raza et al. (2019); D, E from Kee et al. (2019); G–K from Hudson (1963); O, R from Wang et al. (2017).

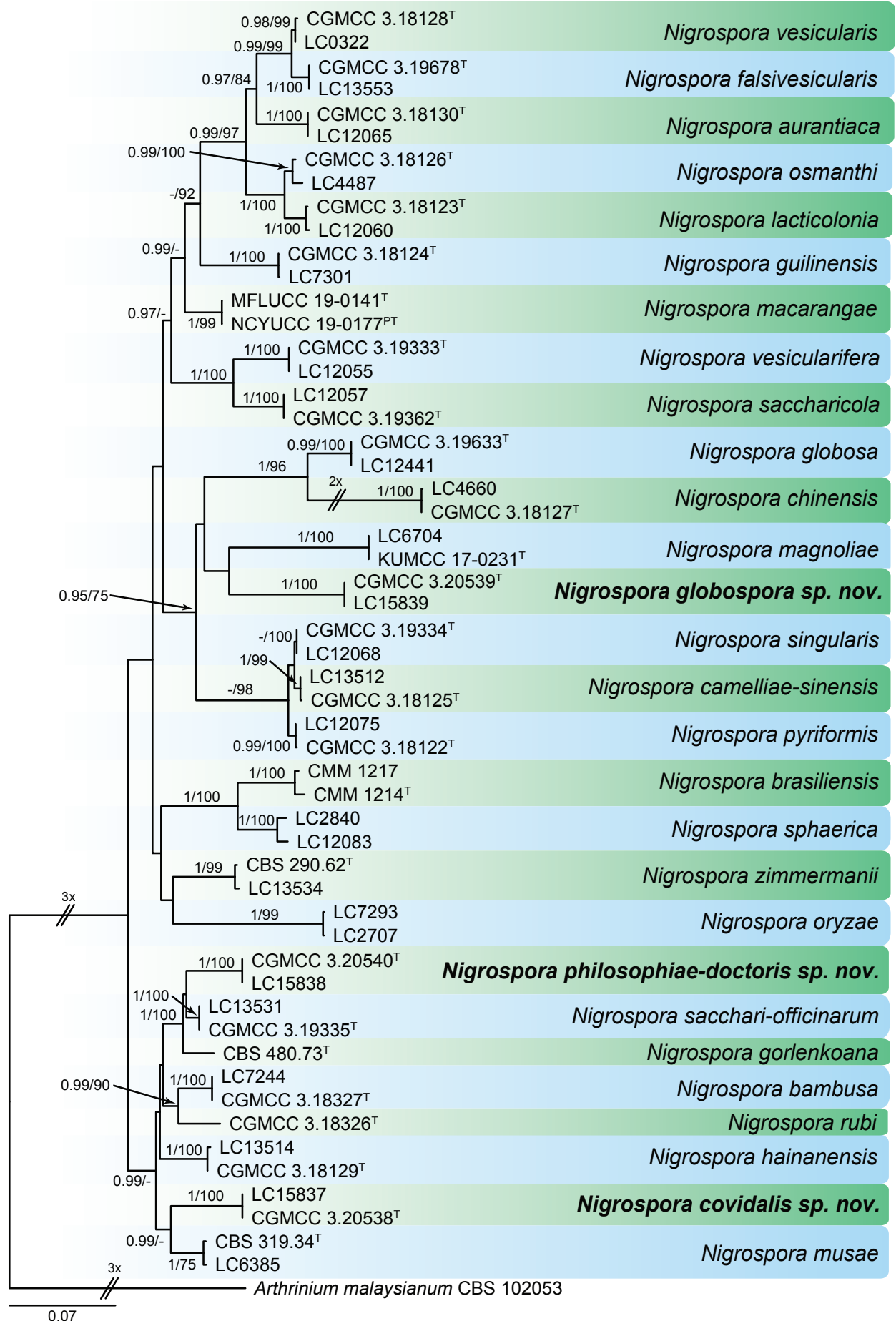


Fig. 41. RAxML phylogram constructed from ITS (521 bp), *tub2* (433 bp) and *tef1* (543 bp) sequences of all accepted species of *Nigrospora*. Maximum likelihood bootstrap support values (> 70 %) and Bayesian posterior probability scores (> 0.95) are indicated on the branches. The novel taxa are printed in bold. The phylogenetic tree was rooted to *Arthrinium malaysianum* CBS 102053. GenBank accession numbers are indicated in Table 12. ^T and ^{PT} indicate ex-type and ex-paratype strains, respectively. TreeBASE: S26190.

Table 12. DNA barcodes of accepted *Nigrospora* spp.

Species	Isolates ¹	GenBank accession numbers ²			References
		ITS	tub2	tef1	
<i>Nigrospora aurantiaca</i>	CGMCC 3.18130 ^T	KX986064	KY019465	KY019295	Wang <i>et al.</i> (2017)
	LC 12065	MN215771	MN329935	MN264010	Raza <i>et al.</i> (2019)
<i>N. bambusae</i>	CGMCC 3.18327 ^T	KY385307	KY385319	KY385313	Wang <i>et al.</i> (2017)
	LC 7244	KY385306	KY385320	KY385314	Wang <i>et al.</i> (2017)
<i>N. brasiliensis</i>	CMM 1214 ^T	KY569629	MK720816	MK753271	Crous <i>et al.</i> (2019)
	CMM 1217	KY569630	MK720817	MK753272	Crous <i>et al.</i> (2019)
<i>N. camelliae-sinensis</i>	CGMCC 3.18125 ^T	KX985986	KY019460	KY019293	Wang <i>et al.</i> (2017)
	LC 13512	MN215775	MN329939	MN264014	Raza <i>et al.</i> (2019)
<i>N. chinensis</i>	CGMCC 3.18127 ^T	KX986023	KY019462	KY019422	Wang <i>et al.</i> (2017)
	LC 4660	KX986026	KY019548	KY019445	Wang <i>et al.</i> (2017)
<i>N. covidalis</i>	CGMCC 3.20538 = LC 4566 ^T	OK335209	OK431479	OK431485	Present study
	LC 158337	OK335210	OK431480	OK431486	Present study
<i>N. falsivesicularis</i>	CGMCC 3.19678 ^T	MN215778	MN329942	MN264017	Raza <i>et al.</i> (2019)
	LC 13553	MN215779	MN329943	MN264018	Raza <i>et al.</i> (2019)
<i>N. globosa</i>	CGMCC 3.19633 ^T	MK329121	MK336134	—	Zhang <i>et al.</i> (2021)
	LC 12441	MK329122	MK336135	—	Zhang <i>et al.</i> (2021)
<i>N. globospora</i>	CGMCC 3.20539 = LC 8397 ^T	OK335211	OK431481	OK431487	Present study
	LC 15839	OK335212	OK431482	OK431488	Present study
<i>N. gorlenkoana</i>	CBS 480.73 ^T	KX986048	KY019456	KY019420	Wang <i>et al.</i> (2017)
<i>N. guilinensis</i>	CGMCC 3.18124 ^T	KX985983	KY019459	KY019292	Wang <i>et al.</i> (2017)
	LC 7301	KX986063	KY019608	KY019404	Wang <i>et al.</i> (2017)
<i>N. hainanensis</i>	CGMCC 3.18129 ^T	KX986091	KY019464	KY019415	Wang <i>et al.</i> (2017)
	LC 13514	MN215780	MN329944	MN264019	Raza <i>et al.</i> (2019)
<i>N. lacticolonia</i>	CGMCC 3.18123 ^T	KX985978	KY019458	KY019291	Wang <i>et al.</i> (2017)
	LC 12060	MN215784	MN329948	MN264023	Raza <i>et al.</i> (2019)
<i>N. macarangae</i>	MFLUCC 19–0141 ^T	MW114318	—	—	Tennakoon <i>et al.</i> (2021)
	NCYUCC 19–0177 ^{PT}	MW114319	—	—	Tennakoon <i>et al.</i> (2021)
<i>N. magnoliae</i>	MFLUCC 19–0112 = KUMCC 17–0246 ^T	MW285092	MW438334	—	de Silva <i>et al.</i> (2021)
	LC 6704	KX986047	KY019571	KY019373	Wang <i>et al.</i> (2017)
<i>N. musae</i>	CBS 319.34 ^T	KX986076	KY019455	KY019419	Wang <i>et al.</i> (2017)
	LC 6385	KX986042	KY019567	KY019371	Wang <i>et al.</i> (2017)
<i>N. oryzae</i>	LC 7293	KX985931	KY019601	KY019396	Wang <i>et al.</i> (2017)
	LC 2707	KX985954	KY019481	KY019307	Wang <i>et al.</i> (2017)
<i>N. osmanthi</i>	CGMCC 3.18126 ^T	KX986010	KY019461	KY019421	Wang <i>et al.</i> (2017)
	LC 4487	KX986017	KY019540	KY019438	Wang <i>et al.</i> (2017)
<i>N. philosophiae-doctoris</i>	CGMCC 3.20540 = LC 13398 ^T	OK335213	OK431483	OK431489	Present study
	LC 15838	OK335214	OK431484	OK431490	Present study
<i>N. pyriformis</i>	CGMCC 3.18122 ^T	KX985940	KY019457	KY019290	Wang <i>et al.</i> (2017)
	LC 12075	MN215787	MN329988	MN264026	Raza <i>et al.</i> (2019)
<i>N. rubi</i>	CGMCC 3.18326 ^T	KX985948	KY019475	KY019302	Wang <i>et al.</i> (2017)
<i>N. sacchari-officinarum</i>	CGMCC 3.19335 ^T	MN215791	MN329954	MN264030	Raza <i>et al.</i> (2019)
	LC 13531	MN215792	MN329955	MN264031	Raza <i>et al.</i> (2019)
<i>N. saccharicola</i>	CGMCC 3.19362 ^T	MN215788	MN329951	MN264027	Raza <i>et al.</i> (2019)
	LC 12057	MN215789	MN329952	MN264028	Raza <i>et al.</i> (2019)
<i>N. singularis</i>	CGMCC 3.19334 ^T	MN215793	MN329956	MN264032	Raza <i>et al.</i> (2019)
	LC 12068	MN215794	MN329957	MN264033	Raza <i>et al.</i> (2019)
<i>N. sphaerica</i>	LC 2840	KX985965	KY019492	KY019318	Wang <i>et al.</i> (2017)

Table 12. (Continued).

Species	Isolates ¹	GenBank accession numbers ²			References
		ITS	<i>tub2</i>	<i>tef1</i>	
<i>N. vesicularifera</i>	LC 12083	MN215811	MN329974	MN264050	Raza <i>et al.</i> (2019)
	CGMCC 3.19333 ^T	MN215812	MN329975	MN264051	Raza <i>et al.</i> (2019)
<i>N. vesicularis</i>	LC 12055	MN215814	MN329977	MN264053	Raza <i>et al.</i> (2019)
	CGMCC 3.18128 ^T	KX986088	KY019463	KY019294	Wang <i>et al.</i> (2017)
<i>N. zimmermanii</i>	LC 0322	KX985939	KY019467	KY019296	Wang <i>et al.</i> (2017)
	CBS 290.62 ^T	KY385309	KY385317	KY385311	Wang <i>et al.</i> (2017)
	LC 13534	MN215824	MN329987	MN264063	Raza <i>et al.</i> (2019)

¹ CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CMM: Culture Collection of Phytopathogenic Fungi Prof. Maria Menezes; CGMCC: China General Microbiological Culture Collection Center, Institute of Microbiology, Beijing, China; LC: Dr Lei Cai's personal collection deposited in laboratory, housed at Chinese Academy of Sciences (CAS), China. ^T and ^{PT} indicate ex-type and ex-paratype strains, respectively.

²ITS: internal transcribed spacers and intervening 5.8S nrDNA; *tub2*: partial β -tubulin gene; *tef1*: partial translation elongation factor 1- α gene.

Arthrinium and *Apiospora* (Minter 1985, Crous & Groenewald 2013, Wang *et al.* 2017, Raza *et al.* 2019, Pintos & Alvarado 2021).

References: Hudson 1963 (sexual connection), Wang *et al.* 2017, Crous *et al.* 2019a, Raza *et al.* 2019, Pintos & Alvarado 2021 (morphology and phylogeny), Kee *et al.* 2019 (morphology and pathogenicity).

Nigrospora covidalis M. Raza, Qian Chen & L. Cai, *sp. nov.* MycoBank MB 840804. Fig. 42.

Etymology: Refers to the COVID-19 pandemic.

Asexual morph on SNA: Hyphae branched, septate, guttulate, hyaline to pale brown, 2–4 μ m diam. *Conidiophores* micronematous or semi-macronematous, flexuous or straight, hyaline to pale brown. *Conidiogenous cells* monoblastic, solitary, discrete, pale brown, doliform to ampulliform, 5–8.5 \times 4.5–7 μ m (av. = 6.70 \pm 1.4 \times 5.91 \pm 1.2). *Conidia* sparse, discrete on aerial hyphae, pale brown to black, globose or subglobose, 9–14 μ m diam (av. = 12.03 \pm 1.3).

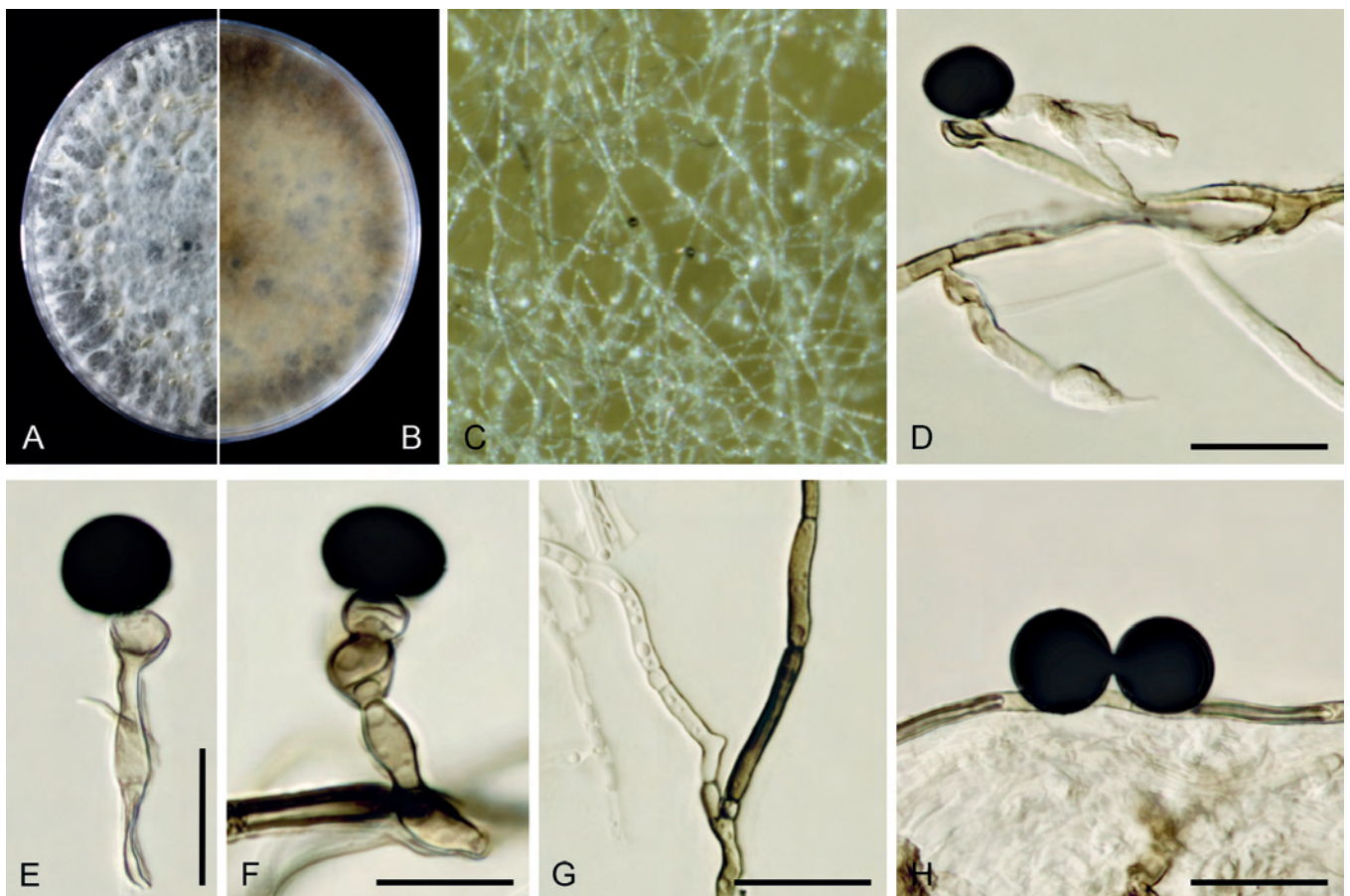


Fig. 42. *Nigrospora covidalis* (ex-type CGMCC 3.20538). A, B. Colony on PDA (front and reverse). C. Sporulation on SNA medium. D–F. Conidiophores with conidia. G. Hyphal growth. H. Conidia. Scale bars = 5 μ m.

Culture characteristics: Colony on PDA fast growing, reaching 86 mm diam in 1 wk after incubation at 25 ± 1 °C; colony sparse, rough surface with fimbriate edge, elevation raised, floccose and irregular at margin; colony from above rough, sparse, white; from below white to black, not producing pigment in PDA media.

Cardinal temperature for growth: Optimum 25 °C, maximum 37 °C, minimum 5 °C.

Typus: China, Jiangxi Province, on *Lithocarpus* sp. (*Fagaceae*), Oct. 2013, Y.H. Gao, N. Zhou & Y. Zhang (**holotype** HMAS 350622, culture ex-type CGMCC 3.20538 = LC 4566).

Additional material examined: China, Jiangxi Province, on *Lithocarpus*, Oct. 2013, Y.H. Gao, N. Zhou & Y. Zhang, culture LC 158337.

Notes: *Nigrospora covidalis* clustered in a well-supported clade closely related to *N. musae* (Fig. 41). Morphologically, *N. covidalis* can be differentiated from *N. musae* in the smaller size of its conidiogenous cells ($5\text{--}8.5 \times 4.5\text{--}7$ μm vs $6.5\text{--}14 \times 6\text{--}9$ μm) and conidia ($9\text{--}14$ μm vs $15\text{--}19.5$ μm). Additionally, vesicles were present in *N. musae* but absent in *N. covidalis*.

Nigrospora globospora M. Raza, Qian Chen & L. Cai, **sp. nov.**
Mycobank MB 840805. Fig. 43.

Etymology: Refers to the globose shape of its conidia.

Asexual morph on SNA: Hyphae smooth, septate, branched, hyaline to pale brown, 1.5–4.5 μm diam. Conidiophores reduced to conidiogenous cells. Conidiogenous cells monoblastic, solitary,

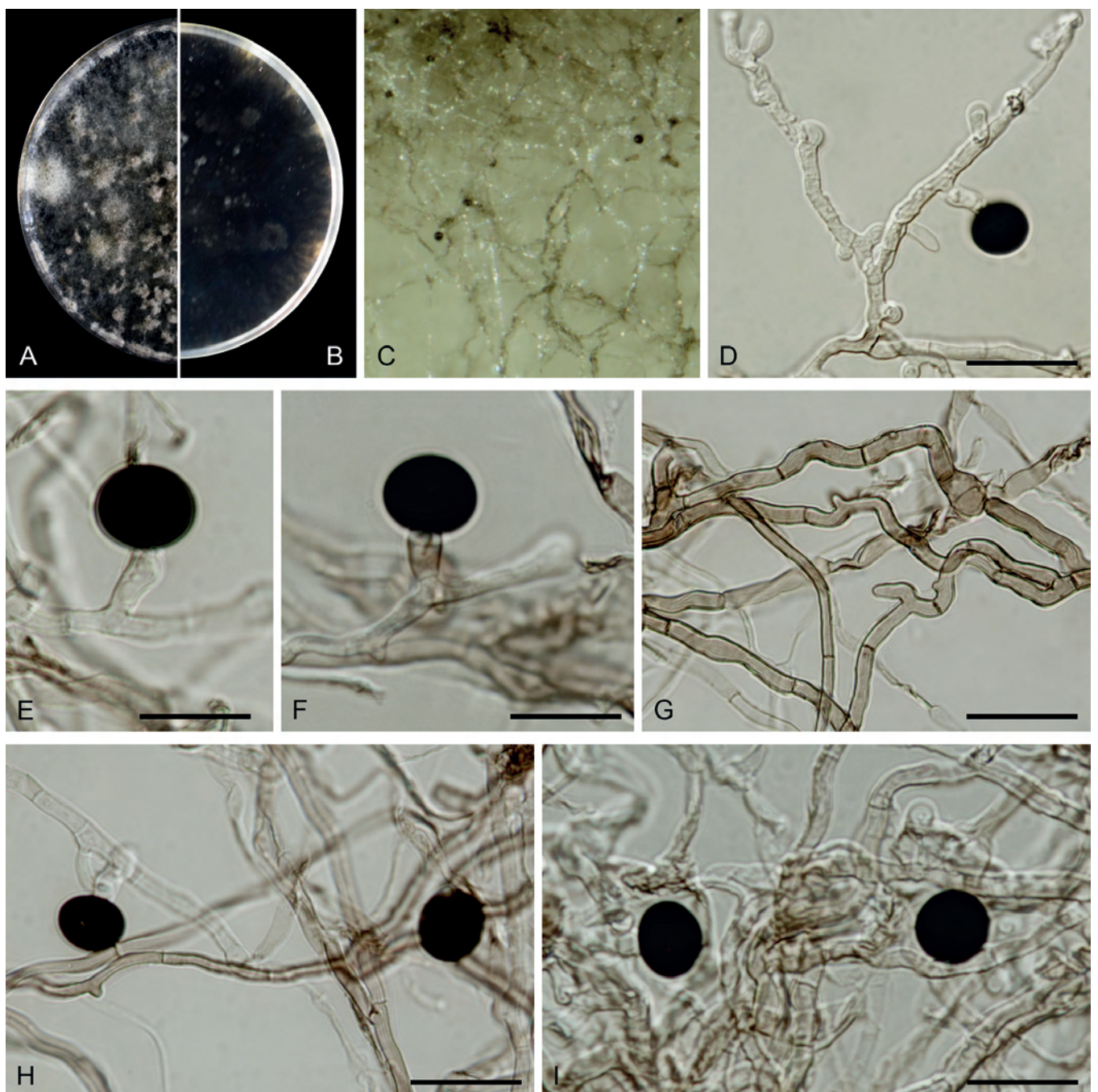


Fig. 43. *Nigrospora globospora* (ex-type CGMCC 3.20539). **A, B.** Colony on PDA (front and reverse). **C.** Sporulation on SNA medium. **D–F.** Conidiophores with conidia. **G.** Hyphal growth. **H, I.** Conidia. Scale bars = 5 μm .

discrete, determinate, sub-spherical or ampulliform, $8.5\text{--}9 \times 3\text{--}4.5 \mu\text{m}$ (av. = $7.39 \pm 1.1 \times 3.8 \pm 0.4$). *Conidia* sparse, discrete on aerial hyphae, black, shiny, mostly ellipsoidal, $8.5\text{--}12 \times 10.5\text{--}13.5 \mu\text{m}$ (av. = $10.51 \pm 0.9 \times 12.11 \pm 0.6$).

Culture characteristics: Colony on PDA fast growing, reaching 89 mm diam in 1 wk after incubation at $25 \pm 1 \text{ }^\circ\text{C}$, colony with rough surface and erose edge, elevation raised, effuse and strongly irregular at margin; colony from above rough, whitish black; from below white to black, not producing pigment in PDA media.

Cardinal temperature for growth: Optimum $25 \text{ }^\circ\text{C}$, maximum $37 \text{ }^\circ\text{C}$, minimum $5 \text{ }^\circ\text{C}$.

Typus: China, Fujian Province, Fuzhou, Wuyishan country, on *Petasites hybridus* (Asteraceae), Aug. 2016, L. Cai (**holotype** HMAS 350624, culture ex-type CGMCC 3.19633 = LC 8397).

Additional material examined: China, Fujian Province, Fuzhou, Wuyishan country, on *Petasites hybridus*, Aug. 2016, L. Cai, culture LC 12441.

Notes: *Nigrospora globospora* clustered with *N. magnoliae* and formed a distinct clade (Fig. 41). Morphologically, *N. globospora* can be differentiated from *N. magnoliae* by its larger conidiogenous cells ($8.5\text{--}9 \times 3\text{--}4.5 \mu\text{m}$ vs $5\text{--}7 \times 5\text{--}6 \mu\text{m}$) and smaller conidia ($8.5\text{--}12 \times 10.5\text{--}13.5 \mu\text{m}$ vs $10\text{--}14 \times 10\text{--}13 \mu\text{m}$).

Nigrospora philosophiae-doctoris M. Raza, Qian Chen & L. Cai, **sp. nov.** MycoBank MB 840803. Fig. 44.

Etymology: Refers to a PhD career in academia, PhD represents the Latin phrase "*philosophiae doctor*".

Asexual morph on SNA: *Hyphae* septate, branched, flexuous or straight, hyaline to pale brown, $1.5\text{--}3.5 \mu\text{m}$ diam. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* monoblastic, discrete, solitary, pale brown, subglobose to ampulliform, $4\text{--}9.5 \times 3\text{--}7.5 \mu\text{m}$ (av. = $6.66 \pm 1.6 \times 5.83 \pm 1.4$). *Conidia* discrete on aerial hyphae, sparse, pale brown to brown, globose or subglobose, $11\text{--}16 \times 8\text{--}14 \mu\text{m}$ (av. = $14.02 \pm 1.4 \times 11.38 \pm 1.6$).

Culture characteristics: Colony on PDA fast growing, reaching 88 mm diam in 1 wk after incubation at $25 \pm 1 \text{ }^\circ\text{C}$, colony medium sparse, rough surface with fimbriate edge, elevation raised, downy, funiculate, floccose and irregular at margin; colony from above; rough, sparse, white; from below; black, not producing pigment in PDA media.

Cardinal temperature for growth: Optimum $25 \text{ }^\circ\text{C}$, maximum $37 \text{ }^\circ\text{C}$, minimum $5 \text{ }^\circ\text{C}$.

Typus: China, Guangxi Region, Baise, Leye country, on *Disporum sessile* (Colchicaceae), Aug. 2017, Z.Y. Ma & L.W. Hou (**holotype** HMAS 350623, culture ex-type CGMCC 3.20540 = LC 13398).

Additional materials examined: China, Guangxi Region, Baise, Leye country, on *Disporum sessile*, Aug. 2017, Z.Y. Ma and L.W. Hou, culture LC 15838.

Notes: *Nigrospora philosophiae-doctoris* clustered in a well-supported clade closely related to *N. sacchari-officinarum* and *N.*

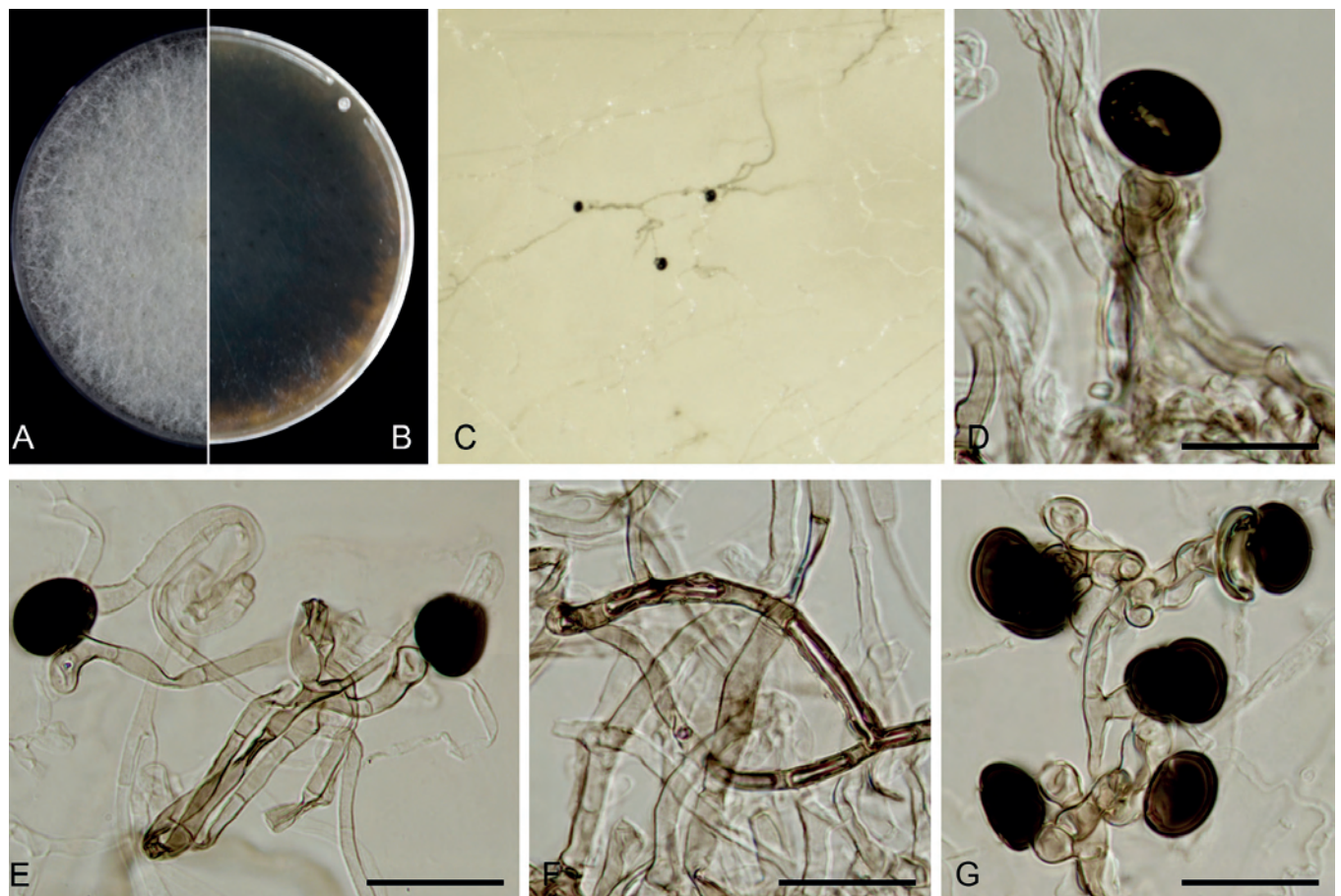


Fig. 44. *Nigrospora philosophiae-doctoris* (ex-type CGMCC 3.20540). **A, B.** Colony on PDA (front and reverse). **C.** Sporulation on SNA medium. **D, E.** Conidiophores with conidia. **F.** Hyphal growth. **G.** Conidia. Scale bars = $5 \mu\text{m}$.

gorkenkoana (Fig. 41). *Nigrospora philosophiae-doctoris* produces smaller conidiogenous cells when compared to those in *N. sacchari-officinorum* and *N. gorkenkoana* ($4\text{--}9.5 \times 3\text{--}7.5 \mu\text{m}$ in *N. philosophiae-doctoris*; $7\text{--}15.5 \times 9\text{--}9.5 \mu\text{m}$ in *N. sacchari-officinorum*; $7\text{--}13.5 \times 4\text{--}9 \mu\text{m}$ in *N. gorkenkoana*), and smaller conidia than those of *N. sacchari-officinorum*. Additionally, vesicles were present in *N. sacchari-officinorum* but absent in *N. philosophiae-doctoris*.

Genome sequenced strain: Nigrospora sphaerica. Unknown, from fruit of *Musa × paradisiaca* (= *Musa sapientum*), collection date and collector unknown, culture CBS 166.26. This Whole Genome Shotgun project has been deposited at GenBank under the accession JALRMJ000000000 (BioProject: PRJNA827019, BioSample: SAMN27594418; present study).

Authors: M. Raza, Q. Chen & L. Cai

Pezizula Tul & C. Tul., *Select. fung. carpol.* (Paris) 3: 182. 1865. Fig. 45.

Classification: *Leotiomyces*, *Leotiomycetidae*, *Helotiales*, *Dermateaceae*.

Type species: Pezizula carpinea (Pers.) Tul. & C. Tul. ex Fuckel., basionym: *Peziza carpinea* Pers., *Syn. meth. fung.*: 673. 1801. Holotype: L 910.261-293. Epitype and ex-epitype strain designated by Chen *et al.* (2016): CBS H-17476, CBS 923.96.

DNA barcodes (genus): ITS, LSU.

DNA barcode (species): *rpb2*. Table 13. Fig. 46.

Ascomata apothecial, erumpent, solitary or in clusters, sessile to short pedicellate. *Disc* pruinose, circular to irregular, pale whitish, orange, yellow, olivaceous, or orange brown to dark brown. *Receptacle* dark brown to olivaceous black, with entire margin, persistent or irregular, often with slightly raised rim. *Peridium* thickened, unequally, two-layered, outer layer comprising of hyaline to dark brown, thick-walled cells, inner layer comprising of thin-walled, hyaline to brown cells. *Hamathecium* comprising smooth, septate, filiform, septate or branched, filamentous paraphyses, tapering towards apex. *Asci* 8- or 4-spored, cylindrical-clavate to clavate, inoperculate, short pedicellate with knob-like pedicle, sometimes crozier present, apically well-developed, thickened, amyloid, with a J+. *Ascospores* smooth, thin-walled, straight or curved, ovoid, fusoid or ellipsoidal, hyaline, guttulate, aseptate to septate, or muriform. *Conidiomata* erumpent, single or clustered, immersed, subglobose, irregular pulvinate to conical or claviform, sometimes stromatic acervular, plane to pustulate. *Conidiophores* smooth, hyaline, simple, branched, acrogenous or acropleurogenous. *Conidiogenous cells* determinate, discrete or integrated, phialidic or indeterminate, proliferating percurrently, cylindrical to ampulliform, giving rise to macro- or microconidia. *Macroconidia* usually present, smooth, thin-walled, aseptate to septate, hyaline, ellipsoidal, pyriform, fusoid or claviform, rounded or pointed at apex, attenuated or rounded with protruding scar at base, guttulate, sometimes form microconidia from minute opening. *Microconidia* usually present, hyaline, smooth, aseptate, thin-walled, cylindrical, rounded at apex, truncate at base, content granular (adapted from Verkley 1999, Chen *et al.* 2016).

Cultural characteristics: Colonies on OA growing fast compared to MEA. Colonies on OA, flat, entire or discrete margins, aerial

mycelium absent or weakly developed with patches, hyaline to buff, reverse concolourous. Colonies on MEA, flat, slightly raised, entire or discrete margins, moderately to well-developed white aerial mycelium, pigmented or non-pigmented.

Optimal media and cultivation conditions: OA and MEA at 18 °C with nuv-light (12 h light, 12 h dark).

Distribution: Worldwide.

Hosts: Pathogens, saprophytes or endophytes on a variety of hosts such as *Abies alba*, *A. balsamea*, *Larix decidua*, *Tsuga canadensis* (*Pinaceae*), *Acer spicatum* (*Sapindaceae*), *Alnus crispa*, *A. glutinosa*, *Carpinus betulus* (*Betulaceae*), *Chamaecyparis* sp. (*Cupressaceae*), *Cornus rugosa* (*Cornaceae*), *Eucalyptus* sp. (*Myrtaceae*), *Fagus sylvatica*, *Quercus robur*, *Castanea sativa* (*Fagaceae*), *Gaultheria shallon* (*Ericaceae*), *Taxus baccata* (*Taxaceae*), *Tilia cordata* (*Malvaceae*), *Rhamnus frangula* (*Rhamnaceae*), *Rubus* sp. (*Rosaceae*).

Disease symptoms: Cankers, but also saprobic.

Notes: *Pezizula*, a discomycetous genus typified by *Pe. carpinea* was established by Tulasne & Tulasne (1865). The type species of *Cryptosporiopsis* (*Cryp. nigra*) was considered the asexual morph of *Pezizula ocellata* (Chen *et al.* 2016), *Cryptosporiopsis* has therefore been synonymised under *Pezizula* (Johnston *et al.* 2014). Previous studies considered *Pezizula*, *Phlyctema* and *Rhizoderma* as congeneric to *Neofabraea*, but these groups present great variation in morphology (Rěblová *et al.* 2011, Johnston *et al.* 2014). Recently, Chen *et al.* (2016) emphasised the usefulness of *rpb2* in resolving the phylogenetic relationships among *Cryptosporiopsis*, *Neofabraea*, and *Pezizula*, and concluded that *Pezizula* represents a separate genus. The genera *Neofabraea* and *Pezizula* have similar apothecia but the excipular tissues are less differentiated in *Neofabraea*. Phialidic conidiogenous cells and strongly curved macroconidia are present in *Neofabraea* species while species of *Pezizula* have two types of conidiogenesis (determinate and phialidic or indeterminate and proliferating percurrently). Species of *Pezizula* and related genera vary in host specificity, but most studies to date have focussed on northern America or Europe. Epitypification of species from *Pezizula* and related genera therefore remains of great importance to stabilise the application of names in this generic complex.

References: Verkley 1999, Abeln *et al.* 2000, Chen *et al.* 2016, Ekanayaka *et al.* 2016 (morphology and phylogeny).

Genome sequenced strain: Pezizula carpinea. Germany, Bad Bentheim, Bentheimer relictwald, near Kuhort, on recently fallen *Carpinus betulus*, 9 Jul. 1996, G. Verkley, culture ex-epitype CBS 923.96. This Whole Genome Shotgun project has been deposited at GenBank under the accession JALRMK000000000 (BioProject: PRJNA827019, BioSample: SAMN27594419; present study).

Authors: M. Raza & L. Cai

Phaeomoniella Crous & W. Gams, *Phytopathol. Medit.* 39: 113. 2000. Fig 47.

Classification: *Eurotiomycetes*, *Chaetothyriomycetidae*, *Phaeomoniellales*, *Celotheliaceae*.



Fig. 45. *Pezicula* spp. **A–G.** Sexual morph. **A, B.** Living on substrate. **A.** Ascomata of *Pezicula chiangraiensis* (holotype MFLU 15-3566). **B.** Dry apothecium of *Pezicula neocinnamomea* (ex-type CBS 100248). **C.** Section through apothecium of *Pezicula ocellata* (CBS 949.97). **D.** Section through peridium of *Pezicula ocellata* (CBS 949.97). **E.** Asci and paraphyses of *Pezicula carpinea* (ex-epitype CBS 923.96). **F.** Fusoid ascospore of *Pezicula chiangraiensis* (holotype MFLU 15-3566). **G.** Ascospores of *Pezicula ocellata* (CBS 949.97). **H–L.** Asexual morph. **H.** Conidiophores, macro- and microconidiogenous cells of *Pezicula fagacearum* (ex-type CBS 112400). **I.** Macroconidiogenous cells giving rise to macroconidia with phialides of *Pezicula fagacearum* (ex-type CBS 112400). **J.** Microconidiogenous cells giving rise to microconidia with phialides of *Pezicula fagacearum* (ex-type CBS 112400). **K.** Macroconidia of *Pezicula neocinnamomea* (ex-type CBS 100248). **L.** Microconidia of *Pezicula pseudocinnamomea* (ex-type CBS 101000). Scale bars: C = 100 μ m, E = 20 μ m, F–I, K, L = 10 μ m, J = 5 μ m. Pictures A, F taken from Ekanayaka *et al.* (2016); B–E, G–L from Chen *et al.* (2016).

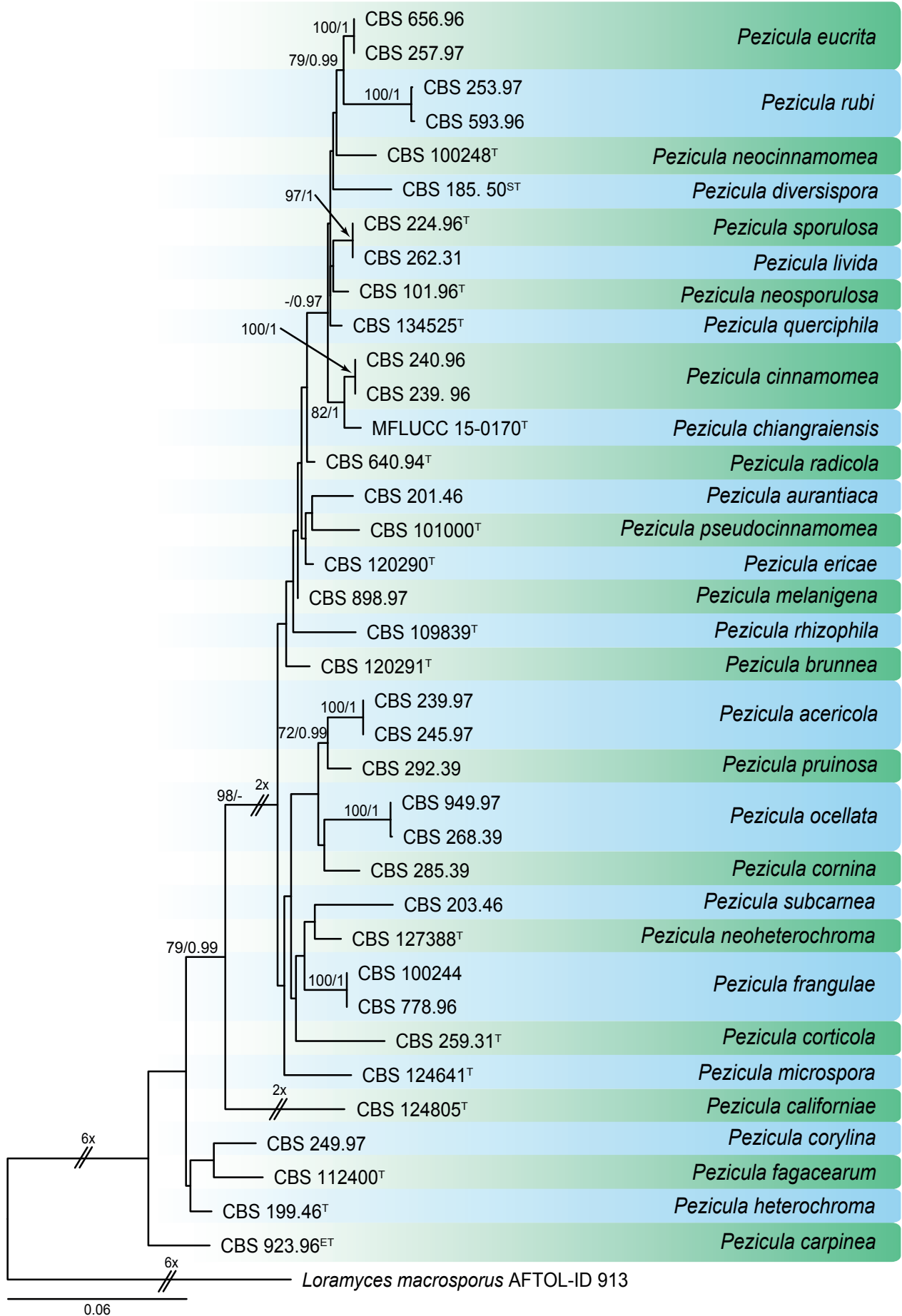


Fig. 46. RAxML phylogram constructed from ITS (490 bp), LSU (799 bp) and *rpb2* (1 045 bp) sequences of all accepted species of *Pezicula*. Maximum likelihood bootstrap support values (> 70 %) and Bayesian posterior probability scores (> 0.95) are indicated on the branches. The tree was rooted to *Loramyces macrosporus* AFTOL-ID 913. GenBank accession numbers are indicated in Table 13. ^T, ^{ET} and ST, indicate ex-type, ex-epitype and ex-sytype strains, respectively. TreeBASE: S26191.

Table 13. DNA barcodes of accepted *Pezizula* spp.

Species	Isolates ¹	GenBank accession numbers ²			References
		ITS	LSU	<i>rpb2</i>	
<i>Pezizula acericola</i>	CBS 239.97	KF376154	KR858884	KF376214	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
	CBS 245.97	KF376153	KR858889	KF376213	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
<i>Pe. aurantiaca</i>	CBS 201.46	KF376150	KR858893	KF376210	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
<i>Pe. brunnea</i>	CBS120291 ^T	KR859103	KR858894	—	Chen <i>et al.</i> (2016)
<i>Pe. californiae</i>	CBS 124805 ^T	KR859104	KR858895	KR859332	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
<i>Pe. carpinea</i>	CBS 923.96 ^{ET}	KR859108	KR858899	KF376158	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
<i>Pe. chiangraiensis</i>	MFLUCC 15-0170 ^T	KU310621	KU310622	KU310623	Ekanayaka <i>et al.</i> (2016)
<i>Pe. cinnamomea</i>	CBS 239.96	KF376102	KR858915	KF376165	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
	CBS 240.96	KF376105	KR858916	KF376163	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
<i>Pe. cornina</i>	CBS 285.39	AF141182	—	—	Abeln <i>et al.</i> (2000)
<i>Pe. corticola</i>	CBS 259.31 ^T	KR859164	KR858956	—	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
<i>Pe. corylina</i>	CBS 249.97	KF376106	KR858960	KF376161	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
<i>Pe. diversispora</i>	CBS 185.50 ST	KR859170	KR858962	—	Chen <i>et al.</i> (2016)
<i>Pe. ericae</i>	CBS120290 ^T	KR859173	KR858965	—	Chen <i>et al.</i> (2016)
<i>Pe. eucrita</i>	CBS 656.96	KF376144	KR858977	KF376208	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
	CBS 257.97	KR859177	KR858969	—	Chen <i>et al.</i> (2016)
<i>Pe. fagacearum</i>	CBS 112400 ^T	KR859201	KR858993	—	Chen <i>et al.</i> (2016)
<i>Pe. frangulae</i>	CBS 778.96	KF376151	KR859001	KF376212	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
	CBS 100244	KF376152	KR858996	KF376211	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
<i>Pe. heterochroma</i>	CBS 199.46 ^T	KR859210	KR859002	—	Chen <i>et al.</i> (2016)
<i>Pe. livida</i>	CBS 262.31	AF141180	—	—	Abeln <i>et al.</i> (2000)
<i>Pe. melanigena</i>	CBS 898.97	KR859211	KR859003	—	Chen <i>et al.</i> (2016)
<i>Pe. microspora</i>	CBS 124641 ^T	KR859212	KR859004	KR859337	Chen <i>et al.</i> (2016)
<i>Pe. neocinnamomea</i>	CBS 100248 ^T	KR859213	KR859005	KF376209	Chen <i>et al.</i> (2016)
<i>Pe. neoheterochroma</i>	CBS 127388 ^T	KR859221	KR859013	KR859338	Chen <i>et al.</i> (2016)
<i>Pe. neosporulosa</i>	CBS 101.96 ^T	KR859223	KR859015	KF376193	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
<i>Pe. ocellata</i>	CBS 949.97	KF376149	KR859025	KF376215	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
	CBS 268.39	KR859232	KR859024	KR859339	Chen <i>et al.</i> (2016)
<i>Pe. pruinosa</i>	CBS 292.39	AF141188	KR859026	—	Abeln <i>et al.</i> (2000), Chen <i>et al.</i> (2016)
<i>Pe. pseudocinnamomea</i>	CBS 101000 ^T	KR859235	KR859027	KR859340	Chen <i>et al.</i> (2016)
<i>Pe. querciphila</i>	CBS 134525 ^T	JX144750	—	—	Chen <i>et al.</i> (2016)
<i>Pe. radicolica</i>	CBS 640.94 ^T	KR859236	KR859028	—	Chen <i>et al.</i> (2016)
<i>Pe. rhizophila</i>	CBS 109839 ^T	KR859238	KR859030	—	Chen <i>et al.</i> (2016)
<i>Pe. rubi</i>	CBS 253.97	KF376100	KR859042	KF376204	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
	CBS 593.96	KF376101	KR859045	KF376203	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
<i>Pe. sporulosa</i>	CBS 224.96 ^T	AF141172	KR859053	KF376201	Chen <i>et al.</i> (2016), Ekanayaka <i>et al.</i> (2016)
<i>Pe. subcarnea</i>	CBS 203.46	AF141171	KR859059	—	Abeln <i>et al.</i> (2000), Chen <i>et al.</i> (2016)

¹ CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand.

^T, ^{ET} and ST indicate ex-type, ex-epitype and ex-syntype strains, respectively.

² ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial 28S large subunit nrRNA gene; *rpb2*: partial RNA polymerase II second largest subunit gene.

Type species: Phaeomoniella chlamydospora (W. Gams *et al.*) Crous & W. Gams, basionym: *Phaeoacremonium chlamydosporum* W. Gams *et al.*, Mycologia 88: 792. 1996. Holotype and ex-type strain: CBS H-5709, CBS 229.95.

DNA barcode (genus): LSU.

DNA barcodes (species): ITS and *tef1*. Table 14. Fig. 48.

Mycelium consisting of branched, septate hyphae. *Hyphae* simple, or occurring in strands, verruculose to tuberculate, green-brown, becoming paler to hyaline towards the conidiogenous region. Chlamydospore-like structures present, forming microsclerotia on water agar. *Conidiophores* micronematous, arising from aerial or



Fig. 47. *Phaeoconiella chlamydospora* (culture STE-U 6384). **A–C.** Symptoms of Petri disease on grapevines. **A, B.** Brown-black discoloration of vascular tissue of grapevine rootstock. **C.** Brown-black streaking in vertical section of an infected rootstock. **D, E.** Conidiomata on grapevine wood. **F.** Section through a conidioma. **G, H.** Conidiogenous cells from conidiomata. **I.** Conidia from conidiomata. **J–R.** Structures from the hyphomycetous stage. **J.** Mycelium and conidial droplets. **K–M, O.** Conidiophores. **N, P.** Conidiogenous cells. **Q.** Adelophialide. **R.** Conidia. Scale bars: D = 500 µm; E, J = 100 µm; F, G, I, K, O, P, R = 10 µm. G applies to H; K applies to L–N; P applies to Q.

submerged hyphae, erect, simple, subcylindrical, green-brown, becoming paler toward the tip, verruculose to smooth, septate. *Conidiogenous cells* terminal, monophialidic, elongate-ampulliform to lageniform or subcylindrical, with a terminal, narrowly funnel-shaped collarette. *Conidia* becoming aggregated into round,

slimy heads at the apices of conidiogenous cells, pigmented, aseptate, smooth-walled, oblong-ellipsoidal to obovate, straight. *Synasexual morph* phoma-like, induced in culture and on infected canes. *Conidiomata* brown, pycnidial, globose, up to 70 µm diam. *Conidiophores* pale brown, subcylindrical, smooth, 1-

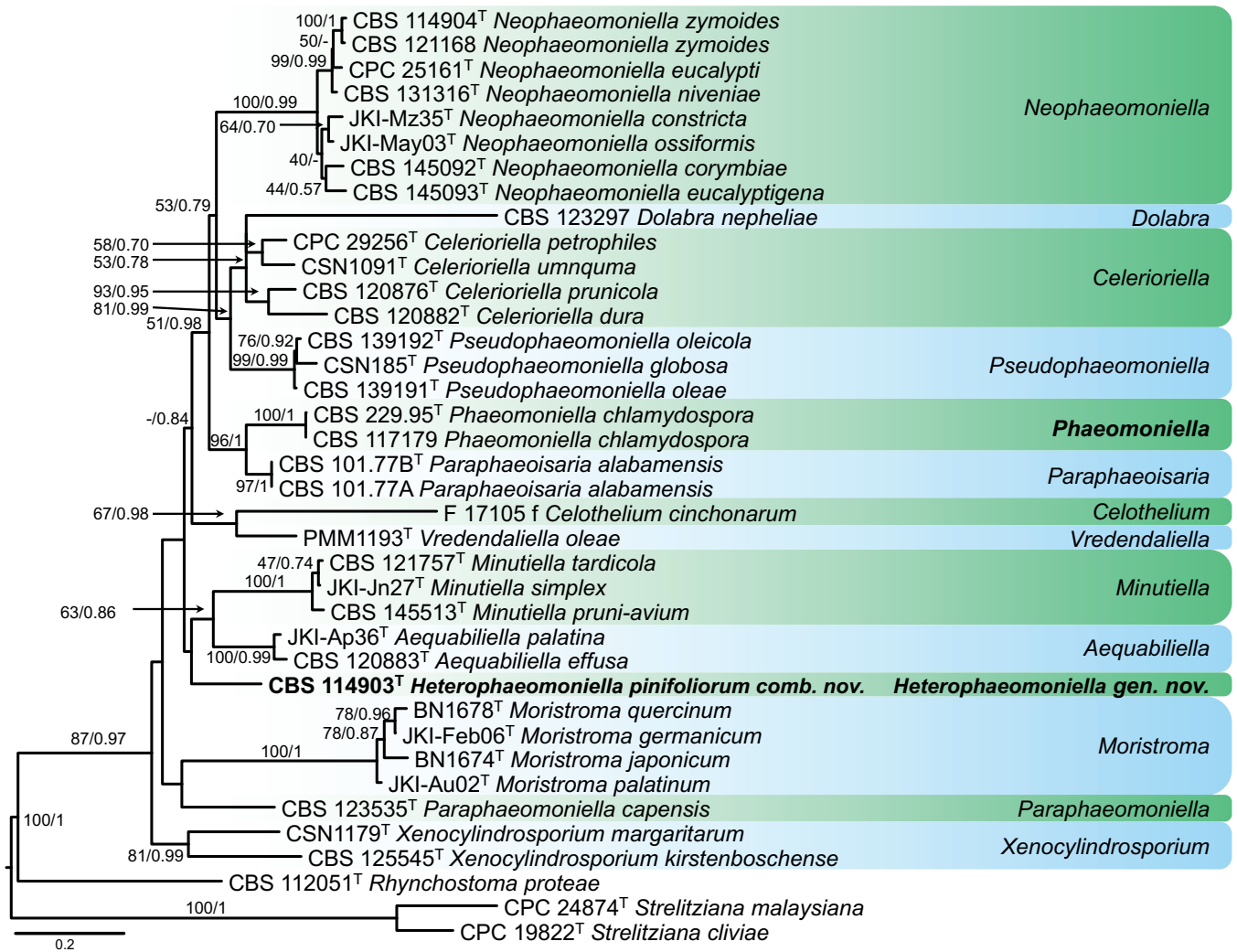


Fig. 48. Maximum likelihood phylogram of the *Phaeomoniellales* constructed from ITS (636 bp), 28S (869 bp), *tef1* (274 bp) and *tub2* (423 bp) sequences. Maximum likelihood bootstrap support values (> 40 %) and Bayesian posterior probability scores (> 0.70) are shown at the nodes. The novel taxon is printed in **bold**. The phylogenetic tree was rooted to *Rhynchostoma proteae* CBS 112051, *Strelitziana cliviae* CPC 19822 and *S. malaysiana* CPC 24874. GenBank accession numbers of *Phaeomoniella* and *Heterophaeomoniella* are listed in Table 14. † indicates ex-type strain. TreeBASE: S27583.

Table 14. DNA barcodes of accepted species in *Phaeomoniella* and *Heterophaeomoniella*.

Species	Isolates ¹	GenBank accession numbers ²				References
		ITS	LSU	<i>tef1</i>	<i>tub2</i>	
<i>Phaeomoniella chlamydospora</i>	CBS 229.95 [†]	NR_155612	NG_066265	—	AF253968	Groenewald <i>et al.</i> (2001), Vu <i>et al.</i> (2019)
	CBS 117179	KF764544	—	KF764636	KF764683	Úrbez-Torres <i>et al.</i> (2014)
<i>Heterophaeomoniella pinifoliorum</i>	CBS 114903 [†]	DQ270240	MN861685	MN861678	KR260452	Lee <i>et al.</i> (2006), Úrbez-Torres <i>et al.</i> (2015), present study

¹ CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; † indicates ex-type strain.

² ITS: internal transcribed spacer regions, including the 5.8S nrDNA; LSU: partial 28S large subunit nrRNA gene; *tef1*: partial translation elongation factor 1- α gene.

multiseptate. *Conidiogenous cells* monopialidic, terminal and intercalary, variable in shape, but frequently subcylindrical to oblong-ellipsoidal. *Conidia* exuding from pycnidia in a droplet or cirrus, hyaline, oblong-ellipsoidal to obovate, permanently straight. *Sexual morph* unknown.

Cultural characteristics: Colonies on MEA (reverse) grey olivaceous to olivaceous black, with sparse aerial mycelium.

Optimal media and cultivation conditions: PDA or MEA to induce sporulation of the asexual morph, while for the synasexual morph WA with sterilised pine needles is recommended, incubated at 25 °C.

Distribution: Worldwide.

Hosts: Mainly pathogen of grapevine (*Vitis vinifera* and *Vitis* spp.; *Vitaceae*). One of the causal agents of Petri disease and esca on

grapevines. Once reported on kiwi fruit in Italy (di Marco *et al.* 2000) and olive trees in California (Úrbez-Torres *et al.* 2013).

Disease symptoms: Brown to black discolouration of vascular tissue; streaking symptoms when vertically sectioned and brown to black spots (goo-like) when cross-sectioned. Young vines with Petri disease show stunted growth, shoot dieback and in severe conditions, the young vines can die.

Notes: Currently only one species resides in the genus *Phaeomoniella*. *Phaeomoniella pinifoliorum* groups together with *Paraphaeomoniella capensis*, being distinctly different from *Pa. chlamydospora*. Several species described in *Phaeomoniella* were placed into new genera including *Aequabiliella*, *Celerioriella*, *Minutiella*, *Neophaeomoniella* and *Paraphaeomoniella*. Morphological variation motivated the introduction of new genera with some genera that only formed the coelomycetous morph and no hyphomycete morph (Crous *et al.* 2015c). Available sequence data mostly include ITS and LSU, only limited *tef1* sequences are available.

Genome sequenced strain: *Phaeomoniella chlamydospora*. USA, California, Riverside County, Coachella Valley, 33.617467 N, 116.065139 W, Nov. 2011, collector unknown, isolate UCR-PC4. This Whole Genome Shotgun project has been deposited at GenBank under the accession LCWF00000000 (BioProject: PRJNA261774, BioSample: SAMN03077702; Morales-Cruz *et al.*, 2015).

Heterophaeomoniella L. Mostert, C.F.J. Spies, Halleen & Gramaje, **gen. nov.** MycoBank MB 835744. Table 14. Fig. 48.

Etymology: “Heter” meaning other; morphologically similar, but phylogenetically different from *Phaeomoniella*.

Mycelium densely interwoven, forming globular to ovoid vesicles. **Phialides** commonly simple, inflated, sometimes integrated as swollen cells into toruloid hyphal segments, usually without an obvious collarette. **Conidia** hyaline, cylindrical to ovoid, often slightly curved to allantoid, potentially reproducing in a yeast-like fashion after dehiscence, secondary conidiation common with the yeast-like conidia arising mostly from phialidic apertures at the ends of primary conidia. Vesicular **chlamydospores** abundant, hyaline or subhyaline, globose to subglobose, formed singly or in chains (from Lee *et al.* 2006).

Type species: *Heterophaeomoniella pinifoliorum* (Hyang B. Lee *et al.*) L. Mostert, C.F.J. Spies, Halleen & Gramaje. Holotype and ex-type culture: SFC P00327, CBS 114903 = SFCCW202.

Notes: A new genus name is proposed for *Phaeomoniella pinifoliorum*. Only one isolate of *Phaeomoniella pinifoliorum* has been found to date. This isolate is phylogenetically distant from *Phaeomoniella* (Fig. 48). *Phaeomoniella zymoides* and *Pa. pinifoliorum* were described by Lee *et al.* (2006) from pine needles in Korea. *Phaeomoniella zymoides* was renamed as *Neophaeomoniella zymoides* (H.B. Lee *et al.*) Crous (Crous *et al.* 2015c), being distinct from *Pa. chlamydospora*, although it was initially a sister clade to *Pa. chlamydospora* when less taxa were included the phylogeny of Lee *et al.* (2006). *Phaeomoniella pinifoliorum* was found to differ from *Pa. chlamydospora* in optimal growth in culture (Lee *et al.* 2006). Furthermore, *Pa. pinifoliorum* produced little to no aerial mycelium in comparison with *Pa. chlamydospora* (Lee *et al.* 2006).

Heterophaeomoniella pinifoliorum (Hyang B. Lee *et al.*) L. Mostert, C.F.J. Spies, Halleen & Gramaje, **comb. nov.** MycoBank MB 835759.

Basionym: *Phaeomoniella pinifoliorum* Hyang B. Lee *et al.*, Mycologia 98: 605. 2006.

Description and illustration: Lee *et al.* (2006).

Typus: Korea, Mount Juwang, Gyung-sangbug-do, on needles of *Pinus densiflora* (Pinaceae), 20 Jan 2004, H.B. Lee (**holotype** SFC P00327, culture ex-type CBS 114903 = SFCCW202).

References: Crous *et al.* 1996, Crous & Gams 2000, Damm *et al.* 2010, Chen *et al.* 2015a, Crous *et al.* 2015c (morphology and systematics); Larignon & Dubos 1997, Mugnai *et al.* 1999, Pascoe & Cottral 2000, Gatica *et al.* 2001, Halleen *et al.* 2003, Luque *et al.* 2009, Gramaje *et al.* 2010, White *et al.* 2011, Diaz & Latorre 2014 (symptoms and pathogenicity); Groenewald *et al.* 2000, Ridgway *et al.* 2002, Whiteman *et al.* 2002, Overton *et al.* 2004, Retief *et al.* 2005, Martos *et al.* 2011, Martin *et al.* 2012, Pouzoulet *et al.* 2013, Úrbez-Torres *et al.* 2015 (detection); Mostert *et al.* 2000, Tegli *et al.* 2000, Borie *et al.* 2002, Pottinger *et al.* 2002, Tello *et al.* 2010 (genetic diversity); Antonielli *et al.* 2014, Morales-Cruz *et al.* 2015 (genomes).

Authors: L. Mostert, C.F.J. Spies, F. Halleen & D. Gramaje

Phytophthora de Bary, J. Roy. Agric. Soc. England 12: 240. 1876. Figs 49–51.

Classification: Stramenipila, Oomycota, Peronosporomycetes, Peronosporales, Peronosporaceae.

Fig. 49. Morphological structures of *Phytophthora*. **A.** Coenocytic, irregular coralloid hyphae of *Phytophthora xheterohybrida*. **B.** Catenulate, globose to subglobose and irregular hyphal swellings of *Phytophthora pseudosyringae*. **C., D.** Papillate, slightly asymmetric caducous sporangia of *Phytophthora tropicalis* with basal plug. **C.** Elongated-ovoid with medium-length pedicel. **D.** Pyriform with long pedicel. **E.** Compound sympodium of *Phytophthora tropicalis* sporangia. **F.** Bipapillate, laterally attached distorted sporangium of *Phytophthora citrophthora*. **G.** Semipapillate, ovoid to obpyriform sporangium of *Phytophthora plurivora*. **H.** Ovoid nonpapillate sporangium of *Phytophthora xcambivora*. **I.** Internal extended sporangial proliferation of *Phytophthora xcambivora*. **J.** Internal nested sporangial proliferation of *Phytophthora xcambivora* and release of zoospores with flagella (arrows). **K.** Zoospore cysts of *Phytophthora cinnamomi* germinating directly with a hypha and after release of a secondary zoospore (arrow; diplanetism). **L.** Zoospore cysts of *Phytophthora cinnamomi* germinating directly with hyphae or by forming a microsporangium (arrow). **M.** Terminal thin-walled chlamydospore of *Phytophthora cinnamomi*. **N.** Lateral, sessile thick-walled chlamydospore of *Phytophthora meadii*. **O.** Elongated oogonium of *Phytophthora attenuata* with long-tapering curved base, a conspicuous basal plug, a subglobose plerotic oospore containing a lipid globule, and a paragynous antheridium. **P.** Globose oogonium of *Phytophthora plurivora* with tapering curved base, a plerotic oospore containing a lipid globule and a paragynous antheridium with finger-like projection (arrow). **Q.** Oogonium of the heterothallic *Phytophthora cinnamomi* resulting from an A1×A2 cross, with golden-brown wall, thick-walled plerotic oospore containing multiple lipid globules, and an amphigynous bicellular antheridium. **R.** Oogonia of the heterothallic *Phytophthora xcambivora* resulting from an A1×A2 cross, with an ornamented-wavy wall, a plerotic oospore and a bicellular amphigynous antheridium (arrow) or smooth-walled with an aplerotic oospore and a unicellular amphigynous antheridium. **S.** Oogonium of *Phytophthora uniformis* with a thin stalk and wavy wall, an aplerotic oospore containing a large lipid globule, a bicellular amphigynous and a secondary paragynous (arrow) antheridium. **T.** Comma-shaped oogonium of *Phytophthora xmultiformis*, with ornamented, golden-brown wall and unicellular amphigynous antheridium. Scale bars = 25 µm; T applies to A–D and F–T.



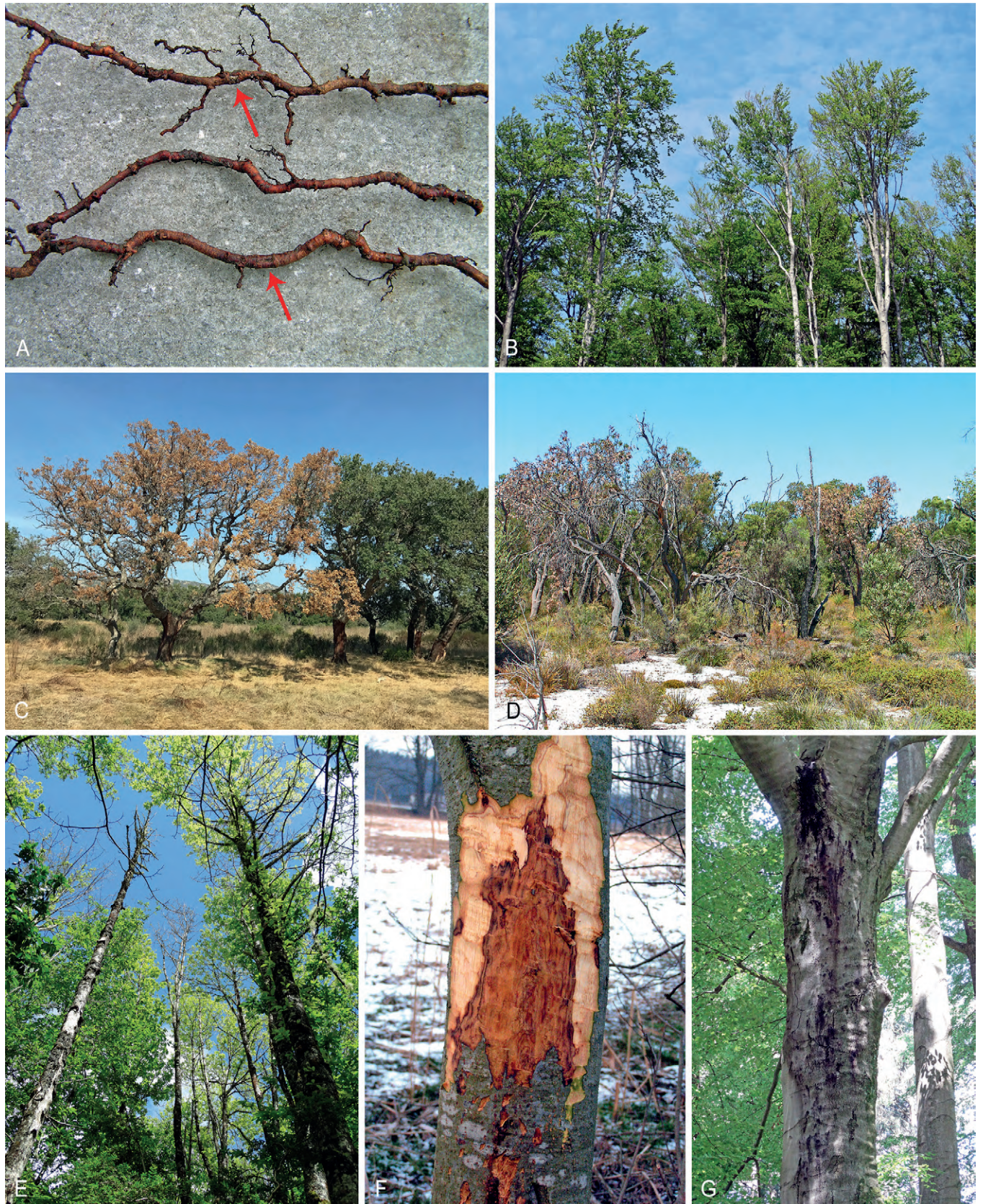


Fig. 50. Phytophthora diseases of forest trees. **A.** Small woody roots of a mature *Quercus robur* with severe losses of fine roots and lateral roots and bark lesions (arrows) caused by *Phytophthora plurivora* and *Phytophthora quercina*. **B.** Chlorosis, microphyllly, thinning and dieback of *Fagus sylvatica* due to root and collar rot caused by *Phytophthora ×cambivora*. **C.** Acute wilting and death of *Quercus suber* due to a girdling collar rot lesion caused by *Phytophthora cinnamomi*. **D.** Extensive dieback and collapse of a *Banksia* woodland caused by *Phytophthora cinnamomi*. **E.** Chlorosis, thinning, dieback and mortality of *Castanea sativa* caused by *Phytophthora cinnamomi*. **F.** Orange-brown, tongue-shaped, active inner bark lesion caused by *Phytophthora ×alni* on *Alnus incana*. **G.** Aerial bleeding canker caused by *Phytophthora ×cambivora* on *Fagus sylvatica*.

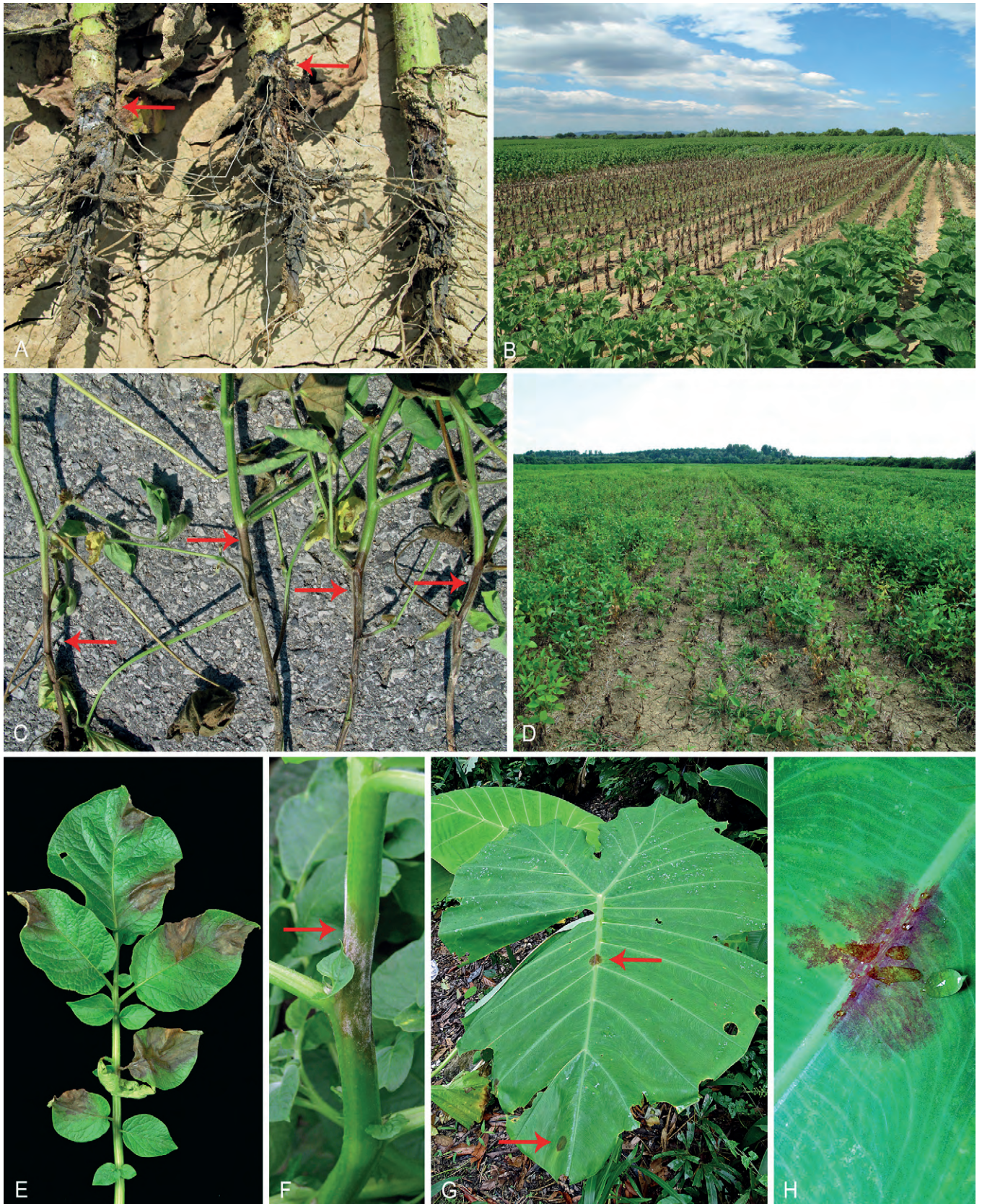


Fig. 51. Phytophthora diseases of agricultural plants. **A.** Root and collar rot (arrows) of *Helianthus annuus* caused by *Phytophthora rosacearum*. **B.** Patch dieback and mortality of *Helianthus annuus* caused by *Phytophthora rosacearum* following heavy rain and temporary waterlogging. **C.** Stem rot (arrows) of *Glycine max* caused by *Phytophthora sojae*. **D.** Patch dieback and mortality of *Glycine max* caused by *Phytophthora sojae* following heavy rain and temporary waterlogging. **E.** Late blight on *Solanum tuberosum* leaves caused by *Phytophthora infestans*. **F.** Late blight on *Solanum tuberosum* stem with white masses of sporangia (arrow). **G, H.** Necrotic lesions (arrows) caused by *Phytophthora colocasiae* on leaves of *Colocasia esculenta*. Pictures A–D courtesy to Dr Željko Tomić, Center for Plant Protection, Zagreb, Croatia; E, F courtesy to Dr David Cooke, The James Hutton Institute, Dundee, UK.

Type species: Phytophthora infestans (Mont.) de Bary, basionym: *Botrytis infestans* Mont., Bull. Sci. Soc. Philom. Paris 13: 313. 1845; **holotype** of *B. infestans*: **France**, from leaves of *Solanum tuberosum* (*Solanaceae*) “Sur les fanes de pomme de terre” M. Vernois, coll. H. Montagne, dep. on 18 Aug. 1845, Hi.C. Montagne FUSION94490 in PC; additional synonym: *Peronospora infestans* (Mont.) Casp., in Rabenhorst, Klotzschii Herb. Viv. Mycol. Ed. II, Cent. 19: no. 1879 (1854). **Netherlands**, from infected *Solanum tuberosum*, 1993, A. Drenth (**epitype** designated here CBS H-24657, MBT 10005612, culture ex-epitype CBS 147289).

DNA barcodes (genus): LSU, ITS, *cox1*.

DNA barcodes (species): ITS, *Btub*, *TigA*, *cox1*. Table 15. Figs 52–56.

Mycelium hyaline, consisting of individual hyphae 3–8 µm diam, generally coenocytic (Fig. 49A) with septa occurring only in ageing cultures. *Hyphae* branched with a conspicuous constriction at the base of lateral hyphae, coralloid, nodose, smooth, swollen, tuberculate or undulate (Fig. 49A); *hyphal swellings* spherical, ellipsoid, appressoria-like or irregular-elongated shape, occurring terminally, laterally or intercalary, often in chains (catenulate; Fig. 49B) or groups; *hyphal aggregations* occasionally present, originated by clusters of lateral hyphae or hyphae twisting around each other. *Sporangia*, or *zoosporangia*, borne on thin-walled sporangiophores, variable in shape and size (Fig. 49C–J), mostly spherical, subspherical, ovoid, obovoid, ellipsoid, elongated, limoniform, pyriform, obpyriform to turbinate, obturbinate, ampulliform and distorted, sometimes containing a large vacuole at maturity; *sporangial tip* either with a conspicuous protruding papilla at the apex (papillate; Fig. 49C–E), sometimes laterally displaced, bipapillate (Fig. 49F) or tripapillate, or with an inconspicuous papilla (semipapillate; Fig. 49G), or nonpapillate (Fig. 49H–I); *sporangial base* round or tapered, often with a prominent plug, a globose swelling or a conspicuous narrowing, and occasionally with laterally attached sporangiophore (Fig. 49F); persistent or caducous breaking off below a basal plug separating a short (< 5 µm), intermediate (5–20 µm; Fig. 49C) or long pedicel (> 20 µm; Fig. 49D) from the bearing sporangiophore; pedicel length mostly species specific; *sporangial proliferation* externally with hyphae arising close to sporangial base and forming monochasial or dichasial, lax or dense-compound sympodia (Fig. 49E), and internally, both in an extended or nested way (Fig. 49I–J), only occurring in species with nonpapillate sporangia; *Phytophthora* species with a primarily aerial lifestyle usually form papillate or semipapillate, caducous sporangia in more or less compound sympodia (Fig. 49E). In contrast, *Phytophthora* species with a primarily aquatic or soilborne lifestyle form nonpapillate or semipapillate, persistent sporangia on unbranched sporangiophores or in lax sympodia; sporangia usually germinate indirectly via release of zoospores or — on solid agar or in oxygen-depleted aqueous solutions — directly with one or more germ tubes which usually emerge at the sporangial apex. *Zoospores* are fully differentiated inside the sporangium and discharged through a narrow to wide exit pore at the sporangial apex into an ephemeral membranous vesicle, reniform (kidney-like), motile with two heterokont flagella developing from the concave side; chemotactically attracted to and encysting on the surface of host tissues; *zoospore cysts* germinate directly by forming hyphae or a secondary microsporangium (Fig. 49K–L) or indirectly by releasing a secondary zoospore (= diplanetism; Fig. 49K). *Chlamydozoospores* are produced by some *Phytophthora*

species, thin-walled in soilborne and aquatic species (Fig. 49M) or thick-walled in aerial species (Fig. 49N), formed either individually or in clusters, differentiated at the tip of hyphae (terminal; Fig. 49M), laterally on short hyphae or sessile (Fig. 49N) or intercalary, with globose, ellipsoid or irregular shape, sometimes with one or multiple radiating hyphal extensions. *Gametangia* produced by homothallic species in single culture and by heterothallic species only when individuals of the opposite compatibility types (= mating types) A1 and A2 are paired; *oogonia* globose to subglobose (Fig. 49P–S), sometimes elongated (Fig. 49O), pyriform, ellipsoid, comma-shaped (Fig. 49T), tubular or excentric, with a tapering (Fig. 49O, Q, T) or rounded base (Fig. 49P, R, S), occasionally with a curved, twisted or long thick oogonial stalk; oogonial wall smooth (Fig. 49P, R), wavy (Fig. 49Q, S), flexuose (Fig. 49O) or ornamented with bullate protuberances (verrucose; Fig. 49R, T), mostly hyaline but they may become pigmented golden- to dark-brown with age (Fig. 49Q, T); *oospores* mostly globose to subglobose (Fig. 49P–T) or less frequently elongated (Fig. 49O), thick-walled, near-plerotic to plerotic (Fig. 49O–Q, T) or aplerotic (Fig. 49R–S), usually containing one large or less frequently multiple smaller lipid globules (ooplasts); *antheridia* attached to the oogonium laterally (paragynous; Fig. 49O–P) or surrounding the oogonial stalk (amphigynous; Fig. 49Q–T)), single- (Fig. 49O–R, T) or two-celled (Fig. 49Q–S), sometimes with finger-like hyphal projections (Fig. 49P); homothallic *Phytophthora* species amphigynous, paragynous or with both types of antheridial insertion; heterothallic *Phytophthora* species always form amphigynous antheridia but sometimes one or multiple additional paragynous antheridia can be observed, in particular when A2 mating type isolates are selfing (main references for morphology: Blackwell 1949, Brasier & Griffin 1979, Erwin & Ribeiro 1996, Jung *et al.* 1999, 2003, 2011, 2017a, b, Jung & Burgess 2009).

Culture characteristics: Colonies always white with chrysanthemum, petallate, petaloid, radiate, stellate, striate, rosaceous, dendroid or uniform patterns; on V8-juice agar (V8A) and carrot agar (CA) appressed, felty, or with limited to fluffy aerial mycelium, in some species umbonate in the centre of the colony, with round or irregular margins; largely submerged on CMA; on PDA and MEA often with slow growth, felty to cottony aerial mycelium, and round to irregular, sometimes submerged margins (Brasier & Griffin 1979, Erwin & Ribeiro 1996, Jung *et al.* 1999, 2002, 2003, 2011, 2017a, b, 2021, Brasier *et al.* 2004, Jung & Burgess 2009, Rea *et al.* 2010, 2011, Bertier *et al.* 2013a, Yang & Hong 2013, Henricot *et al.* 2014, Scanu *et al.* 2014a, 2015, Burgess *et al.* 2018).

Optimal media and cultivation conditions: A range of selective agar media available for *Phytophthora* isolations with PARPNH agar and Synthetic Mucor Agar (SMA) being most commonly used (Elliott *et al.* 1966, Masago *et al.* 1977, Jeffers & Martin 1986, Erwin & Ribeiro 1996, Jung *et al.* 2000, 2002, 2021). V8A, CA prepared from grated carrots or carrot juice and — for *Phy. infestans* — rye agar at 20 °C in the dark to stimulate the production of gametangia (Brasier 1967, Erwin & Ribeiro 1996, Jung *et al.* 1999, Scanu *et al.* 2014a) which, depending on the *Phytophthora* species, predominantly occurs in the centre of the colony, confined to fertile patches of dense mycelium or at the margins of the colony close to the Petri dish walls. Chlamydozoospores and hyphal swellings frequently differentiated at the margins of the colony. V8A or CA discs from growing colonies submerged in nonsterile soil extract water under natural daylight at 18–24 °C to induce the production of sporangia (Erwin & Ribeiro 1996, Jung *et al.* 1996). Release of zoospores from mature sporangia occurs readily in most *Phytophthora* species but

can be stimulated by incubation for 30 min at 5–8 °C and returning to room temperature (chilling; Erwin & Ribeiro 1996). Long-term storage either cryogenic under liquid nitrogen (Mchau & Coffey 1995) or conventional on V8A, CA or PDA, sealed and double-bagged, in Petri dishes, on agar slants or as agar discs in tubes, either submerged in sterile distilled water or non-submerged, or on sterile hemp seeds submerged in sterile distilled water; incubation temperature 15–25 °C for tropical species and 5–14 °C for species from other climatic regions (cf. Boesewinkel 1976, Brasier & Griffin 1979, Erwin & Ribeiro 1996, Aragaki & Uchida 2001, Jung *et al.* 2002, 2017a, 2020, Pérez-Sierra *et al.* 2013, Ann *et al.* 2016).

Distribution: Worldwide.

Hosts: Apart from primarily aquatic species from phylogenetic Clades 6 and 9 with a predominant lifestyle as saprotrophic litter decomposers and opportunistic pathogens (Brasier *et al.* 2003a, Jung *et al.* 2011, 2020, Yang & Hong 2013), most *Phytophthora* species are primary plant pathogens causing serious damage to horticultural, ornamental, forestry and natural terrestrial, riparian and marine ecosystems. The genus *Phytophthora* has a particularly wide range of host plants within the *Dicotyledoneae*, *Monocotyledoneae*, *Acrogymnospermae* and *Polypodiopsida*. Many *Phytophthora* species are host-specific or have very limited host ranges, often within a plant genus or family, *i.e.* *Phy. abietivora* on *Abies fraseri*, *Phy. agathidicida* on *Agathis australis*, *Phy. aleatoria* and *Phy. pinifolia* on *Pinus radiata*, *Phy. amaranthi* on *Amaranthus tricolor*, *Phy. andina*, *Phy. betacei* and *Phy. infestans* on *Solanaceae* species, *Phy. austrocedrae* on *Austrocedrus chilensis* and *Juniperus communis*, *Phy. botryosa* on *Hevea brasiliensis*, *Phy. cajani* on *Cajanus cajan*, *Phy. captiosa* and *Phy. fallax* on *Eucalyptus* spp., *Phy. castanetorum* on *Castanea sativa*, *Phy. clandestina* on *Trifolium subterraneum*, *Phy. chesapeakeensis* and *Phy. gemini* on *Zostera* spp., *Phy. cocois* on *Cocos nucifera*, *Phy. cyperi* on *Cyperus* spp., *Phy. flexuosa* on *Fagus hayatae*, *Phy. fragariae* on *Fragaria* × *ananassa*, *Phy. glovera* on *Nicotiana tabacum*, *Phy. idaei* and *Phy. rubi* on *Rubus idaeus*, *Phy. ilicis* on *Ilex aquifolium*, *Phy. intricata* on *Quercus tarokoensis*, *Phy. ipomoeae* on *Ipomoea* spp., *Phy. lateralis* on *Chamaecyparis* spp. and *Taxus brevifolia*, *Phy. medicaginis* on *Medicago sativa*, *Phy. megakarya* on *Theobroma cacao*, *Phy. mirabilis* on *Mirabilis jalapa*, *Phy. oleae* on *Olea europea*, *Phy. phaseoli* on *Phaseolus lunata*, *Phy. pisi* on *Pisum sativum* and *Vicia faba*, *Phy. pistaciae* on *Pistacia vera*, *Phy. pluvialis* on *Pseudotsuga menziesii* and *Pinus radiata*, *Phy. primulae* on *Primula* spp., *Phy. pseudotsugae* on *Pseudotsuga menziesii*, *Phy. quercina*, *Phy. quercetorum* and *Phy. tyrrhenica* on *Quercus* spp., *Phy. quininea* on *Cinchona* spp., *Phy. sojae* on *Glycine max*, *Phy. terminalis* on *Pachysandra terminalis*, *Phy. trifolii* on *Trifolium* spp., *Phy. tubulina* and *Phy. vulcanica* on *Fagus sylvatica*, *Phy. vignae* on *Vigna unguiculata* and *V. angularis*, *Phy. ×alni*, *Phy. ×multiformis* and *Phy. uniformis* on *Alnus* spp. (Crandall 1947, Buddenhagen & Young 1957, Amin *et al.* 1978, Brasier & Griffin 1979, Hamm & Hansen 1983, Galindo & Hohl 1985, Taylor *et al.* 1985, Hansen & Maxwell 1991, Wilcox *et al.* 1993, Kennedy & Duncan 1995, Erwin & Ribeiro 1996, Jung *et al.* 1999, 2000, 2017a, b, 2018a, Mirabolfathy *et al.* 2001, Hansen *et al.* 2000, 2012, Flier *et al.* 2002, Brasier *et al.* 2004, Dick *et al.* 2006, Greslebin *et al.* 2007, Tyler 2007, Balci *et al.* 2008, Durán *et al.* 2008, Abad *et al.* 2011, Man in't Veld *et al.* 2011, 2015, 2019, Forbes *et al.* 2013, Green *et al.* 2013, 2015, Heyman *et al.* 2013, Reeser *et al.* 2013, Scanu *et al.* 2014b, Scott & Williams 2014, Weir *et al.* 2015, Ann *et al.* 2016, Mideros *et al.* 2018, Ruano-Rosa *et al.* 2018, Li *et al.* 2019, Scott *et al.* 2019). Species from Clade 8b, *Phy. brassica*, *Phy. cichorii*, *Phy. dauci*, *Phy. lactucae*, *Phy. porri*, *Phy.*

pseudolactucae and interspecific hybrids between them are host specific pathogens of various vegetable species (Erwin & Ribeiro 1996, Man in't Veld *et al.* 2002, Bertier *et al.* 2013a, b, Rahman *et al.* 2015). In contrast, the notorious *Phy. cinnamomi* arguably has the widest host range of all plant pathogens infecting more than 5 000 woody and herbaceous, dicotyledonous, monocotyledonous and coniferous plant species (Erwin & Ribeiro 1996, Shearer *et al.* 2004, Cahill *et al.* 2008, Jung *et al.* 2013a, Hardham & Blackman 2018). Numerous *Phytophthora* species infect multiple plant species, *i.e.* *Phy. arenaria*, *Phy. attenuata*, *Phy. bisheria*, *Phy. capsici*, *Phy. castaneae*, *Phy. chlamydospora*, *Phy. citricola*, *Phy. condilina*, *Phy. constricta*, *Phy. crassamura*, *Phy. elongata*, *Phy. erythroseptica*, *Phy. europaea*, *Phy. gonapodyides*, *Phy. gregata*, *Phy. gibbosa*, *Phy. hedraiandra*, *Phy. hibernalis*, *Phy. inundata*, *Phy. kernoviae*, *Phy. lacustris*, *Phy. litoralis*, *Phy. heveae*, *Phy. kwongonina*, *Phy. meadii*, *Phy. pachypleura*, *Phy. parvispora*, *Phy. pseudorosacearum*, *Phy. pseudosyringae*, *Phy. psychrophila*, *Phy. rosacearum*, *Phy. sansomeana*, *Phy. syringae*, *Phy. tentaculata*, *Phy. thermophila* and *Phy. versiformis* (Mchau & Coffey 1995, Erwin & Ribeiro 1996, Abad *et al.* 2008, Jung *et al.* 2002, 2003, 2011, 2013b, 2016, 2017a, c, 2018a, b, 2020, Brasier *et al.* 2003b, 2005, de Cock & Lévesque 2004, Rea *et al.* 2010, 2011, Nechwatal *et al.* 2013, Pérez-Sierra *et al.* 2013, Henricot *et al.* 2014, Scanu *et al.* 2014a, 2015, Hansen *et al.* 2012, 2015, Paap *et al.* 2017, Burgess *et al.* 2018) and some have diverse host ranges of up to 100 and more woody and herbal plant species, *i.e.* *Phy. cactorum*, *Phy. citrophthora*, *Phy. cryptogea*, *Phy. drechsleri*, *Phy. megasperma*, *Phy. nicotianae*, *Phy. palmivora*, *Phy. plurivora*, *Phy. ramorum*, *Phy. tropicalis* and *Phy. ×cambivora* (Brasier & Griffin 1979, Erwin & Ribeiro 1996, Aragaki & Uchida 2001, Grünwald *et al.* 2008, Jung & Burgess 2009, Panabières *et al.* 2016, Jung *et al.* 2018a). The emerging pathogens *Phy. multivora* and *Phy. niederhauserii* have rapidly expanding host ranges (Scott *et al.* 2009, Abad *et al.* 2014). Generally, the *Cupressaceae*, *Ericaceae*, *Fabaceae*, *Fagaceae*, *Lauraceae*, *Myrtaceae*, *Nothofagaceae*, *Proteaceae* and *Rosaceae* families contain many susceptible woody hosts of *Phytophthora* spp.

Disease symptoms: Soilborne *Phytophthora* species cause damping-off, losses of fine roots and small lateral roots (Fig. 50A), necrotic bark lesions on woody roots (Fig. 50A), root rots (Fig. 51A), collar and stem rots (Fig. 50F, 51A, C) and bark lesions along the stem up to the canopy (aerial bark cankers or stem cankers; Fig. 50G) (Day 1938, Crandall *et al.* 1945, Tsao 1990, Shearer & Tippet 1989, Erwin & Ribeiro 1996, Harris 1991, Jung *et al.* 1996, 1999, 2000, 2013a, b, 2017c, 2018a, b, 2020, Hansen *et al.* 2000, 2012, Jung & Blaschke 2004, Tyler 2007, Jung 2009, Green *et al.* 2013, 2015, Pérez-Sierra *et al.* 2013, Ginetti *et al.* 2014, Bellgard *et al.* 2016). On woody plants collar rot and aerial bark lesions are characterised by orange-brown to black exudations at the surface of the bark and orange to dark-brown, tongue-shaped lesions of the inner bark (Fig. 50F, G; Crandall *et al.* 1945, Erwin & Ribeiro 1996, Hansen *et al.* 2000, Jung 2009, Jung *et al.* 2013a, b, 2018a, 2020, Green *et al.* 2013, Bellgard *et al.* 2016). In *Acacia*, *Citrus* and *Prunus* species bark cankers on stems and branches are characterised by gum-like exudations (gummosis; Erwin & Ribeiro 1996, Graham & Menge 2000, Pérez-Sierra *et al.* 2010, Jung *et al.* 2016, Puglisi *et al.* 2017, Albuquerque Alves *et al.* 2019). Since *Phytophthora* pathogens are advancing first in the cambium layer, the front of active lesions in the cambium and inner bark is usually considerably ahead of the exudate spots on the bark surface. Depending on the proportion of circumference, affected bark lesions on stems cause starvation of parts of the root system and reduced water transport.

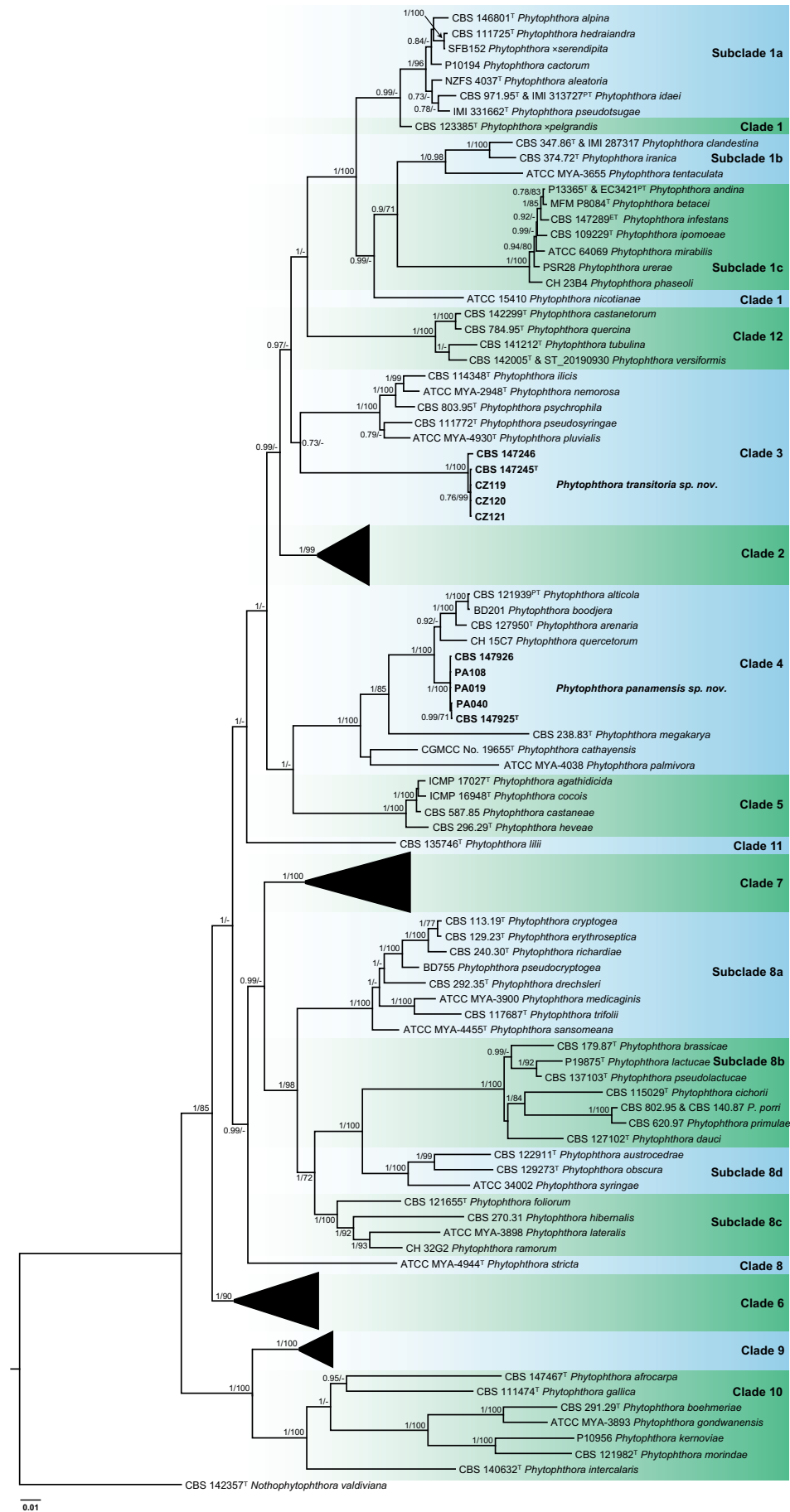


Fig. 52. Bayesian Inference phylogram constructed from ITS (1 185 bp), *Btub* (1 136 bp), *tiga* (1 669 bp) and *cox1* (867 bp) sequences of all accepted species of *Phytophthora*. Bayesian posterior probability scores (> 0.90) and RAxML bootstrap support values (> 70 %) are shown at the nodes. Detailed structures of Clades 2, 6, 7 and 9 are shown in Figs 53–56, respectively. The novel taxa are printed in **bold**. The phylogenetic tree was rooted to *Nothophytophthora valdiviana* CBS 142357. GenBank accession numbers are listed in Table 15. T, ET and PT indicate ex-type, ex-epitype and ex-paratype strains, respectively. TreeBASE: S28641.

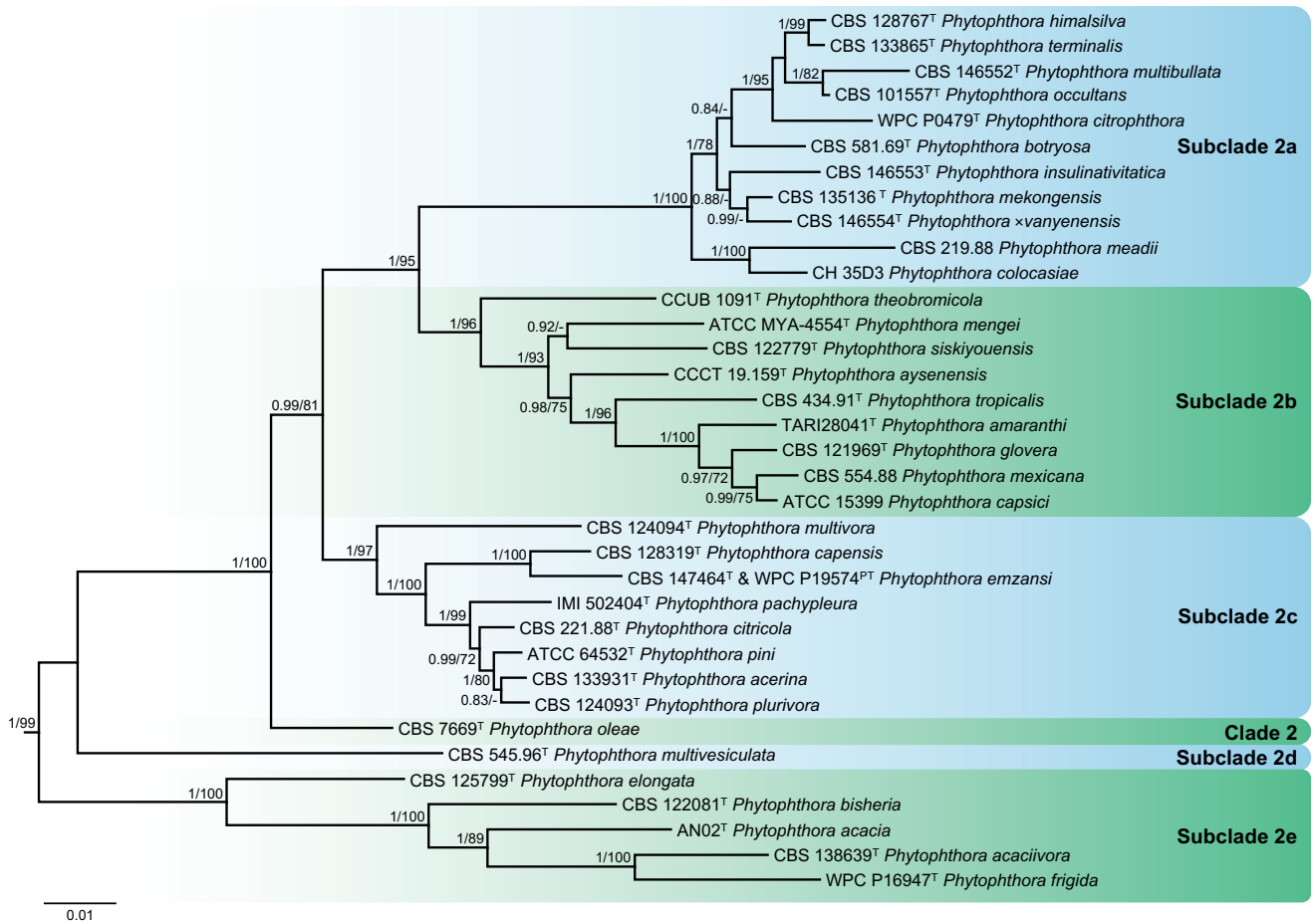


Fig. 53. Structure of *Phytophthora* Clade 2 in the Bayesian Inference phylogram constructed from ITS (1 185 bp), *Btub* (1 136 bp), *tigA* (1 669 bp) and *cox1* (867 bp) sequences of all accepted species of *Phytophthora* (Fig. 52). Bayesian posterior probability scores (> 0.90) and RAxML bootstrap support values (> 70 %) are shown at the nodes. GenBank accession numbers are listed in Table 15. ^T and ^{PT} indicate ex-type and ex-paratype strains, respectively. TreeBASE: S28641.

Reduced water uptake due to fine root losses and reduced water transport cause non-specific symptoms of drought and malnutrition in the crown such as increased transparency of the crown, sparse ramification resulting in whip-like branches, chlorotic, wilting, small-sized leaves which often cluster at the ends of branches (Fig. 50B–E; Erwin & Ribeiro 1996, Jung *et al.* 2000, 2013b, 2016, 2017c, 2018a, b, 2020, Jönsson *et al.* 2005, Jung 2009, Pérez-Sierra *et al.* 2010, 2013, Orlikowski *et al.* 2011, Pérez-Sierra & Jung 2013, Scanu *et al.* 2015, Bellgard *et al.* 2016, Milenković *et al.* 2018, Corcobado *et al.* 2020). In mature trees it can take decades of multicyclic inoculum build-up and infections until the destruction of the fine root system results in visible above-ground symptoms. Eventually trees and whole ecosystems can show dieback and die (Fig. 50B–E; Erwin & Ribeiro 1996, Shearer & Tippett 1989, Jung *et al.* 1996, 2000, 2013a, b, 2018a, b, Jung 2009). Girdling of large roots or the stem by bark lesions results in acute wilting and mortality (Fig. 50C, D). Temporary waterlogging after heavy or prolonged rain or flooding provides ideal conditions for continuous zoospore production and infections often leading to acute patch dieback and mortality, in particular in agricultural ecosystems with highly susceptible, often clonal crops (Fig. 51A–D) and in riparian ecosystems (Davison 1988, Harris 1991, Shearer & Tippett 1989, Erwin & Ribeiro 1996, Streito *et al.* 2002, Jung & Blaschke 2004, Dorrance 2013, Jung *et al.* 2018a). Splash-dispersal of soilborne sporangia and zoospores by heavy rain or sprinkler irrigation can cause leaf necroses, shoot dieback and fruit rot up to 2 m above the

ground (Erwin & Ribeiro 1996, Nechwatal *et al.* 2011, Pérez-Sierra & Jung 2013).

Airborne *Phytophthora* species cause necrotic lesions on leaves, shoots and fruits (Fig. 51E–H), shoot dieback, defoliations, bleeding bark lesions and also root and foot rot (Erwin & Ribeiro 1996, Aragaki & Uchida 2001, Werres *et al.* 2001, Rizzo *et al.* 2002, Brasier *et al.* 2005, Brown & Brasier 2007, Brasier & Webber 2010, Reeser *et al.* 2013, Scanu & Webber 2016, Jung *et al.* 2016, 2018a, 2021, Hansen *et al.* 2017). Analogous to fine root diseases *Phytophthora*-induced leaf and fruit diseases are multicyclic and prolonged foggy and rainy periods or excessive sprinkler irrigation can result in epidemic disease outbreaks in temperate crops like *Solanum tuberosum* (late blight of leaves, shoots and tubers), *Solanum lycopersicum* (buckeye fruit rot, leaf blight) and *Piper nigrum* (damping-off, root, foot and fruit rot); tropical crops like *Artocarpus altilis* (leaf blight, fruit rot), *Theobroma cacao* (Black pod), *Cocos nucifera* (bud rot), *Durio zibethinus* (leaf blight, fruit rot, stem canker), *Artocarpus heterophyllus* (root rot, trunk cankers and gummosis, chlorosis, wilt, leaf blight, defoliation, fruit rot), *Carica papaya* (damping-off, leaf and shoot blight, pod rot), *Hevea brasiliensis* (early leaf fall, pod rot, black stripe and stem canker) and *Colocasia esculenta* (leaf blight) by *Phy. botryosa*, *Phy. colocasiae*, *Phy. meadii*, *Phy. palmivora* and *Phy. tropicalis*; forest trees and shrubs like *Larix kaempferi* and *Larix × eurolepis* (defoliation, bark cankers on twigs and stems), *Rhododendron ponticum* and *Umbellularia californica* laurel (leaf and shoot blight) by *Phy. ramorum*, *Pinus radiata* by *Phy. pinifolia* and *Phy. pluvialis*

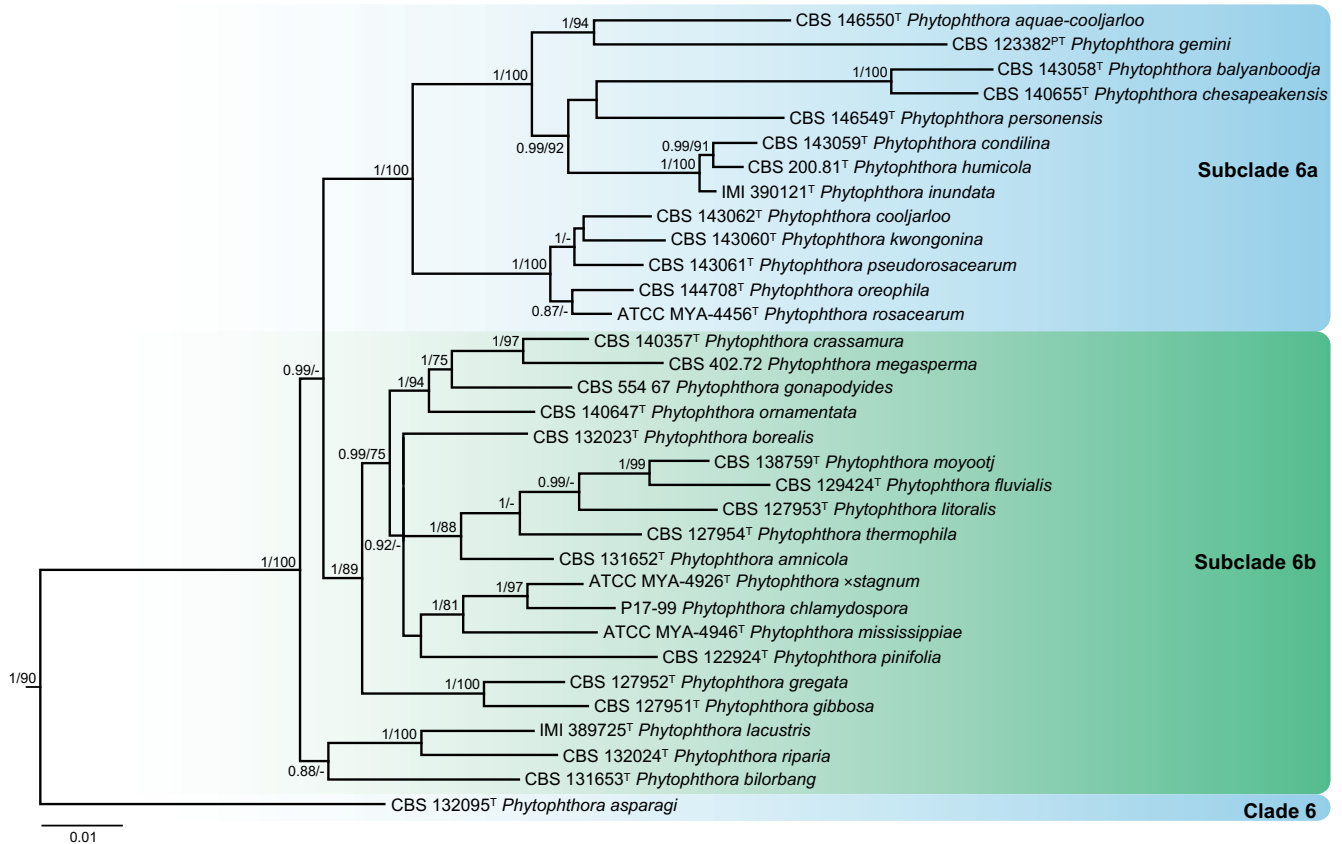


Fig. 54. Structure of *Phytophthora* Clade 6 in the Bayesian Inference phylogram constructed from ITS (1 185 bp), *Btub* (1 136 bp), *tigA* (1 669 bp) and *cox1* (867 bp) sequences of all accepted species of *Phytophthora* (Fig. 52). Bayesian posterior probability scores (> 0.90) and RAxML bootstrap support values (> 70 %) are shown at the nodes. GenBank accession numbers are listed in Table 15. ^T and ^{PT} indicate ex-type and ex-paratype strains, respectively. TreeBASE: S28641.

(needle cast), *Chamaecyparis* spp. by *Phy. lateralis* (needle and shoot necroses) or *Ilex aquifolium* by *Phy. ilicis* (leaf and shoot blight, fruit rot); and many ornamental plants like *Rhododendron* spp. (Brasier & Griffin 1979, Erwin & Ribeiro 1996, Aragaki & Uchida 2001, Werres *et al.* 2001, Rizzo *et al.* 2002, Drenth & Guest 2004, Durán *et al.* 2008, Grünwald *et al.* 2008, Brasier & Webber 2010, Robin *et al.* 2011, Webber *et al.* 2012, Forbes *et al.* 2013, Granke *et al.* 2013, Miyasaka *et al.* 2013, Sanogo & Bosland 2013, Jung *et al.* 2016, 2018a, Akrofi 2015, Tri *et al.* 2015, Puglisi *et al.* 2017).

Notes: The potato late blight epidemic caused by *Phy. infestans* was responsible for the Irish potato famine, which resulted in death and emigration of millions of people from Ireland (Haas *et al.* 2009). Worldwide control measure expenses and crop losses are estimated to be \$6.7 billion per year (Haverkort *et al.* 2008). When the genus *Phytophthora* (Greek for 'plant destroyer') was established in 1876 by Anton de Bary with *Phy. infestans*, the causal agent of potato late blight, as type species, no culture was retained linked to this specimen. Therefore, we designate here an epitype for *Phy. infestans*. Isolate CBS 147289 (= T30–4) was chosen as ex-epitype strain because it has an A1 mating type, like the original strains causing the potato late blight epidemic of the 19th century studied by de Bary, with known parents resulting from a sexual cross between two Dutch *Phy. infestans* isolates from late-blighted potatoes, 80029 (A1 mating type, race 2.4.7, isolated in 1980) and 88133 (A2 mating type, race 1.3.7.10.11, isolated in 1988) performed in potato leaves under natural conditions (Drenth *et al.* 1995); it was used in numerous studies including the sequencing of the *Phy. infestans* reference genome ASM14294v1 (genome size 240 Mbp; GenBank assembly accession GCA_000142945.1,

RefSeq assembly accession GCF_000142945.1) (Haas *et al.* 2009); and proved to contain all six avirulence genes studied in the experiments of van der Lee *et al.* (2001).

Until the end of the 20th century the number of described *Phytophthora* species was gradually increasing to 50 (Erwin & Ribeiro 1996, Jung *et al.* 1999). However, during the past two decades the number of new species descriptions was skyrocketing and the genus currently comprises 192 described and accepted culturable species (Table 15; Figs 52–56) and six unculturable species (*Phy. cyperi*, *Phy. cyperi-bulbosi*, *Phy. leporinae*, *Phy. leersiae*, *Phy. polygoni* and *Phy. verrucosa*). The latter were not included in the phylogenetic analyses of the present study. Several factors contributed to this exponential increase of *Phytophthora* species numbers. The advent and advance of molecular sequencing techniques and phylogenetic inference analyses allowed the sorting out of several morphospecies complexes (*cf.* Brasier *et al.* 2003b, Jung *et al.* 2003, 2011, 2017b, Man In't Veld 2002, 2007, Hansen *et al.* 2009, 2015, Hong *et al.* 2009, 2011, Jung & Burgess 2009, Scott *et al.* 2009, Rea *et al.* 2010, Bertier *et al.* 2013a, Nechwatal *et al.* 2013, Scanu *et al.* 2014b, Burgess *et al.* 2018) and correct identifications of isolates in culture collections (Burgess *et al.* 2009, Rahman *et al.* 2015). Further, surveys in previously unexplored natural and semi-natural ecosystems in Africa, Asia, Australia, Europe, the USA and South America uncovered an unprecedented diversity of both known and unknown *Phytophthora* species (*cf.* Jung *et al.* 1999, 2000, 2002, 2003, 2011, 2017a–d, 2018b, 2020, Hansen *et al.* 2003, 2012, Dick *et al.* 2006, Balci *et al.* 2008, Reeser *et al.* 2011, 2013, Vettraino *et al.* 2011, Oh *et al.* 2013, Ginetti *et al.* 2014, Scanu *et al.* 2015, Paap *et al.* 2017, Burgess *et al.* 2017, 2018) supporting the prediction of 200–600 unknown *Phytophthora* species in natural ecosystems (Brasier 2009).

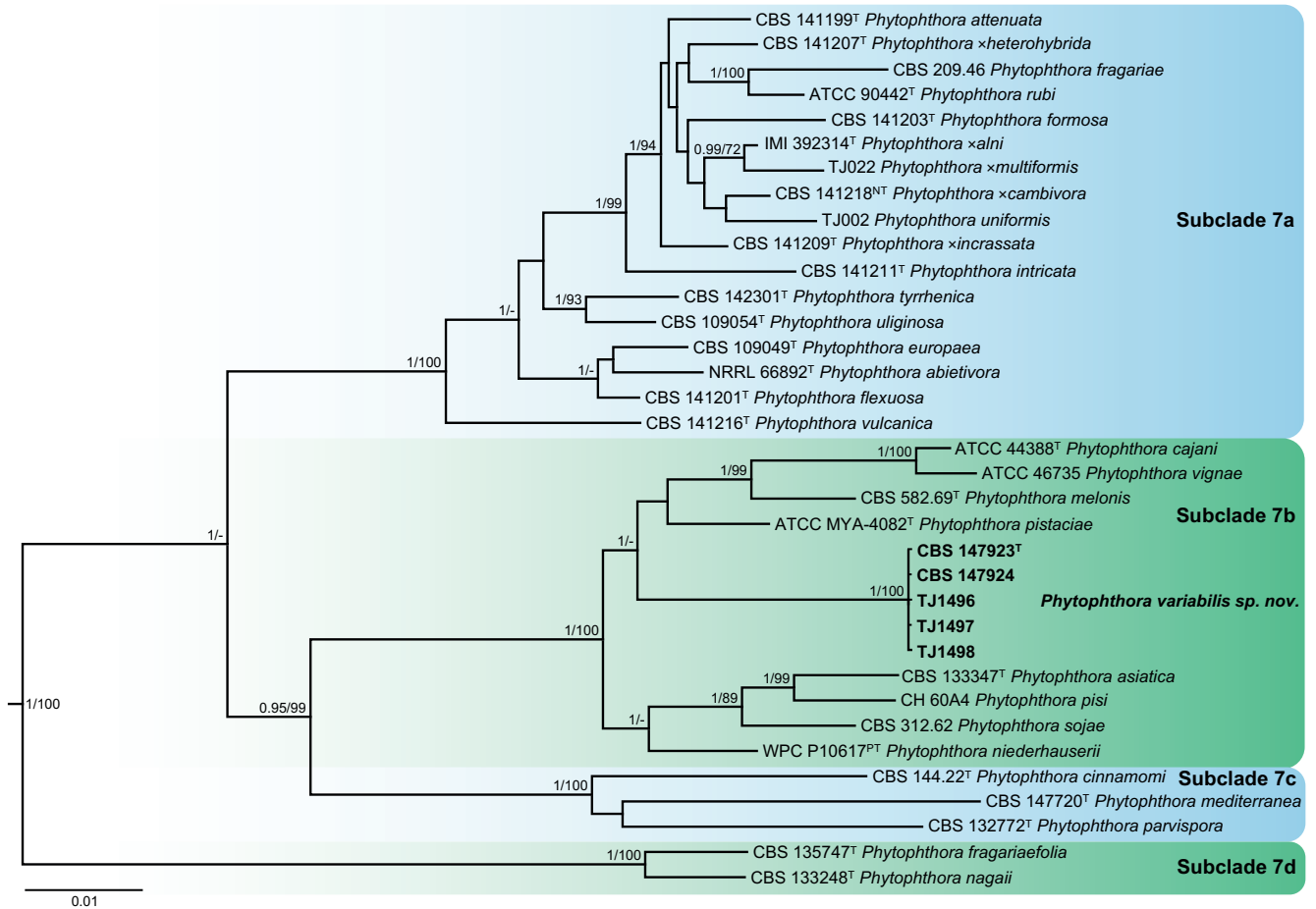


Fig. 55. Structure of *Phytophthora* Clade 7 in the Bayesian Inference phylogram constructed from ITS (1 185 bp), *Btub* (1 136 bp), *tigA* (1 669 bp) and *cox1* (867 bp) sequences of all accepted species of *Phytophthora* (Fig. 52). Bayesian posterior probability scores (> 0.90) and RAxML bootstrap support values (> 70 %) are shown at the nodes. The novel taxon is printed in **bold**. GenBank accession numbers are listed in Table 15. ^T, ^{PT} and ^{NT} indicate ex-type, ex-paratype and ex-neotype strains, respectively. TreeBASE: S28641.

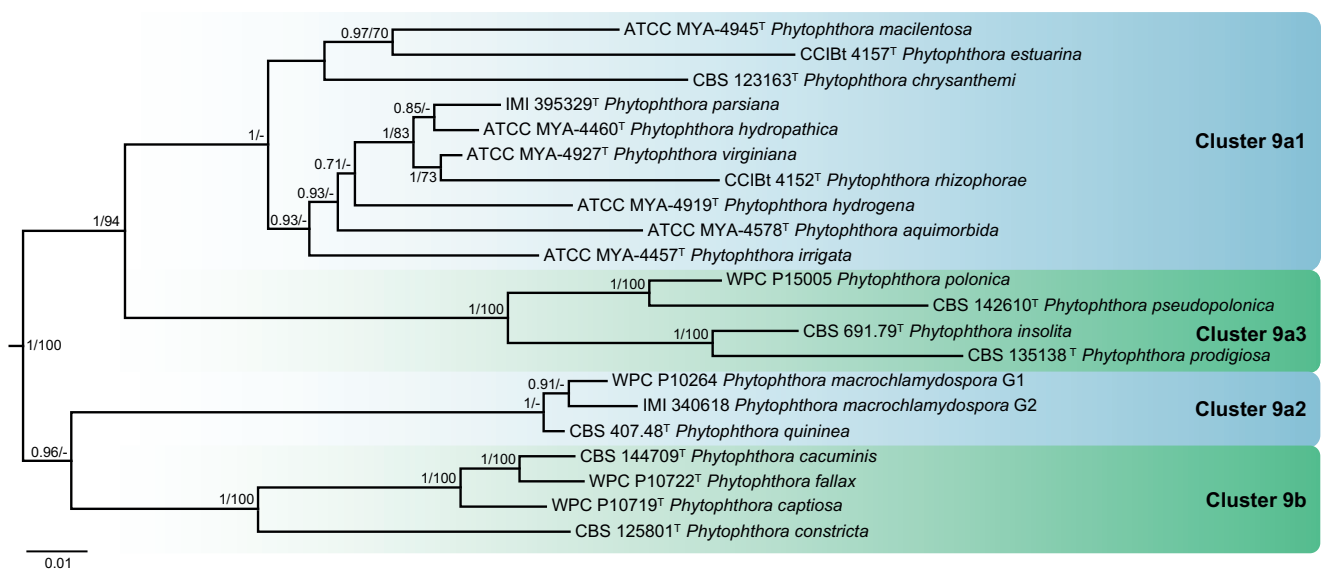


Fig. 56. Structure of *Phytophthora* Clade 9 in the Bayesian Inference phylogram constructed from ITS (1 185 bp), *Btub* (1 136 bp), *tigA* (1 669 bp) and *cox1* (867 bp) sequences of all accepted species of *Phytophthora* (Fig. 52). Bayesian posterior probability scores (> 0.90) and RAxML bootstrap support values (> 70 %) are shown at the nodes. GenBank accession numbers are listed in Table 15. ^T indicates ex-type strain. TreeBASE: S28641.

Table 15. DNA barcodes of accepted *Phytophthora* spp.

Species	(Sub) clade	Isolates ¹	GenBank accession numbers ²				References
			<i>cox1</i>	ITS	<i>Btub</i>	<i>tigA</i>	
<i>Phy. abietivora</i>	7a	NRRL 66892 ^T	MK164270	MK163944	MK164274	—	Li <i>et al.</i> (2019)
<i>Phy. acaciae</i>	2d	AN02 ^T	KX396267	KX396303	KX396338	—	Albuquerque Alves <i>et al.</i> (2019)
<i>Phy. acaciivora</i>	2d	CBS 138639 ^T	MN991991	KX011264	MN991984	—	Paap <i>et al.</i> (2017), Burgess <i>et al.</i> (2020)
<i>Phy. acerina</i>	2c	CBS 133931 ^T	MH620026	JX951285	KX250713	KX250718	Ginetti <i>et al.</i> (2014), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. afrocarpa</i>	10	CBS 147467 ^T	MT762315	MT762306	MT762324	—	Bose <i>et al.</i> (2021)
<i>Phy. agathidicida</i>	5	ICMP 17027 ^T	MH620036	KP295308	KX251077	KX251082	Weir <i>et al.</i> (2015), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. alpina</i>	1a	CBS 146801 ^T	MT729668	MT707332	MT729673	—	Bregant <i>et al.</i> (2020)
<i>Phy. alticola</i>	4	CBS 121939 ^{PT}	KF317106	KF317084	KX251007	KX251012	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. amaranthi</i>	2b	TARI28041 ^T	MH477739	GU111585	KJ179949	—	Ann <i>et al.</i> (2016)
<i>Phy. amnicola</i>	6b	CBS 131652 ^T	MH620041	MH620126	KX251168	KX251173	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. andina</i>	1c	WPC P13365 ^T EC3421 ^{PT}	— AY564160	FJ801734	EU080183	EU080188	Blair <i>et al.</i> (2008) Kroon <i>et al.</i> (2004)
<i>Phy. aquae-cooljarloo</i>	6a	CBS 146550 ^T	MT210466	MT210484	MT210475	—	Crous <i>et al.</i> (2020a)
<i>Phy. aquimorbida</i>	9a (cluster 9a1)	ATCC MYA-4578 ^T	GQ294536	FJ666127	KX252239	KX252244	Hong <i>et al.</i> (2012)
<i>Phy. arenaria</i>	4	CBS 127950 ^T	MH620034	MH620120	KX251014	KX251019	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. asiatica</i>	7b	CBS 133347 ^T	MH620062	MH620142	KX251666	KX251671	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. asparagi</i>	6	CBS 132095 ^T	MH620053	MH620137	KX251474	KX251479	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. attenuata</i>	7a	CBS 141199 ^T	MH620054	KU517154	KX251610	KX251615	Jung <i>et al.</i> (2017a), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. austrocedrae</i>	8d	CBS 122911 ^T	KF358233	KF358220	KX252169	KX252174	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. aysenensis</i>	2b	CCCT 19.159 ^T	—	MN557838	MN557840	—	Crous <i>et al.</i> (2020b)
<i>Phy. balyanboodja</i>	6a	CBS 143058 ^T	MF326863	KJ372258	MF326806	—	Burgess <i>et al.</i> (2018)
<i>Phy. betaceae</i>	1c	MFM-P8084 ^T	—	JAANHX010000146 ³	JAANHX010000299 ³	JAANHX010000345 ³	Mideros <i>et al.</i> (2018)
<i>Phy. bilorbang</i>	6b	CBS 131653 ^T	MH620042	MH620127	KX251182	KX251186	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. bisheria</i>	2d	CBS 122081 ^T	MH620030	MH620116	EU080742	EU080747	Blair <i>et al.</i> (2008), Yang & Hong (2018)
<i>Phy. boehmeriae</i>	10	CBS 291.29 ^T	KT183047	KT183036	EU080162	EU080167	Blair <i>et al.</i> (2008), Yang <i>et al.</i> (2016)
<i>Phy. boodjera</i>	4	BD201	MZ736426	MZ753913	MZ736452	MZ736479	Present study
<i>Phy. borealis</i>	6b	CBS 132023 ^T	MH620043	MH620128	KX251188	KX251193	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. botryosa</i>	2a	CBS 581.69 ^T	MH620019	MH620107	KX250538	KX250543	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. brassicae</i>	8b	CBS 179.87 ^T	MH620082	MH620158	KX252001	KX252006	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. cactorum</i>	1a	WPC P10194	MH620014	MH620100	KX250370	KX250375	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. cacuminis</i>	9b	CBS 144709 ^T	MG543010	MG542997	MG543045	—	Khaliq <i>et al.</i> (2019)
<i>Phy. cajani</i>	7b	ATCC 44388 ^T	MH620063	MH620143	KX251687	KX251692	Yang <i>et al.</i> (2017), Yang & Hong (2018)

Table 15. (Continued).

Species	(Sub) clade	Isolates ¹	GenBank accession numbers ²				References
			<i>cox1</i>	ITS	<i>Btub</i>	<i>tigA</i>	
<i>Phy. capensis</i>	2c	CBS 128319 ^T	MH620027	MH620113	KX250727	KX250732	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. capsici</i>	2b	ATCC 15399	KF317094	KF317073	KX250636	KX250641	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. captiosa</i>	9b	WPC P10719 ^T	KC733449	MH620174	EU079659	EU079664	Blair <i>et al.</i> (2008), Yang <i>et al.</i> (2014a), Yang & Hong (2018)
<i>Phy. castaneae</i>	5	CBS 587.85	AY564190	MH620122	KX251098	KX251103	Kroon <i>et al.</i> (2004), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. castanetorum</i>	12	CBS 142299 ^T	MZ736427	MF036182	MZ736453	MZ736480	Jung <i>et al.</i> (2017b), present study
<i>Phy. cathayensis</i>	4	CGMCC No. 19655 ^T	MN692211	MN385741	MT063102	—	Morales-Rodríguez <i>et al.</i> (2020)
<i>Phy. chesapeakeensis</i>	6a	CBS 140655 ^T	KX172096	KX172092	—	—	Man In't Veld <i>et al.</i> (2019)
<i>Phy. chlamydospora</i>	6b	P17-99	CM022726	JAABLK010000522 ³	JAABLK010000021 ³	JAABLK010000299 ³	Mc Gowan <i>et al.</i> (2020)
<i>Phy. chrysanthemi</i>	9a (cluster 9a1)	CBS 123163 ^T	MH620093	KT183038	KX252267	KX252272	Yang <i>et al.</i> (2016, 2017), Yang & Hong (2018)
<i>Phy. cichorii</i>	8b	CBS 115029 ^T	MH620083	MH620159	KX252008	KX252013	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. cinnamomi</i>	7c	CBS 144.22 ^T	MH620070	MH620147	KX251812	KX251817	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. citricola</i>	2c	CBS 221.88 ^T	KF317095	KF317074	KX250748	KX250753	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. citrophthora</i>	2a	WPC P0479 ^T	MH136872	MG865476	MH493923	—	https://idtools.org/id/phytophthora/
<i>Phy. clandestina</i>	1b	CBS 347.86 ^T	—	MH620101	EU079867	EU079872	Blair <i>et al.</i> (2008), Yang & Hong (2018)
		IMI 287317	AY564172				Kroon <i>et al.</i> (2004)
<i>Phy. cocois</i>	5	ICMP 16948 ^T	MH620037	KP295304	KX251105	KX251110	Weir <i>et al.</i> (2015), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. colocasiae</i>	2a	CH 35D3	KF317097	KF317076	KX250566	KX250571	Yang <i>et al.</i> (2014a, 2017)
<i>Phy. condilina</i>	6a	CBS 143059 ^T	MF326843	KJ372262	MF326814	—	Burgess <i>et al.</i> (2018)
<i>Phy. constricta</i>	9b	CBS 125801 ^T	KC733450	MH620175	KX252562	KX252567	Yang <i>et al.</i> (2014a, 2017), Yang & Hong (2018)
<i>Phy. cooljarloo</i>	6a	CBS 143062 ^T	HQ012881	HQ012957	MF326816	—	Jung <i>et al.</i> (2011), Burgess <i>et al.</i> (2018)
<i>Phy. crassamura</i>	6b	CBS 140357 ^T	MH620044	KP863493	KX251202	KX251207	Scanu <i>et al.</i> (2015), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. cryptogea</i>	8a	CBS 113.19 ^T	MH620075	MH620151	KX251868	KX251873	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. dauci</i>	8b	CBS 127102 ^T	MH620084	MH620160	KX252015	KX252020	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. drechsleri</i>	8a	CBS 292.35 ^T	MH620076	MH620152	KX251889	KX251894	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. elongata</i>	2d	CBS 125799 ^T	MH620031	MH620117	KX250895	KX250900	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. emzansi</i>	2c	CBS 147464 ^T	MT762309	MT762301	—	—	Bose <i>et al.</i> (2021)
		WPC P19574 ^{PT}	—	—	KX250860	KX250865	Yang <i>et al.</i> (2017)
<i>Phy. erythroseptica</i>	8a	CBS 129.23 ^T	MH620077	MH620153	KX251896	KX251901	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. estuarina</i>	9a (cluster 9a1)	CCIBt 4157 ^T	KT886051	KT886034	—	—	Li <i>et al.</i> (2016)
<i>Phy. europaea</i>	7a	CBS 109049 ^T	MH620055	MH620138	KX251523	KX251528	Yang <i>et al.</i> (2017), Yang & Hong (2018)

Table 15. (Continued).

Species	(Sub) clade	Isolates ¹	GenBank accession numbers ²				References
			<i>cox1</i>	ITS	<i>Btub</i>	<i>tigA</i>	
<i>Phy. fallax</i>	9b	WPC P10722 ^T	KC733451	MH620176	KX252569	KX252574	Blair <i>et al.</i> (2008), Yang <i>et al.</i> (2014a), Yang & Hong (2018)
<i>Phy. flexuosa</i>	7a	CBS 141201 ^T	MH620056	KU517152	KX251617	KX251622	Jung <i>et al.</i> (2017a), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. fluvialis</i>	6b	CBS 129424 ^T	MH620045	MH620129	KX251209	KX251214	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. foliorum</i>	8c	CBS 121655 ^T	EU124918	MH620164	KX252113	KX252118	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. formosa</i>	7a	CBS 141203 ^T	MH620057	KU517153	KX251624	KX251629	Jung <i>et al.</i> (2017a), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. fragariae</i>	7a	CBS 209.46 ^T	MH620058	MH620139	KX251544	KX251549	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. fragariaefolia</i>	7d	CBS 135747 ^T	MH620073	MH620149	KX251854	KX251859	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. frigida</i>	2d	WPC P16947 ^T	KF317098	KF317077	KX250916	KX250921	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. gallica</i>	10	CBS 111474 ^T	KF317112	KF317090	KX252590	KX252595	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. gemini</i>	6a	CBS 123382 ^{PT}	MH620038	FJ217680	KX251126	KX251131	Man In't Veld <i>et al.</i> (2011), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. gibbosa</i>	6b	CBS 127951 ^T	MH620046	MH620130	KX251223	KX251228	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. glovera</i>	2b	CBS 121969 ^T	MH620022	MH620110	KX250650	KX250655	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. gonapodyides</i>	6b	CBS 554.67	KC733448	KF112854	KX251237	KX251242	Yang <i>et al.</i> (2013, 2014a, 2017)
<i>Phy. gondwanensis</i>	10	ATCC MYA-3893	KT183046	KT183035	KX252604	KX252609	Yang <i>et al.</i> (2016, 2017)
<i>Phy. gregata</i>	6b	CBS 127952 ^T	MH620047	MH620131	KX251251	KX251256	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. hedraiandra</i>	1a	CBS 111725 ^T	AY769115	AY707987	KX250398	KX250403	de Cock & Lévesque (2004), Yang <i>et al.</i> (2017)
<i>Phy. heveae</i>	5	CBS 296.29 ^T	AY564182	MH620123	KX251112	KX251117	Kroon <i>et al.</i> (2004), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. hibernalis</i>	8c	CBS 270.31	MH620088	KT183039	KX252120	KX252125	Yang <i>et al.</i> (2016, 2017), Yang & Hong (2018)
<i>Phy. himalsilva</i>	2a	CBS 128767 ^T	MH620020	MH620108	KX250573	KX250578	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. humicola</i>	6a	CBS 200.81 ^T	KF112862	KF112855	KX251140	KX251145	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. hydrogena</i>	9a (cluster 9a1)	ATCC MYA-4919 ^T	KC249962	KC249959	KX252281	KX252286	Yang <i>et al.</i> (2014b, 2017)
<i>Phy. hydropathica</i>	9a (cluster 9a1)	ATCC MYA-4460 ^T	KC733452	EU583793	KX252295	KX252300	Hong <i>et al.</i> (2010), Yang <i>et al.</i> (2014b, 2017)
<i>Phy. idaei</i>	1a	CBS 971.95 ^T IMI 313727 ^{PT}	— AY564185	FJ801946	EU080130	EU080135	Blair <i>et al.</i> (2008) Kroon <i>et al.</i> (2004)
<i>Phy. ilicis</i>	3	CBS 114348 ^T	JX524159	JX524158	KX250951	KX250956	Yang <i>et al.</i> (2017)
<i>Phy. infestans</i>	1c	CBS 147289 ^{ET}	MZ736428	MZ753914	MZ736454	MZ736481	Present study
<i>Phy. insolita</i>	9a (cluster 9a3)	CBS 691.79 ^T	AY564188	GU111612	EU080176	EU080181	Kroon <i>et al.</i> (2004), Blair <i>et al.</i> (2008)
<i>Phy. insulinativatica</i>	2a	CBS 146553 ^T	MT583646	KY212028	MT583631	—	Dang <i>et al.</i> (2021)
<i>Phy. intercalaris</i>	10	CBS 140632 ^T	KT163315	KT163268	KX252611	KX252616	Yang <i>et al.</i> (2016, 2017)
<i>Phy. intricata</i>	7a	CBS 141211 ^T	MH620059	KU517155	KX251631	KX251636	Jung <i>et al.</i> (2017a), Yang <i>et al.</i> (2017), Yang & Hong (2018)

Table 15. (Continued).

Species	(Sub) clade	Isolates ¹	GenBank accession numbers ²				References
			<i>cox1</i>	ITS	<i>Btub</i>	<i>tigA</i>	
<i>Phy. inundata</i>	6a	IMI 390121 ^T	KF112863	KF112856	KX251154	KX251159	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. ipomoeae</i>	1c	CBS 109229 ^T	MH620016	MH620104	EU080831	EU080836	Blair <i>et al.</i> (2008), Yang & Hong (2018)
<i>Phy. iranica</i>	1b	CBS 374.72 ^T	AY564189	MH620102	KX250440	KX250445	Kroon <i>et al.</i> (2004), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. irrigata</i>	9a (cluster 9a1)	ATCC MYA-4457 ^T	KC733453	EU334634	KX252316	KX252321	Hong <i>et al.</i> (2008), Yang <i>et al.</i> (2014b, 2017)
<i>Phy. kernoviae</i>	10	WPC P10956	KT183048	MH620177	EU080042	KX252631	Blair <i>et al.</i> (2008), Yang <i>et al.</i> (2016), Yang & Hong (2018)
<i>Phy. kwongonina</i>	6a	CBS 143060 ^T	MF326847	JN547636	MF326824	—	Aghighi <i>et al.</i> (2012), Burgess <i>et al.</i> (2018)
<i>Phy. lactucae</i>	8b	WPC P19875 ^T	MH620085	MH620161	KX252043	KX252048	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. lacustris</i>	6b	IMI 389725 ^T	JF896561	AF266793	EU080531	EU080536	Cooke <i>et al.</i> (2000), Blair <i>et al.</i> (2008), Nechwatal <i>et al.</i> (2013)
<i>Phy. lateralis</i>	8c	ATCC MYA-3898	MH620089	MH620165	KX252134	KX252139	Yang (2017), Yang & Hong (2018)
<i>Phy. lillii</i>	11	CBS 135746 ^T	AB856786	MG865523	AB856782	AB856800	Rahman <i>et al.</i> (2015)
<i>Phy. litchii</i>	4	CPHST BL 145 ^T	MH136919	MG865524	—	—	https://idtools.org/id/phytophthora/
<i>Phy. litoralis</i>	6b	CBS 127953 ^T	MH620048	MH620132	KX251279	KX251284	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. macilentosa</i>	9a (cluster 9a1)	ATCC MYA-4945 ^T	KF192708	KF192700	KX252344	KX252349	Yang <i>et al.</i> (2014a, 2017)
<i>Phy. macrochlamydo-spora-G1</i>	9a (cluster 9a2)	WPC P10264	KC733454	KC733445	KX252511	KX252515	Yang <i>et al.</i> (2014a, 2017)
<i>Phy. macrochlamydo-spora-G2</i>	9a (cluster 9a2)	IMI 340618	MH620098	MH620172	KX252517	KX252521	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. meadii</i>	2a	CBS 219.88	AY564192	MH620109	KX250594	KX250599	Kroon <i>et al.</i> (2004), Yang <i>et al.</i> (2017), Yang & Hong 2018
<i>Phy. medicaginis</i>	8a	ATCC MYA-3900	KF358236	KF358223	KX251903	KX251908	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. mediterranea</i>	7c	CBS 147720 ^T	MW900447	MW892398	MW900443	—	Bregant <i>et al.</i> (2021)
<i>Phy. megakarya</i>	4	CBS 238.83 ^T	MH620035	MH620121	KX251035	KX251040	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. megasperma</i>	6b	CBS 402.72	MH620049	MH620133	KX251286	—	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. mekongensis</i>	2a	CBS 135136 ^T	MZ813273	LC595792	MZ813274	MZ813275	present study
<i>Phy. melonis</i>	7b	CBS 582.69 ^T	MH620064	KT183041	KX251708	KX251713	Yang <i>et al.</i> (2016, 2017), Yang & Hong (2018)
<i>Phy. mengei</i>	2b	ATCC MYA-4554 ^T	MH620023	EU748545	KX250657	KX250662	Hong <i>et al.</i> (2009), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. mexicana</i>	2b	CBS 554.88	MH620024	MH620111	KX250671	KX250676	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. mirabilis</i>	1c	ATCC 64069	MH620017	MH620105	KX250482	KX250487	Yang <i>et al.</i> (2017), Yang & Hong 2018
<i>Phy. mississippiae</i>	6b	ATCC MYA-4946 ^T	KF112860	KF112852	KX251306	KX251311	Yang <i>et al.</i> (2013, 2017)
<i>Phy. morindae</i>	10	CBS 121982 ^T	KT183050	MH620178	KX252634	KX252639	Yang <i>et al.</i> (2016, 2017), Yang & Hong (2018)
<i>Phy. moyooij</i>	6b	CBS 138759 ^T	KJ396702	KJ372256	KJ372303	—	Crous <i>et al.</i> (2014)
<i>Phy. multibullata</i>	2a	CBS 146552 ^T	MT583658	MT568655	MT583643	—	Dang <i>et al.</i> (2021)

Table 15. (Continued).

Species	(Sub) clade	Isolates ¹	GenBank accession numbers ²				References
			<i>cox1</i>	ITS	<i>Btub</i>	<i>tigA</i>	
<i>Phy. multivesiculata</i>	2e	CBS 545.96 ^T	MH620032	MH620118	EU080066	EU080071	Blair <i>et al.</i> (2008), Yang & Hong (2018)
<i>Phy. multivora</i>	2c	CBS 124094 ^T	FJ237508	FJ237521	KX250776	KX250781	Scott <i>et al.</i> (2009), Yang <i>et al.</i> (2017)
<i>Phy. nagaii</i>	7d	CBS 133248 ^T	MH620074	MH620150	KX251861	KX251866	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. nemorosa</i>	3	ATCC MYA-2948 ^T	KF317104	KF317082	KX250965	KX250970	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. nicotianae</i>	1	ATCC 15410	KF317091	KF317070	KX250510	KX250515	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. niederhauserii</i>	7b	WPC P10617 ^{PT}	MH620065	MH620144	KX251729	KX251734	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. obscura</i>	8d	CBS 129273 ^T	MH620091	MH620167	KX252176	KX252181	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. occultans</i>	2a	CBS 101557 ^T	MH620021	JX978155	KX250601	KX250606	Man In 't Veld <i>et al.</i> (2015), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. oleae</i>	2	CBS 7669 ^T	MF083569	KY982930	—	—	Ruano-Rosa <i>et al.</i> (2018)
<i>Phy. oreophila</i>	6a	CBS 144708 ^T	MG543002	MG542976	MG543037	—	Khaliq <i>et al.</i> (2019)
<i>Phy. ornamentata</i>	6b	CBS 140647 ^T	MH620050	KP863496	KX251320	KX251325	Scanu <i>et al.</i> (2015), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. pachypleura</i>	2c	IMI 502404 ^T	MH620028	MH620114	KX250790	KX250795	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. palmivora</i>	4	ATCC MYA-4038	KF317108	KF317086	KX251056	KX251061	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. panamensis</i>	4	CBS 147925 ^T	MZ736433	MZ753919	MZ736459	MZ736486	Present study
		CBS 147926	MZ736432	MZ753918	MZ736458	MZ736485	Present study
		PA19	MZ736429	MZ753915	MZ736455	MZ736482	Present study
		PA40	MZ736430	MZ753916	MZ736456	MZ736483	Present study
		PA108	MZ736431	MZ753917	MZ736457	MZ736484	Present study
<i>Phy. parsiana</i>	9a (cluster 9a1)	IMI 395329 ^T	KC733455	KC733446	KX252358	KX252363	Yang <i>et al.</i> (2014a, 2017)
<i>Phy. parvispora</i>	7c	CBS 132772 ^T	MH620071	KC478667	KX251840	KX251845	Scanu <i>et al.</i> (2014), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. personensis</i>	6a	CBS 146549 ^T	HQ012877	EU301169	MF326805	—	Jung <i>et al.</i> (2011), Crous <i>et al.</i> (2020b)
<i>Phy. phaseoli</i>	1c	CH 23B4	MH620018	MH620106	KX250496	KX250501	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. pini</i>	2c	ATCC 64532 ^T	KF317100	KF317079	KX250811	KX250816	Yang <i>et al.</i> (2014a, 2017)
<i>Phy. pinifolia</i>	6b	CBS 122924 ^T	JN935960	MH620134	KX251334	KX251339	Aghighi <i>et al.</i> (2012), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. pisi</i>	7b	CBS 130350 ^T	MH620066	KT183042	KX251736	KX251741	Yang <i>et al.</i> (2016, 2017), Yang & Hong (2018)
<i>Phy. pistaciae</i>	7b	ATCC MYA-4082 ^T	MH620067	KT183043	KX251749	KX251754	Yang <i>et al.</i> (2016), Yang & Hong (2018)
<i>Phy. plurivora</i>	2c	CBS 124093 ^T	Contig MH136959_KC855435	FJ665225	MZ736460	MZ736487	Jung & Burgess (2009), present study
<i>Phy. pluvialis</i>	3	ATCC MYA-4930 ^T	MH620033	MH620119	KX250972	KX250977	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. polonica</i>	9a (cluster 9a3)	WPC P15005	KC733456	KF358225	KX252546	EU080262	Blair <i>et al.</i> (2008), Yang <i>et al.</i> (2014a)
<i>Phy. porri</i>	8b	CBS 802.95	KC478717	KC478747	—	—	Bertier <i>et al.</i> (2013a)

Table 15. (Continued).

Species	(Sub) clade	Isolates ¹	GenBank accession numbers ²				References
			<i>cox1</i>	ITS	<i>Btub</i>	<i>tigA</i>	
		CBS 140.87	—	—	LC595879	—	—
<i>Phy. primulae</i>	8b	CBS 620.97	KF358238	KF358226	KX252064	KX252069	Yang <i>et al.</i> (2014a, 2017)
<i>Phy. prodigiosa</i>	9a (cluster 9a3)	CBS 135138 ^T	LC595937	LC595799	LC595880	—	-
<i>Phy. pseudocryptogea</i>	8a	BD755	MZ736434	MZ753920	MZ736461	MZ736488	Present study
<i>Phy. pseudolactucae</i>	8b	CBS 137103 ^T	AB894396	AB894388	—	—	Rahman <i>et al.</i> (2015)
<i>Phy. pseudopolonica</i>	9a (cluster 9a3)	CBS 142610 ^T	—	KY707115	KY707104	—	Li <i>et al.</i> (2017)
<i>Phy. pseudorosacearum</i>	6a	CBS 143061 ^T	MF326858	KJ372267	MF326827	—	Burgess <i>et al.</i> (2018)
<i>Phy. pseudosyringae</i>	3	CBS 111772 ^T	KF317105	KF317083	KX250979	KX250984	Yang <i>et al.</i> (2014a, 2017)
<i>Phy. pseudotsugae</i>	1a	IMI 331662 ^T	AY564199	FJ802112	EU080427	EU080432	Kroon <i>et al.</i> (2004), Blair <i>et al.</i> (2008)
<i>Phy. psychrophila</i>	3	CBS 803.95 ^T	KF358239	KF358227	KX250993	KX250998	Yang <i>et al.</i> (2014a, 2017)
<i>Phy. quercetorum</i>	4	CH 15C7	KF358240	KF358228	KX251063	KX251068	Yang <i>et al.</i> (2014a, 2017)
<i>Phy. quercina</i>	12	CBS 784.95 ^T	KF358241	KF358229	KX252655	KX252660	Yang <i>et al.</i> (2014a, 2017)
<i>Phy. quininea</i>	9a (cluster 9a2)	CBS 407.48 ^T	MH620099	MH620173	EU079803	EU079807	Blair <i>et al.</i> (2008), Yang & Hong (2018)
<i>Phy. ramorum</i>	8c	CH 32G2	MH620090	MH620166	KX252148	KX252153	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. rhizophorae</i>	9a (cluster 9a1)	CCIBt 4152 ^T	KT886048	KT886031	—	—	Li <i>et al.</i> (2016)
<i>Phy. richardiae</i>	8a	CBS 240.30 ^T	MH620078	MH620154	KX251924	KX251929	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. riparia</i>	6b	CBS 132024 ^T	MH620051	MH620135	KX251348	KX251353	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. rosacearum</i>	6a	ATCC MYA-4456 ^T	MH620039	MH620124	KX251446	KX251451	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. rubi</i>	7a	ATCC 90442 ^T	DQ674736	HQ643340	KX251565	KX251570	Man In't Veld (2007), Robideau <i>et al.</i> (2011), Yang <i>et al.</i> (2017)
<i>Phy. sansomeana</i>	8a	ATCC MYA-4455 ^T	MH620079	MH620155	KX251931	KX251936	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. siskiyouensis</i>	2b	CBS 122779 ^T	KF317102	KF317081	KX250678	KX250683	Yang <i>et al.</i> (2014a, 2017)
<i>Phy. sojae</i>	7b	CBS 312.62	MH620068	MH620145	KX251763	KX251768	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. stricta</i>	8	ATCC MYA-4944 ^T	KF192702	KF192694	KX252211	KX252216	Yang <i>et al.</i> (2014a, 2017)
<i>Phy. syringae</i>	8d	ATCC 34002	MH620092	MH620168	KX252197	KX252202	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. tentaculata</i>	1b	ATCC MYA-3655	MH620015	MH620103	KX250454	KX250459	Yang <i>et al.</i> (2017), Yang & Hong 2018
<i>Phy. terminalis</i>	2a	CBS 133865 ^T	JX978168	JX978167	KX250608	KX250613	Man In 't Veld <i>et al.</i> (2015), Yang (2017)
<i>Phy. theobromicola</i>	2b	CCUB 1091 ^T	MW597344	MT074263	MT074223	—	Decloquement <i>et al.</i> (2021)
<i>Phy. thermophila</i>	6b	CBS 127954 ^T	MH620052	MH620136	KX251355	KX251360	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. transitoria</i>	3	CBS 147245 ^T	MZ736439	MZ753925	MZ736466	MZ736493	Present study
		CBS 147246	MZ736435	MZ753921	MZ736462	MZ736489	Present study
		CZ119	MZ736436	MZ753922	MZ736463	MZ736490	Present study
		CZ120	MZ736437	MZ753923	MZ736464	MZ736491	Present study
		CZ121	MZ736438	MZ753924	MZ736465	MZ736492	Present study
<i>Phy. trifolii</i>	8a	CBS 117687 ^T	MH620080	MH620156	KX251959	KX251964	Yang <i>et al.</i> (2017), Yang & Hong (2018)

Table 15. (Continued).

Species	(Sub) clade	Isolates ¹	GenBank accession numbers ²				References
			<i>cox1</i>	ITS	<i>Btub</i>	<i>tigA</i>	
<i>Phy. tropicalis</i>	2b	CBS 434.91 ^T	MH620025	MH620112	KX250699	KX250704	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. tubulina</i>	12	CBS 141212 ^T	MZ736440	MF036196	MZ736467	MZ736494	Jung <i>et al.</i> (2017b), present study
<i>Phy. tyrrhenica</i>	7a	CBS 142301 ^T	MZ736441	KU899188	KU899265	MZ736495	Jung <i>et al.</i> (2017b), present study
<i>Phy. uliginosa</i>	7a	CBS 109054 ^T	MH620060	MH620140	EU080012	KX251573	Blair <i>et al.</i> (2008), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. uniformis</i>	7a	TJ002	MZ736442	KU899173	KU899249	MZ736496	Jung <i>et al.</i> (2017a), present study
<i>Phy. urerae</i>	1c	PSR27 ^T	KR632858	KR632862	KR632888	—	Grünwald <i>et al.</i> (2019)
<i>Phy. variabilis</i>	7b	CBS 147923 ^T	MZ736447	MZ753930	MZ736472	MZ736501	Present study
		CBS 147924	MZ736443	MZ753926	MZ736468	MZ736497	Present study
		TJ1496	MZ736444	MZ753927	MZ736469	MZ736498	Present study
		TJ1497	MZ736445	MZ753928	MZ736470	MZ736499	Present study
<i>Phy. versiformis</i>	12	TJ1498	MZ736446	MZ753929	MZ736471	MZ736500	Present study
		CBS 142005 ^T	KX011222	KX011279	KX011321	—	Paap <i>et al.</i> (2017)
<i>Phy. vignae</i>	7b	ATCC 46735	MH620069	MH620146	KX251777	KX251782	Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. virginiana</i>	9a (cluster 9a1)	ATCC MYA-4927 ^T	KC295546	KC295544	KX252379	KX252384	Yang & Hong (2013), Yang <i>et al.</i> (2017)
<i>Phy. vulcanica</i>	7a	CBS 141216 ^T	MZ736448	MF036209	MZ736473	MZ736502	Jung <i>et al.</i> (2017b), present study
<i>Phytophthora aleatoria</i>	1a	NZFS 4037 ^T	MK294177	MK282209	MK294172	—	Scott <i>et al.</i> (2019)
<i>Phy. *alni</i>	7a	IMI 392314 ^T	KU681017	MH620141	KX251589	KX251594	Jung <i>et al.</i> (2017a), Yang <i>et al.</i> (2017), Yang & Hong (2018)
<i>Phy. *cambivora</i>	7a	CBS 141218 ^{NT}	MZ736422	KU899179	KU899255	MZ736475	Jung <i>et al.</i> (2017a), present study
<i>Phy. *heterohybrida</i>	7a	CBS 141207 ^T	KU517145	KU517151	KX251638	KX251643	Jung <i>et al.</i> (2017a), Yang <i>et al.</i> (2017)
<i>Phy. *incrassata</i>	7a	CBS 141209 ^T	KU517150	KU517156	KX251645	KX251650	Jung <i>et al.</i> (2017a), Yang <i>et al.</i> (2017)
<i>Phy. *multiformis</i>	7a	TJ022	MZ736423	KU899184	KU899261	MZ736476	Jung <i>et al.</i> (2017a), present study
<i>Phy. *pelgrandis</i>	1	CBS 123385 ^T	MZ736424	MZ753911	MZ736450	MZ736477	Present study
<i>Phy. *serendipita</i>	1a	SFB152	MZ736425	MZ753912	MZ736451	MZ736478	Present study
<i>Phy. *stagnum</i>	6b	ATCC MYA-4926 ^T	KC631619	—	KX251376	KX251381	Yang <i>et al.</i> (2014c, 2017)
<i>Phy. *vanyenensis</i>	2a	CBS 146554 ^T	MT583648	MT568651	MT583634	—	Dang <i>et al.</i> (2021)

¹ ATCC: American Type Culture Collection, Virginia, USA; CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; BD and TJ: Dr Thomas Jung's personal culture collection, housed at Mendel University in Brno, Czech Republic and the University of Algarve, Faro, Portugal; CCIBT: Culture collection of the Instituto de Botânica, São Paulo State, Brazil; CCUB: Culture Collection at the University of Brasilia, Brazil; CGMCC: China General Microbial Culture Collection Center, Beijing, China; CH: Chuanxue Hong laboratory at Virginia Polytechnic Institute and State University, Virginia Beach, VA, USA; CPHST BL: USDA-APHIS-PPQ-Center for Plant Health, Science & Technology-Beltsville Laboratory, Beltsville, MD, USA; CZ, PA and SFB: Culture collection of Mendel University in Brno, Czech Republic; ICMP: International Collection of Microorganisms from Plants, Auckland, New Zealand; IMI: International Mycological Institute, Kew, UK; NRRL: ARS Culture Collection, Peoria, IL, USA; NZFS: New Zealand Forest Research Culture Collection, Rotorua, New Zealand; TARI: Taiwan Agricultural Research Institute, Taichung, Taiwan; WPC: The World Phytophthora Genetic Resource Collection at University of California, Riverside, USA; all other codes refer to local collections. ^T, ^{ET}, ^{NT} and ^{PT} indicate ex-type, ex-epitype, ex-neotype and ex-paratype strains, respectively.

² *cox1*: partial cytochrome-c oxidase 1 gene; ITS: internal transcribed spacers and intervening 5.8S nrDNA; *Btub*: partial β -tubulin gene; *tigA*, *tigA*: gene fusion protein. PDL Phytophthora Database (www.phytophthoradb.org).

³ Genome sequences.

The continuously growing imports of rooted plants from overseas to Europe and North America and the increasing intensity and complexity of the international nursery trade have caused the accidental introduction of many exotic *Phytophthora* species and their subsequent widespread dissemination through the nursery industry and into the wider environment (Brasier 2008, Davison *et al.* 2006, Schwingle *et al.* 2007, Moralejo *et al.* 2009, Bienapfl & Balci 2014, Jung *et al.* 2016). Consequently, since the 1960s the number of devastating forest epidemics caused by exotic and often previously unknown, invasive *Phytophthora* species has been exponentially increasing (Jung *et al.* 2018a). Recently, Jung *et al.* (2021) demonstrated that *Phy. ramorum*, the causal agent of the devastating “Sudden Oak Death” and “Sudden Larch Death” epidemics in the USA and the UK, respectively, originates from natural forests in East Asia. The centre of origin of the wide-host range pathogen *Phy. cinnamomi* was recently shown to be in Taiwan and Southeast Asia (Shakya *et al.* 2021).

Before 2000 the genus *Phytophthora* was organised in six non-natural morphological groups, named Waterhouse groups 1–6 (Waterhouse 1963, Erwin & Ribeiro 1996). Based on multigene analyses it is currently structured in 12 phylogenetic clades (Table 15; Fig. 52; Yang *et al.* 2017, Jung *et al.* 2017b). The first ITS-based phylogeny of the genus already suggested that *Peronospora* resides within *Phytophthora* (Cooke *et al.* 2000). Subsequent multigene phylogenetic studies confirmed the paraphyly of *Phytophthora* by demonstrating that the brassicolous downy mildews, the graminicolous downy mildews, the downy mildews with coloured conidia and the downy mildews with pyriform haustoria, altogether comprising ca. 600 species in 19 genera, reside as two distinct clades within *Phytophthora* (Thines & Choi 2016, Bourret *et al.* 2018). The availability of whole genome sequences for a wide range of *Phytophthora* and downy mildew species enabled phylogenomic analyses and also confirmed its paraphyletic structure with downy mildews having evolved from hemibiotrophic phytophthora-like ancestors (McCarthy & Fitzpatrick 2017, Fletcher *et al.* 2018, 2019).

Phytophthora and its recently described sister genus *Nothophytophthora* share many morphological characters like the production of chlamydospores, hyphal swellings, both persistent and caducous sporangia with internal zoospore differentiation and both external and internal extended and nested proliferation, and both amphigynous and paragynous antheridial insertion to the oogonia. The most significant morphological difference between the two genera is the presence of a conspicuous, opaque plug inside the sporangiophore close to the base of most mature sporangia in all known *Nothophytophthora* species enabling sporangial caducity in several *Nothophytophthora* species (Jung *et al.* 2017d, O’ Hanlon *et al.* 2021).

Interspecific hybridisations play an important evolutionary role in *Phytophthora* by facilitating adaptation to new host plants and environments. Nine of 16 new *Phytophthora* taxa detected in natural forests and streams in Taiwan and many *Phytophthora* isolates retrieved from aquatic ecosystems in Australia, South Africa, Chile and Vietnam were shown to be interspecific hybrids (Hüberli *et al.* 2013, Nagel *et al.* 2013, Oh *et al.* 2013, Burgess 2015, Jung *et al.* 2017a, c, 2018b, 2020). Particularly prone to interspecific hybridisations are *Phytophthora* Clades 1 (i.e. *Phy. andina*, *Phy. xpelgrandis*, *Phy. xserendipita*; Goss *et al.* 2011, Man in’ t Veld *et al.* 2012), 2a (*Phytophthora* sp. *xbotryosa*-like, *Phytophthora* sp. *xmeadii*-like; Jung *et al.* 2017c), 6 (*Phy. xstagnum* and multiple hybrids between *Phy. amnicola*, *Phy. chlamydospora*, *Phy. fluvialis*, *Phy. gonapodyides*, *Phy. litoralis*, *Phy. moyooij* and *Phy. thermophila*; Nagel *et al.* 2013, Yang *et al.* 2014c, Burgess 2015, Jung *et al.* 2018b), 7a (*Phy. xalni*, *Phy.*

xcombivora, *Phy. xincrassata*, *Phy. xheterohybrida*, *Phy. xmultiformis*; Brasier *et al.* 2004, Husson *et al.* 2015, Jung *et al.* 2017a, 2020), 7b (hybrids of *Phy. sojae* and *Phy. vignae*; May *et al.* 2003), 8b (multiple hybrids of *Phy. primulae*, *Phytophthora* taxon Parsley and several unknown species; Bertier *et al.* 2013b) and 9 (multiple hybrids of *Phy. insolita*, *Phy. virginiana*, *Phytophthora* sp. Grenada 3, *Phytophthora* sp. kunnunara and *Phytophthora* sp. Peru 4; Jung *et al.* 2017, 2020). All known *Phytophthora* hybrids are allopolyploid with known genome sizes ranging from 236 Mbp in *Phy. xalni*, 230–510 Mbp in *Phy. xcombivora* to 654.3 Mbp in *Phy. xincrassata* (Feau *et al.* 2016; Jung *et al.* 2017a), and resulted from sexual crossings rather than from somatic fusions (cf. May *et al.* 2003, Burgess 2015, Jung *et al.* 2017a, c, 2018b, 2020). *Phytophthora xalni*, *Phy. xcombivora* and *Phy. xmultiformis* are the causal agents of widespread root and collar rot epidemics of *Alnus* and *Fagaceae* forests while *Phy. xpelgrandis*, *Phy. xserendipita* and the Clade 8d hybrids cause serious diseases of ornamentals, vegetables and poplar trees (Brasier *et al.* 2004, Jung & Blaschke 2004, Jung *et al.* 2000, 2013a, 2018a, b, Man in’ t Veld *et al.* 2012, Bertier *et al.* 2013b, Milenković *et al.* 2018). *Phytophthora xincrassata*, *Phy. xheterohybrida* and hybrids of *Phy. sojae* and *Phy. vignae* demonstrated in pathogenicity trials high aggressiveness to forest trees and soybean and cowpea cultivars, respectively (May *et al.* 2003, Jung *et al.* 2017a). Using phylogenomics and genome size estimation, van Poucke *et al.* (2021) confirmed and characterised 27 previously described hybrid species and discovered 16 new hybrid species.

References: Blackwell 1949 (morphology and terminology); Erwin & Ribeiro 1996 (morphology, physiology and pathogenicity); Cooke *et al.* 2000, Yang *et al.* 2017, Bourret *et al.* 2018, van Poucke *et al.* 2021 (phylogeny); Lamour 2013, Jung *et al.* 2018a (pathogenicity); Burgess 2015, Husson *et al.* 2015, van Poucke *et al.* 2021 (hybridization); Jung *et al.* 2017a (hybridization, morphology, phylogeny); Jung *et al.* 2021, Shakya *et al.* 2021 (centre of origin).

Phytophthora transitoria I. Milenković, T. Májek & T. Jung, **sp. nov.** MycoBank MB 839452. Fig. 57.

Etymology: Referring to the transitional role of most primary sporangia releasing their cytoplasm into a secondary emerging sporangium which forms and releases zoospores.

Morphological structures on V8A: *Sporangia* infrequently observed in solid agar of 1–3-mo-old cultures and produced commonly in non-sterile soil extract; $32.5 \pm 4.9 \times 25.7 \pm 3.8 \mu\text{m}$ (overall range 20.0–42.5 \times 14.9–33.3 μm) with a length/breadth ratio of 1.33 ± 0.3 (overall range 1.05–3.0); primary sporangia nonpapillate, borne terminally on unbranched sporangiophores, almost exclusively transitional, releasing their undifferentiated cytoplasm gradually into secondary nonpapillate sporangia instead of releasing zoospores (Fig. 57A–R); secondary sporangia emerging from mature primary sporangia at or near the apex (Fig. 57B–N, P–R, T–V) or laterally (Fig. 57O, S), sessile (Fig. 57J, K, M, N, Q–S) or on short stalks (Fig. 57L, O, P, T–V); nonpapillate (Fig. 57K–M, O–R); primary and secondary sporangia usually with a conspicuous basal plug (Fig. 57C–W) and often 1 or 2 additional plugs inside the sporangiophore close to the sporangial base (Fig. 57D–H, J, M–P, T–V) forming short or medium-length pedicels; despite pedicels non-caducous; sporangial shapes varying from subglobose (8 %; Fig. 57B, C, J, K, O, P, T, U), ovoid or broad-ovoid (60 %; Fig. 57A, D, E, G–I, K–N, Q, R), obpyriform (8 %; Fig. 57F) and pyriform (6 %; Fig. 57S) to limoniform (1 %; Fig. 57O, P); lateral attachment of the sporangiophore to the primary sporangia commonly observed

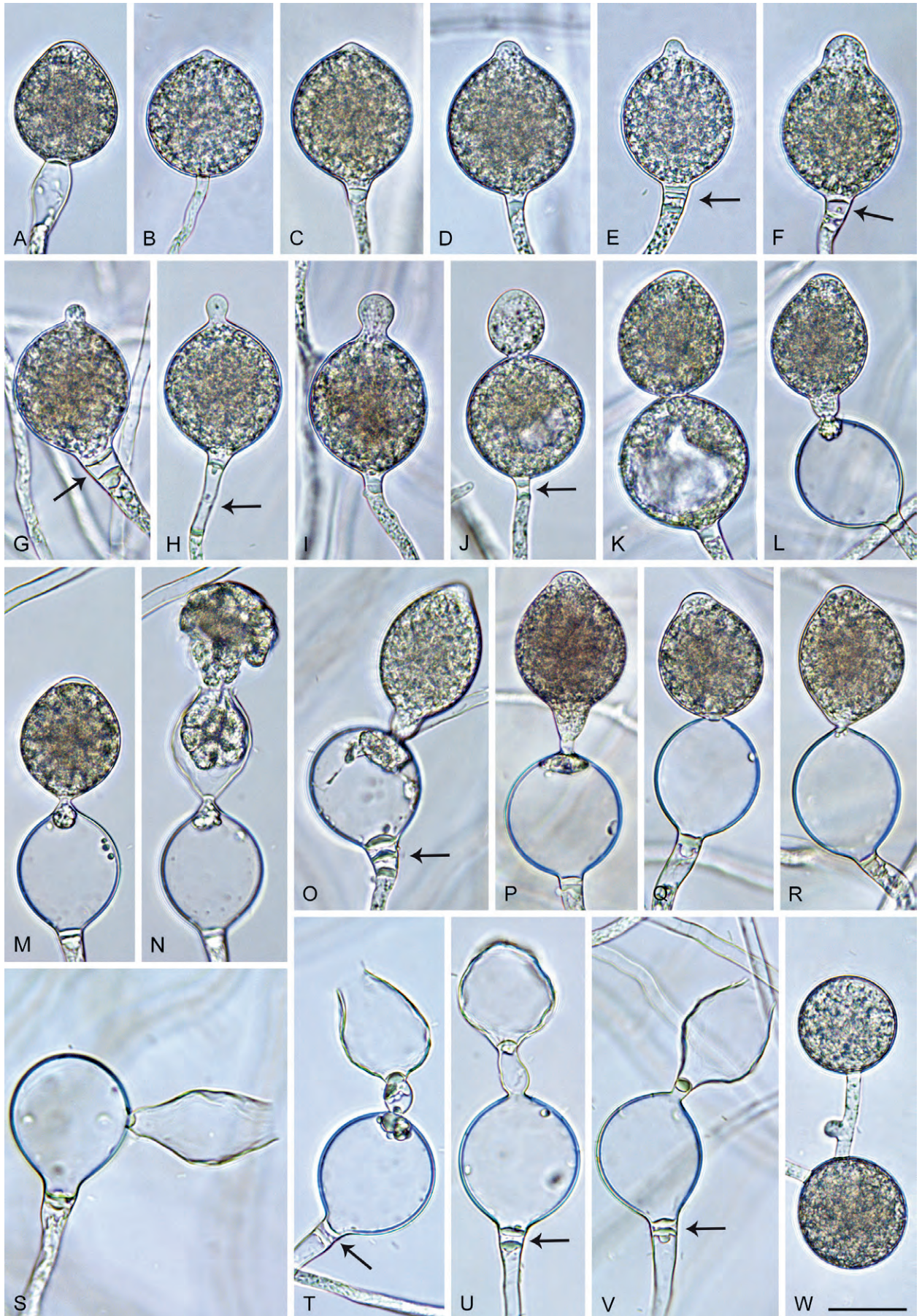


Fig. 57. *Phytophthora transitoria* (ex-type CBS 147245). **A–V.** Sporangia formed on V8 agar (V8A) flooded with soil extract. **A.** Nonpapillate, ovoid primary sporangium with widened sporangiophore. **B–D.** Primary transitional sporangia in different stages of development of secondary sporangia, with conspicuous basal plugs. **E.** With three basal plugs (arrow). **F–H, J.** With pedicels (arrows). **L–R.** Empty, primary transitional sporangia with conspicuous basal plugs and secondary mature sporangia after completion of cytoplasm transfer from the primary sporangia. **N.** Release of zoospores by the secondary sporangium. **O.** With three basal plugs. **S–V.** Empty, primary transitional sporangia and attached, empty secondary sporangia after zoospore release; all sporangia with one or multiple (arrows) basal plugs. **W.** Globose intercalary and terminal chlamydospores formed in solid V8A. Scale bar = 25 μm ; W applies to A–V.

(26 %; Fig. 57G, R). Zoospores differentiate almost exclusively inside secondary sporangia (Fig. 57N–O), discharged through an exit pore 5.2–11.3 µm wide (av. 7.4 ± 1.5 µm; Fig. 57N, S–V), limoniform to reniform whilst motile, becoming spherical (av. diam = 9.9 ± 1.2 µm) on encystment. *Chlamydozoospores* globose to subglobose, 28.9 ± 4.9 µm diam (overall range 17.4–38.1 µm), terminal or intercalary, sometimes catenulate (Fig. 57W). *Gametangia* not observed in single culture or in mating tests with A1 and A2 tester strains of *Phytophthora cinnamomi*, suggesting a sterile breeding system.

Culture characteristics: Colonies on V8A and CA uniform and submerged; on PDA uniform, dense-felty and appressed with irregular submerged margins and slow growth (Fig. 60).

Cardinal temperatures and growth rates: Optimum 22.5 °C with 4.0 mm/d radial growth on V8A, maximum 30 °C, minimum < 10 °C.

Typus: **Czech Republic**, Central Bohemian region, Obříství, isolated from rhizosphere soil of a *Quercus robur* (Fagaceae) seedling, Mar. 2018, I. Milenković (**holotype** CBS H-24578, dried culture on V8A, culture ex-type CBS 147245 = CZ001).

Additional materials examined: **Czech Republic**, Central Bohemian region, Obříství, isolated from rhizosphere soil of nursery-grown *Quercus robur* seedlings, Mar. 2018, I. Milenković (cultures CBS 147246 = CZ118, CZ119, CZ120, CZ121, CZ123).

Notes: *Phytophthora transitoria* differs from all other known *Phytophthora* species by releasing zoospores almost exclusively from secondary sporangia which emerge from primary transient sporangia. In addition, *Phy. transitoria* has a sterile breeding system and produces nonpapillate persistent sporangia differentiating it from all other known species from phylogenetic Clade 3 (Fig. 52) which are homothallic with semipapillate, predominantly caducous sporangia.

Phytophthora panamensis T. Jung, Y. Balci, K. Broders & I. Milenković, **sp. nov.** MycoBank MB 840175. Fig. 58.

Etymology: Name refers to Panama, the country where this species was first isolated.

Morphological structures on V8A: *Sporangia* commonly observed in solid agar and abundantly produced in non-sterile soil extract; borne terminally on long unbranched sporangiophores (8.8 %), in lax sympodia (14.8 %) or on short lateral sporangiophores (70.4 %; Fig. 58E, I) or less frequently intercalary (6.0 %; Fig. 58D); non-caducous, predominantly ovoid or elongated ovoid (94.4 %; Fig. 58A–D, F, G, K), less frequently limoniform (3.6 %; Fig. 58J), obpyriform (1.2 %; Fig. 58I), mouse-shaped (0.4 %; Fig. 58E, H) or distorted (0.4 %); lateral attachment of the sporangiophore (50.4 %; Fig. 58B, C, E) and a conspicuous basal plug (60 %; Fig. 58K) commonly observed; sometimes forming short hyphal appendices (Fig. 58B); apices papillate or rarely bipapillate (<1 %; Fig. 58J), frequently asymmetric to curved (31.2 %; Fig. 58E–I); occasionally external proliferation (Fig. 58I, K); sporangial dimensions averaging $44.1 \pm 5.3 \times 29.8 \pm 3.5$ µm (overall range 28.5–62.9 × 20.3–41.3 µm) with a length/breadth ratio of 1.49 ± 0.16 (overall range 0.95–1.97); sporangial germination usually indirectly with zoospores discharged through an exit pore 3.9–8.3 µm wide (av. 6.2 ± 0.9 µm) (Fig. 58G, K). Zoospores limoniform to reniform whilst motile, becoming spherical (av. diam = 9.5 ± 1.1 µm) on encystment. *Hyphal swellings* subglobose to mostly globose, intercalary, averaging 11.4 ± 3.2 µm (Fig. 58W). *Chlamydozoospores* not observed. *Oogonia* abundantly produced in single culture (homothallic breeding system),

terminal on short to medium-length, often twisted lateral hyphae (Fig. 58L–V), smooth-walled, globose to slightly subglobose (74.4 %; Fig. 58L–Q), less frequently slightly excentric or elongated (25.6 %; Fig. 58R–V), relatively small (mean diam 24.6 ± 2.1 µm, overall range 16.0–31.0 µm); plerotic or almost plerotic (62.8 %; Fig. 58M–P, S) or aplerotic (37.2 %; Fig. 58L, Q, R, T–V). *Oospores* globose with a large lipid globule (Fig. 58L–V), wall thickness 1.9 ± 0.3 µm (overall range 1.1–2.7 µm), oospore wall index 0.43 ± 0.04 ; abortion 16–33 % after 4 wk. *Antheridia* exclusively paragynous and club-shaped to subglobose (Fig. 58L–V), frequently formed on hyphal branches arising close to the oogonia-bearing hyphal branch (Fig. 58V), sometimes with a finger-like projection (1.2 %).

Culture characteristics: Colonies on V8A and CA mostly submerged to appressed, radiate on V8A and uniform on CA; on PDA dense-felty to cottony, petaloid with submerged margins (Fig. 60).

Cardinal temperatures and growth rates: Optimum 27.5 or 30 °C with 9.5–9.7 mm/d radial growth on V8A, maximum 30–32.5 °C, minimum >10–15 °C.

Notes: *Phytophthora panamensis* differs from its closest relative *Phy. quercetorum* in phylogenetic Clade 4 (Fig. 52) by producing on average smaller oogonia and oospores and larger sporangia, having higher minimum and optimum temperatures and lower maximum temperature for growth, showing considerably faster growth between 15 °C and 30 °C and different colony morphology on V8A and CA.

Typus: **Panama**, Parque Nacional Soberania, isolated from necrotic lesion on a naturally fallen leaf of a non-identified tree species in a tropical lowland forest, Nov. 2019, K.D. Broders & Y. Balci (**holotype** CBS H-24773, dried culture on V8A, culture ex-type CBS 147925 = PA328).

Additional materials examined: **Panama**, Parque Nacional Soberania, isolated from necrotic lesions on naturally fallen leaves of non-identified tree species in tropical lowland forests, Nov. 2019, K.D. Broders & Y. Balci (cultures CBS 147926 = PA329, PA019, PA040, PA108).

Phytophthora variabilis T. Jung, M. Horta Jung & I. Milenković, **sp. nov.** MycoBank MB 840174. Fig. 59.

Etymology: Name refers to the variable shapes of the oogonia with both amphigynous and paragynous antheridia.

Morphological structures on V8A: *Sporangia* not observed in solid agar but abundantly produced in non-sterile soil extract; borne terminally on mostly long unbranched or less frequently short lateral sporangiophores (72.4 %; Fig. 59A–J) or via internal nested and extended proliferation (18.8 %; Fig. 59I, J) or external proliferation (8.8 %); nonpapillate, non-caducous, predominantly ovoid, broad ovoid or elongated ovoid (83.2 %; Fig. 59A–D, I), less frequently ellipsoid or elongated ellipsoid (4.8 %; Fig. 59F, G) or elongated obpyriform (0.4 %; Fig. 59E); basal plug common (39.2 %; Fig. 59A, F, H); lateral attachment of the sporangiophore (8.8 %) and a slightly displaced apex (2.8 %) infrequently observed; sporangial dimensions averaging $61.0 \pm 7.0 \times 37.7 \pm 3.9$ µm (overall range 47.2–82.5 × 25.3–47.9 µm) with a length/breadth ratio of 1.62 ± 0.16 (overall range 1.28–2.25); sporangial germination indirectly with zoospores discharged through a wide exit pore of 8.2–18.6 µm (av. 13.1 ± 2.1 µm) into a short-lived vesicle (Fig. 59H, J). Zoospores limoniform to reniform whilst motile (Fig. 59H, J), becoming spherical (av. diam = 10.3 ± 1.0 µm) on encystment. *Hyphal swellings* and

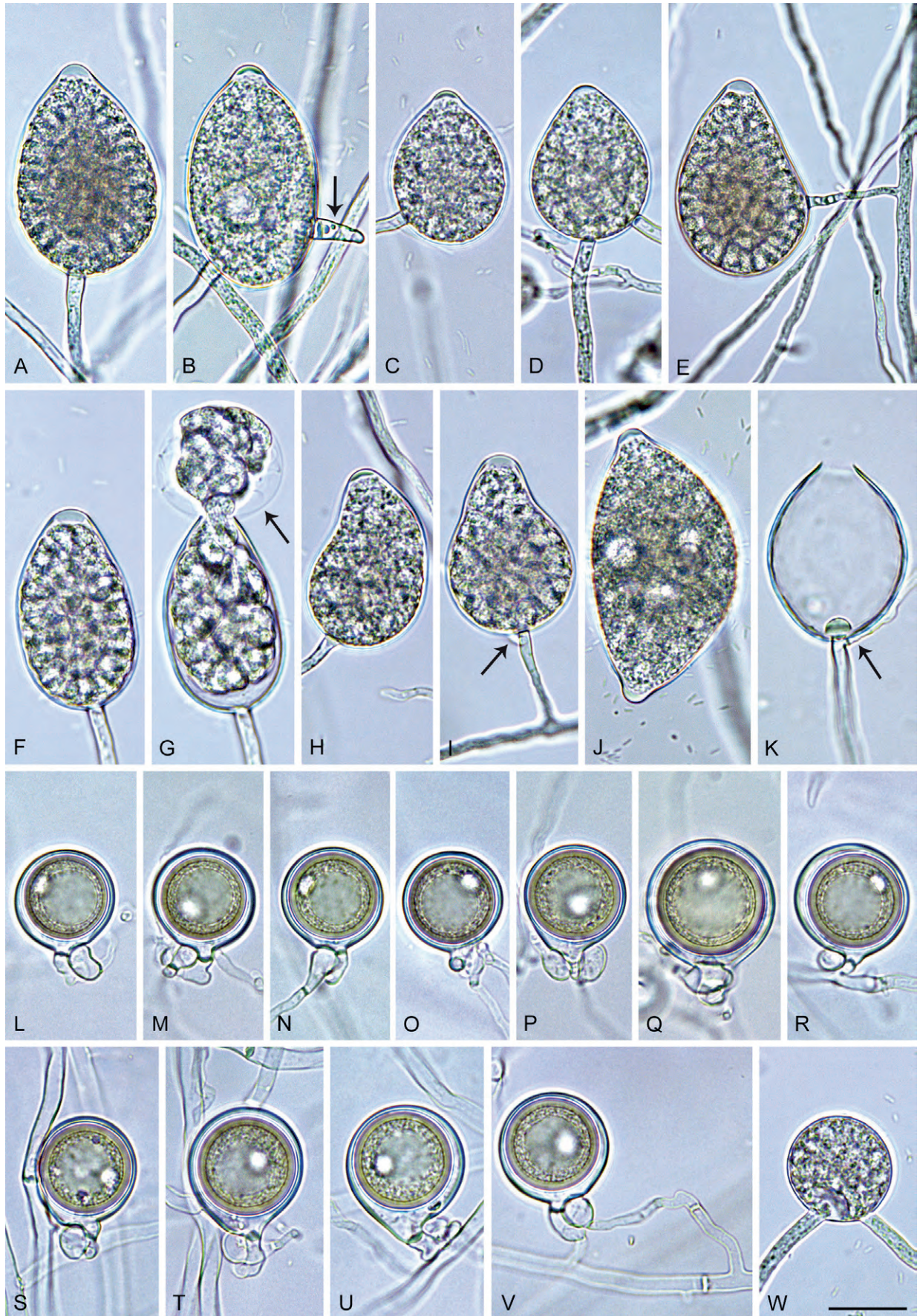


Fig. 58. *Phytophthora panamensis* (ex-type CBS 147925). **A–K.** Papillate sporangia formed on V8 agar (V8A) flooded with soil extract. **A.** Ovoid, with differentiated zoospores inside the sporangium. **B.** Ovoid with hyphal projection (arrow), laterally attached. **C.** Ovoid, laterally attached. **D.** Ovoid, intercalary. **E.** Asymmetric-obpyriform with differentiated zoospores, laterally attached, on short lateral hypha. **F, G.** Elongated-ovoid, releasing zoospores into short-lived vesicle (arrow). **H.** Mouse-shaped. **I.** Obpyriform, with external proliferation (arrow), on short lateral hypha. **J.** Limoniform, bipapillate. **K.** Ovoid, after zoospore release, with conspicuous basal plug and external proliferation (arrow). **L–V.** Oogonia with thick-walled oospores, containing large lipid globules, and paragnathous antheridia, formed in solid V8A. **L–Q.** Globose to subglobose. **R–V.** Slightly excentric or elongated. **M–P, S.** Plerotic or almost plerotic oospores. **Q, R, T–V.** Aplerotic oospores. **W.** Intercalary globose hyphal swelling in solid V8A. Scale bar = 25 μ m; W applies to A–V.



Fig. 59. *Phytophthora variabilis* (ex-type CBS 147923). **A–J.** Non-caducous sporangia formed on V8 agar (V8A) flooded with soil extract. **A–F, I.** Nonpapillate. **A–D.** Ovoid. **D.** On short lateral hypha. **E.** Elongated-obpyriform. **F.** Elongated-ellipsoid. **G, H.** Ellipsoid, releasing zoospores into short-lived vesicle (arrow). **I.** Ovoid, internal extended proliferation. **J.** Internal nested proliferation, zoospore release into short-lived vesicle (arrow). **K–V.** Oogonia containing thick-walled, brown, aplerotic oospores with large lipid globules formed in solid V8A, variable shapes. **K, M, O.** Excentric. **L, P.** Elongated with tapering base. **N.** Comma-shaped. **Q–V.** Globose to slightly subglobose. **K–Q.** Paragynous antheridia. **R–V.** Amphigynous antheridia. Scale bar = 25 µm; V applies to A–U.

chlamydospores not observed. *Oogonia* abundantly produced in single culture (homothallic breeding system), sessile (12.5 %; Fig. 59M, N) or on short stalks which are often unusually thin (Fig. 59S, T) or thick (Fig. 59K, P, Q) and sometimes curved (Fig. 59P, Q); smooth-walled with variable shapes ranging from globose to slightly subglobose (55.5 %; Fig. 59Q–V), elongated (10.5 %; Fig. 59L, P) or excentric (25.5 %; Fig. 59K, M, O) to comma-shaped (19.5 %; Fig. 59N); av. diam. $33.0 \pm 3.9 \mu\text{m}$ with an overall range of 24.0–49.9 μm ; largely aplerotic (Fig. 59K–V). *Oospores* globose to subglobose with a medium-large lipid globule (Fig. 59K–V); wall diam $1.4 \pm 0.2 \mu\text{m}$ (overall range 0.8–2.0 μm) and oospore wall index 0.30 ± 0.04 ; turning brown during maturation (Fig. 59K–V); abortion 2–7 % after 4 wk. *Antheridia* paragynous (68.5 %; Fig. 59K–Q) or amphigynous (31.5 %; Fig. 59R–V), 1-celled, and club-shaped, ovoid, subglobose or elongated to irregular (Fig. 59K–V).

Culture characteristics: Colonies on V8A and CA with limited aerial mycelium, radiate on V8A and uniform on CA; on PDA uniform and cottony (Fig. 60).

Cardinal temperatures and growth rates: Optimum 27.5 °C with 6.1–6.3 mm/d radial growth on V8A, maximum 32.5–35 °C, minimum <10 °C.

Notes: *Phytophthora variabilis* differs from all other species from Clade 7b (Fig. 55) by its distinct phylogenetic position and by having highly variable oogonial shapes. In addition, it is distinguished from the heterothallic *Phy. niederhauserii* and *Phy. melonis* (Erwin & Ribeiro 1996, Mirabolfathy et al. 2001, Abad et al. 2014) by its homothallic breeding system. The production of both amphigynous and paragynous antheridia separate *Phy. variabilis* from *Phy. cajani*, *Phy. melonis*, *Phy. sinensis* and *Phy. vignae* which

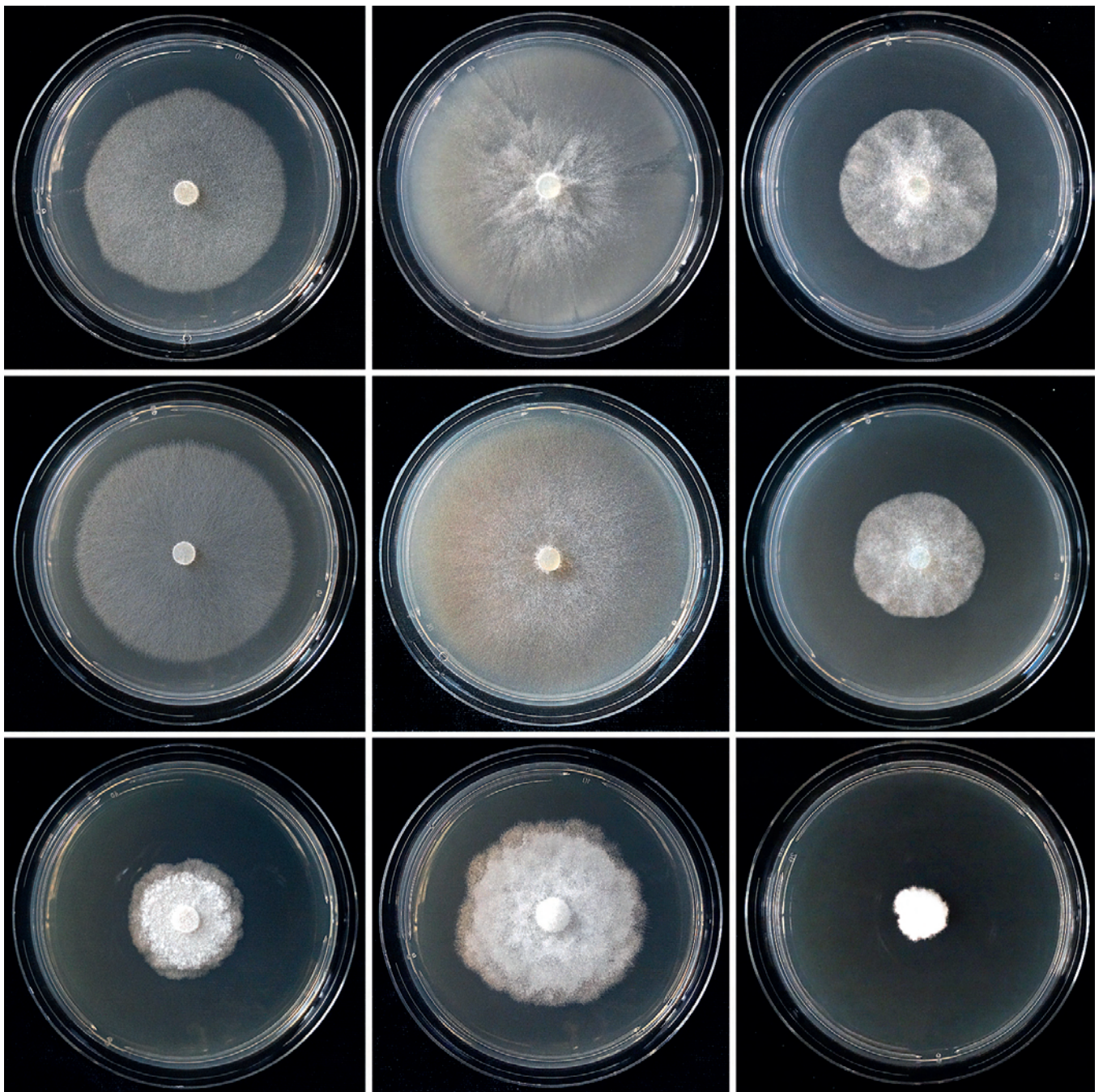


Fig. 60. Colony morphology of *Phytophthora transitoria*, *Phytophthora panamensis* and *Phytophthora variabilis* (from left to right) after 7 d growth at 20 °C in the dark on V8-agar, carrot agar and potato-dextrose agar (from top to bottom).

all have exclusively amphigynous antheridia (Erwin & Ribeiro 1996, Mirabolfathy *et al.* 2001) and from *Phy. asiatica* which produces paragynous antheridia only rarely (Rahman *et al.* 2015).

Typus: **Slovakia**, Bratislava, Marianka, isolated from a commercial tree planting substrate, Jun. 2013, T. Jung (**holotype** CBS H-24772, dried culture on V8A, culture ex-type CBS 147923 = TJ915).

Additional materials examined: **Slovakia**, Bratislava, Marianka, isolated from a commercial tree planting substrate, Jun. 2013, T. Jung (cultures CBS 147924 = TJ1495, TJ1496, TJ1497, TJ1498).

Genome sequenced strain: *Phytophthora infestans*. **Netherlands**, collection information unknown, isolate T30-4 (F_1 individual from a genetic cross used to construct a linkage of *Phy. infestans*). This Whole Genome Shotgun project has been deposited at GenBank under the accession AATU01000000 (BioProject: PRJNA17665, BioSample: SAMN02953670; Haas *et al.* 2009).

Authors: T. Jung, Y. Balci, X. Yang, M. Horta Jung, I. Milenković, K.D. Broders, M. Tomšovský, T. Májek, B. Scanu

Pseudocercospora Spegazzini, Anales Mus. Nac. Buenos Aires, Ser. 3 13: 437. 1911. Fig. 61.

Synonyms: For synonyms see Braun *et al.* (2013).

Classification: *Dothideomycetes*, *Dothideomycetidae*, *Mycosphaerellales*, *Mycosphaerellaceae*.

Type species: *Pseudocercospora vitis* (Lév.) Spegazzini, basionym: *Septonema vitis* Lév., Anns Sci. Nat., Bot., sér. 3 9: 261. 1848. The state of type material is unclear.

DNA barcode (genus): ITS.

DNA barcodes (species): *act*, *rpb2* and *tef1*. Table 16. Fig. 62.

Sexual morph (*vide* Crous 1998, Aptroot 2006) “mycosphaerella-like”. *Ascomata* invariably carbonised, uniformly rather large-cellular with parenchymatous cells, dispersed or aggregated. *Ascomatal wall* extended also below the hamathecium. *Clypeus* not observed. *Ostirole* apical, cells of ostirole arranged regularly. *Hamathecium* filaments (paraphyses, pseudoparaphyses, paraphysoids) always absent. *Asci* bitunicate, pyriform cylindrical, or cylindrical-clavate, variable in size, plerotic, containing 8 ascospores. *Ascospores* arranged irregularly uniseriate to irregularly biseriate or multiseriate, hyaline, median to conspicuously supramedian uniseptate (rarely 3-septate), variable in shape, rounded or slightly pointed at both ends, with thin wall. *Stromata* lacking to well developed, pigmented, subhyaline to dark brown, stomatal, epidermal, erumpent, often with superficial hyphae. *Pycnidial conidioma* rarely formed. *Conidiophores* solitary arising from superficial hyphae or loosely to densely fasciculate from upper part of stromata, rarely synnematos, straight to flexuous or geniculate, subhyaline to dark brown, simple or branched, thin- or thick-walled, smooth to verruculose, aseptate or septate. *Conidiogenous cells* integrated, terminal or intercalary, proliferating sympodially or percurrently, with unthickened conidial loci, rarely cicatrized or ring-shaped. *Conidia* solitary, rarely bearing micro-cyclic conidia in moist condition, holoblastic, cylindrical, acicular to obclavate, straight to mildly curved, subhyaline, pale or dark brown, reddish brown or pale to deep olivaceous, thin- or thick-walled, smooth- to verruculose-walled, aseptate to septate, often more than 10-disto- or euseptate, with unthickened and not darkened hilum, rarely slightly thickened along the rim.

Cultural characteristics: Colonies on PDA and MEA pale grey, smoke grey, grey olivaceous, pale olivaceous grey, pale greenish grey, olivaceous grey to greenish grey (Rayner 1970) on the upper surface, greenish grey, olivaceous black to greenish black on the under surface, floccose, cottony, flat, raised or convex, margin lobate, undulate, entire or sometimes rhizoid. Seldom with citrine green to greyish yellow green diffusible pigmentation in agar medium (Fig. 63).

Optimal media and artificial sporulation: Sterilised banana leaves placed on 1.5 % water agar (WA) or slide cultures of V-8 juice agar under nuv-light to induce sporulation of the asexual morph, while for the sexual morph Sach’s agar (Crous *et al.* 2019d) with sterilised pine needles is recommended, incubated at 20–25 °C, pH 4–9. Inoculation tests using conidia formed on artificial media are required to confirm pathogenicity. Oatmeal agar prepared with host-leaf decoction water (tomato leaf: Hartman *et al.* 1991), sclerotia bodies formed by shake culture (Zinno 1970), and cultivation under nuv-light (Suto 1985). The following method has successfully been used for *Ps. fuligena*: 1) incubate isolate on MEA Petri dish for 1 wk. The medium should be kept somewhat dry; 2) the colony is scratched and spread with a spreader; 3) leaves of the host plant are dipped and lightly waved in boiling water (in the case of tomato leaves, approx. 40 s); 4) leaf pieces are cut out in 5 mm squares, and completely dried under a laminar flow fume hood; 5) several leaf pieces are placed on the spreading colony and incubated for 2 wk under diffused light, without sealing the dishes. Conidia are collected with sterile water and a brush.

Distribution: Worldwide.

Hosts: Wide host range, including ferns, monocots, and dicots.

Disease symptoms: Leaf spots, leaf blight, shot-hole, sooty spots and early defoliation, twig cankers, fruit and husk spots (Fig. 63).

Notes: The taxonomic criteria for distinguishing genera and species of cercosporoid fungi, including *Pseudocercospora*, are sequentially published in a series by Braun *et al.* (2013, 2014, 2015a, b, 2016). The distinguishable morphological characteristics from other cercosporoid fungi are: pale to dark olivaceous caespituli, pigmented conidia with unthickened and not refractive scars on the conidiogenous cells and hila at the basal ends of conidium *in vivo* (Braun *et al.* 2013, Crous *et al.* 2013a, Videira *et al.* 2017). Species criteria of *Pseudocercospora* are based on morphological differences on the host plants as in other cercosporoid fungal genera. This criterion postulates that *Pseudocercospora* species are chiefly host specific. However, inoculation tests on various hosts are largely lacking. Host specificity is supported by the overall DNA phylogeny of *Pseudocercospora* as presented in Crous *et al.* (2013a). Recently, Nakashima *et al.* (2016) indicated that the *rpb2* locus should be added to the concatenated ITS-*actA-tef1* alignment as a robust secondary DNA barcode for recognition of species within the genus *Pseudocercospora*.

References: Deighton 1976 (re-evaluation of the genus *Pseudocercospora*); Crous 1998 (sexual morph); Crous & Braun 2003 (morphology, host range and list of species); Crous *et al.* 2013a (phylogeny); Braun *et al.* 2013, 2014, 2015a, b, 2016 (morphology, host range and list of species by the host family); Nakashima *et al.* 2016 (morphology and DNA barcodes for species); Videira *et al.* 2017 (morphology in culture and phylogeny).

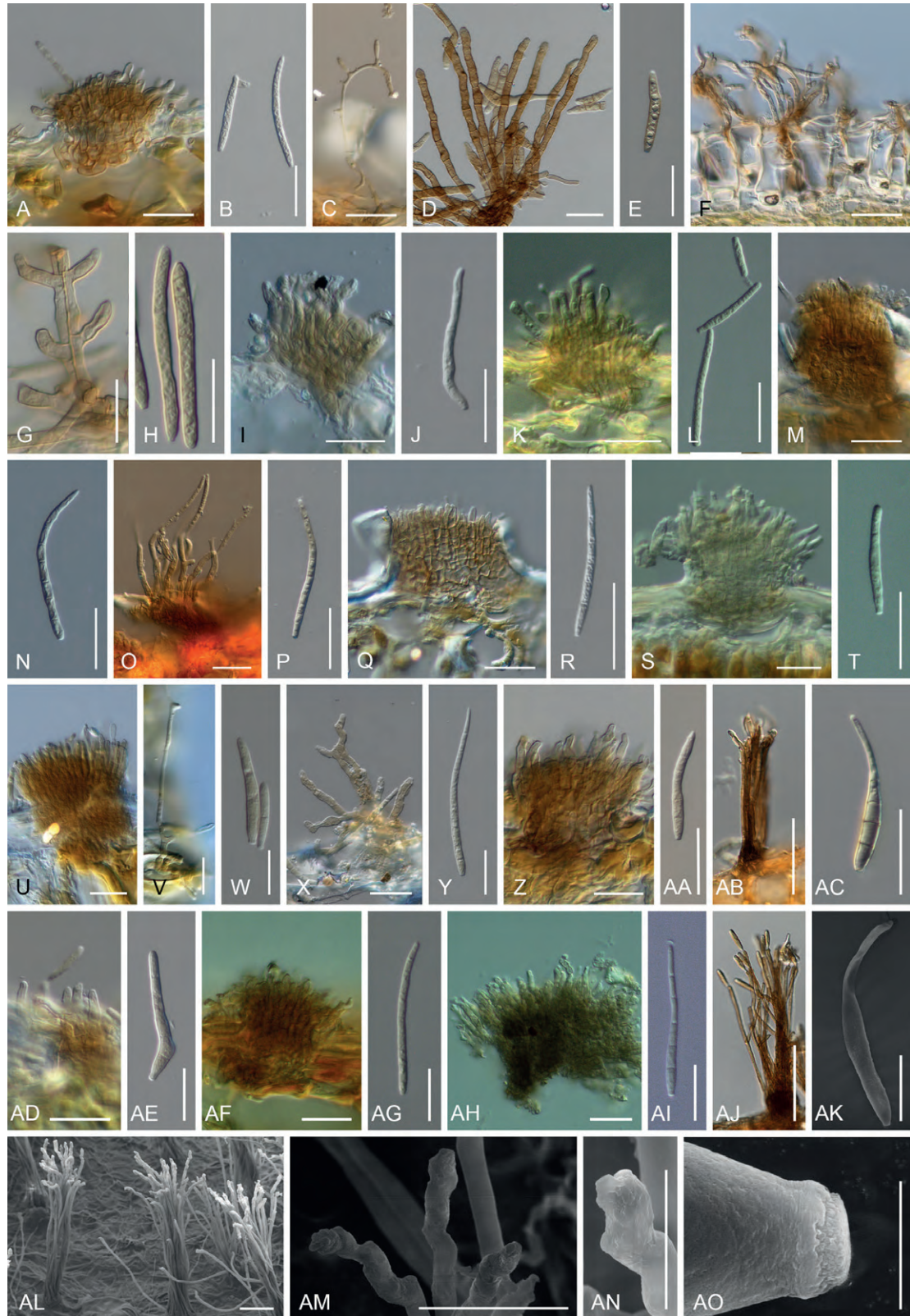


Fig. 61. *Pseudocercospora* spp. on host plants. **A, I, K, M, O, Q, S, U, Z, AF, AH, AJ.** Substomatal or erumpent stromata. **D, F, G, X, AB, AD.** Small stromata composed of few brown cells. **A, D, F, I, K, M, O, Q, S, U, X, Z, AB, AD, AF, AH, AJ.** Conidiophores emerging from stromata. **C, F, G, V.** Short conidiophores branched from superficial hypha. **AB, AJ, AL.** Synnematos conidiophores. **B, E, H, J, L, N, P, R, T, W, Y, AA, AC, AE, AG, AI, AK.** Conidia. **AM.** Sympodially proliferating conidiogenous cell. **AN.** Unthickened and truncated conidiogenous loci at the shoulder of conidiogenous cells. **AO.** Unthickened basal end of conidia. **A–C.** *Pseudocercospora amelanchieris* (holotype TSU-MUMH11539). **D, E.** *Pseudocercospora araliae* (epitype TFM: FPH-8094). **F.** *Pseudocercospora avicenniae* (isotype CPC17304). **G, H.** *Pseudocercospora bruceae* (TSU-MUMH11880). **I, J.** *Pseudocercospora chibaensis* (holotype TFM: FPH-6914). **K, L.** *Pseudocercospora chionanthi-retusi* (epitype NCHUP 3205). **M, N.** *Pseudocercospora daphniphylli* (holotype TFM: FPH-4431). **O, P.** *Pseudocercospora elaeocarpicola* (holotype TFM: FPH-7447). **Q, R.** *Pseudocercospora eriobotryae* (epitype TSU-MUMH11284). **S, T.** *Pseudocercospora eriobotryicola* (epitype NCHUP 3201). **U–W.** *Pseudocercospora hiratsukana* (epitype TNS-F-61275). **X, Y.** *Pseudocercospora houttuyniae* (holotype TNS-F-243809). **Z, AA.** *Pseudocercospora humuli* (holotype NIAES C487). **AB, AC.** *Pseudocercospora pruni-grayanae* (epitype TSU-MUMH11475). **AD, AE.** *Pseudocercospora stephanandrae* (holotype TFM: FPH-4411). **AF, AG.** *Pseudocercospora linea* (epitype NCHUP 3203). **AH, AI.** *Pseudocercospora violamaculans* (neotype TSU-MUMH11409). **AJ–AO.** *Pseudocercospora vitis* (TSU-MUMH 11593). Pictures A–E, G–J, M–AC, AF–AK were taken from Nakashima *et al.* (2016). Scale bars: A–AL = 20 µm; AM, AN = 5 µm, AO = 2.5 µm.

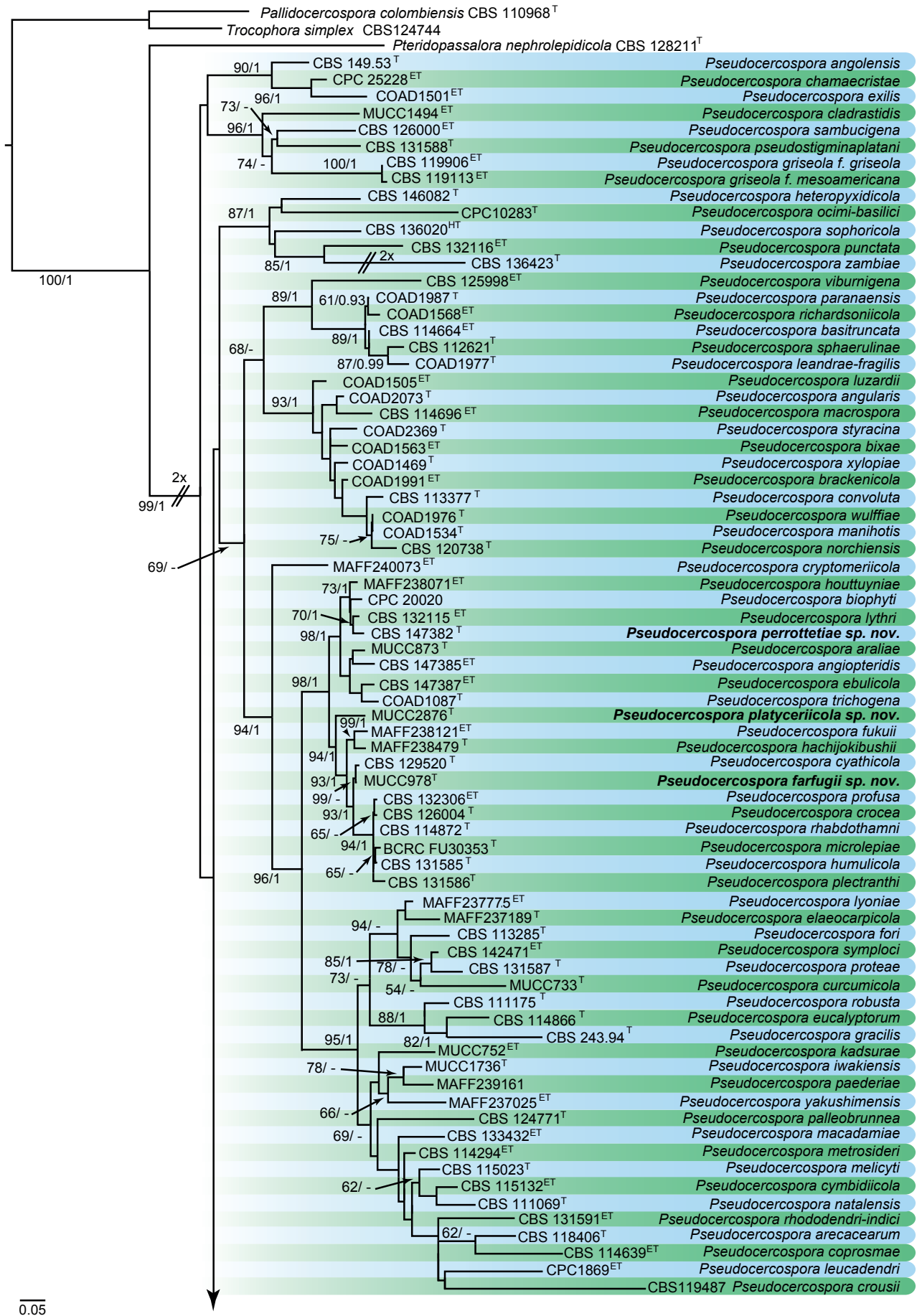


Fig. 62. Maximum Likelihood (ML) phylogram constructed from *actA* (254 bp), ITS (520 bp), *tef1* (615 bp), and *rpb2* (676 bp) sequences of all accepted species of *Pseudocercospora*. Maximum Likelihood bootstrap support values (> 50 %) and Bayesian posterior probability scores (> 0.90) are shown at the nodes. The novel taxa are printed in bold. The phylogenetic tree was rooted to *Pallidocercospora colombiensis* CBS 110968 and *Trocophora simplex* CBS 124744. GenBank accession numbers are indicated in Table 16. ^T, ^{ET}, ^{ISOT} and ^{NT} indicate ex-type, ex-epitype, ex-isotype and ex-neotype strains, respectively. TreeBASE: S27432.

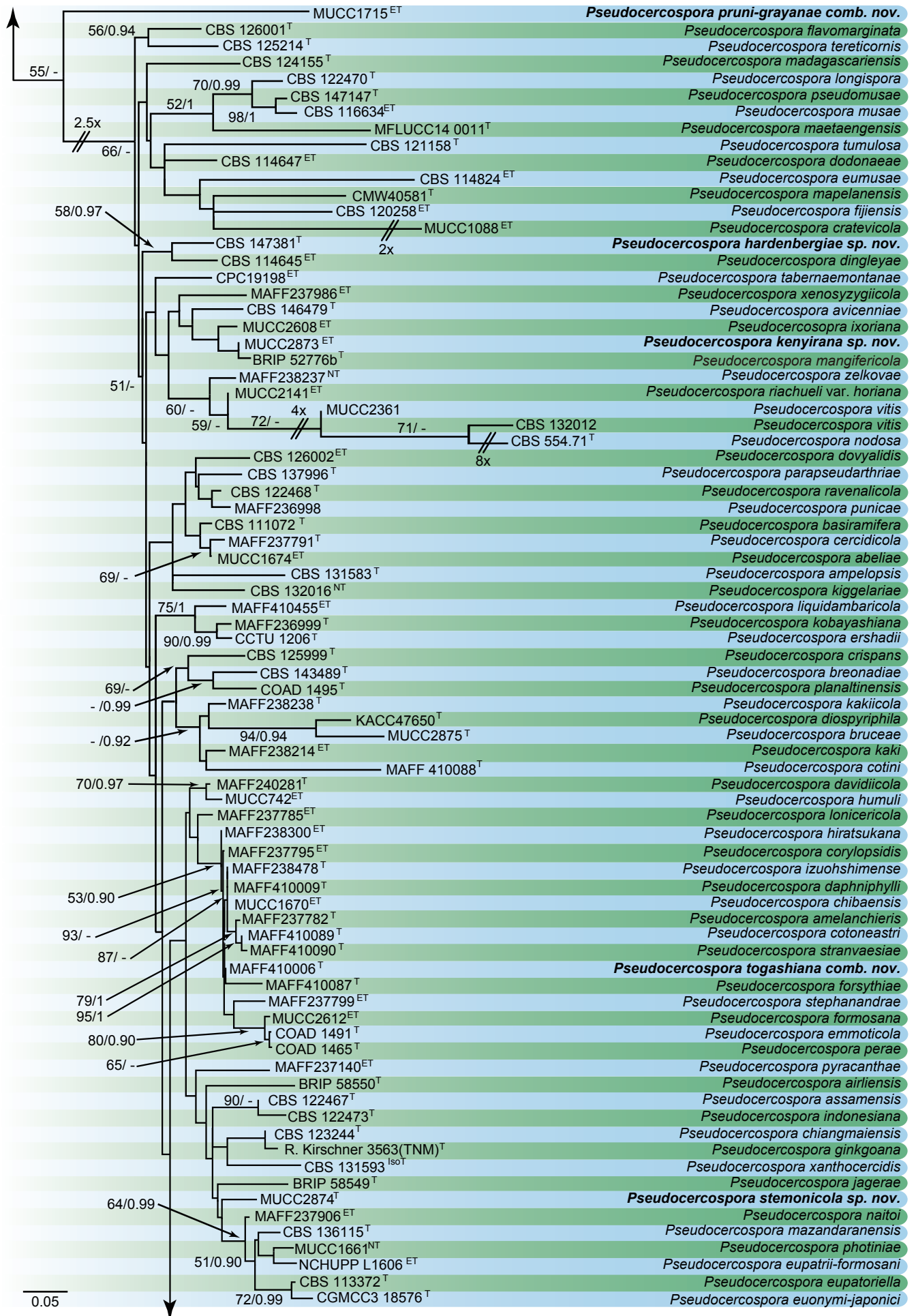


Fig. 62. (Continued).

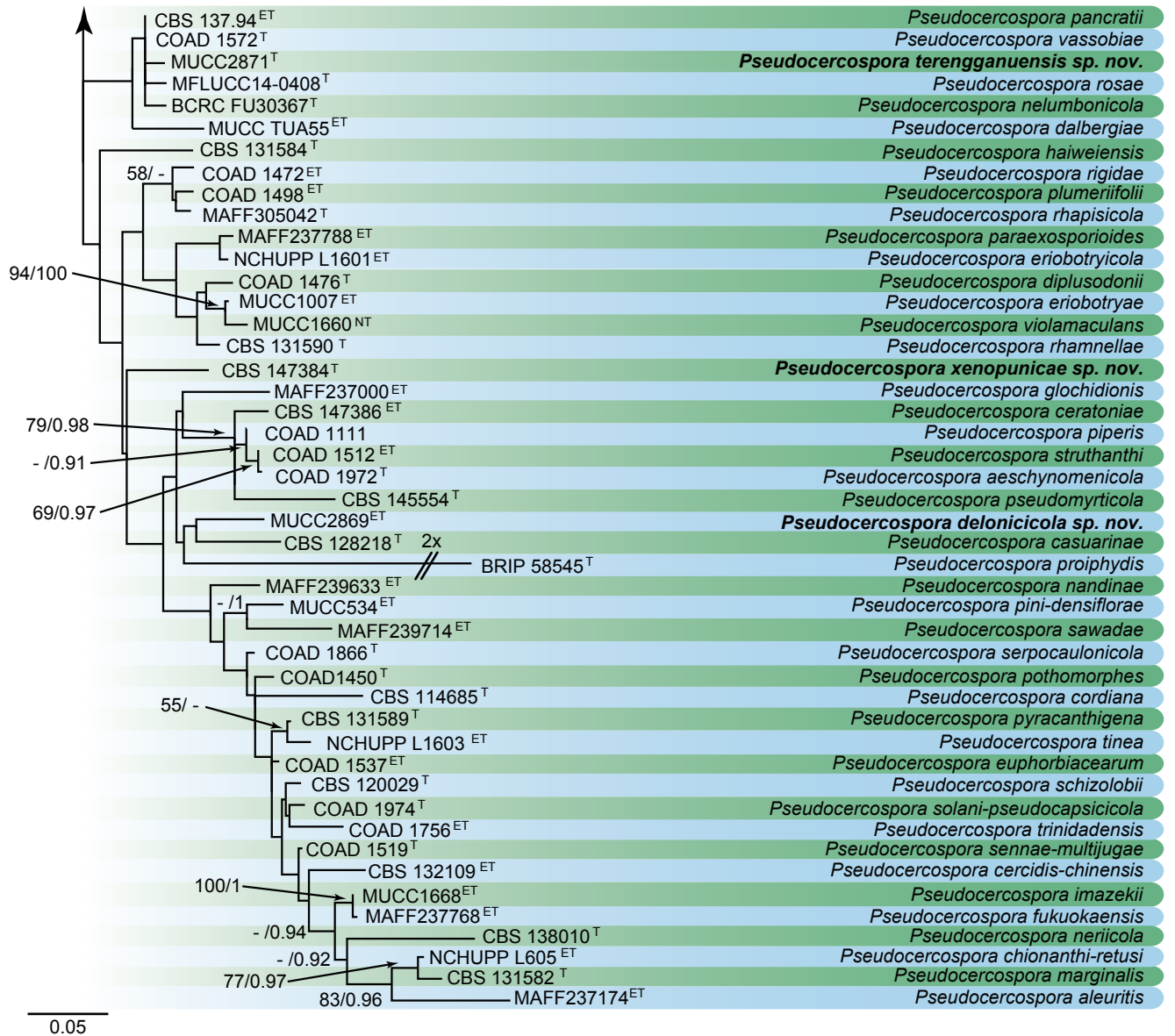


Fig. 62. (Continued).

Table 16. DNA barcodes of accepted *Pseudocercospora* spp.

Species	Isolates ¹	GenBank accession numbers ²					References
		LSU	ITS	actA	tef1	rpb2	
<i>Ps. abeliae</i>	MUCC1674 ^{ET}	—	LC599330	LC599407	LC599448	LC599587	Present study
<i>Ps. aeshynomenicola</i>	CPC 25227 = COAD 1972 ^T	KT290173	KT290146	KT313501	KT290200	—	Silva <i>et al.</i> (2016)
<i>Ps. ailiensis</i>	BRIP 58550 ^T	KM055433	KM055429	—	KM055436	—	Shivas <i>et al.</i> (2015)
<i>Ps. aleuritidis</i>	MAFF237174 = MUCC1230 ^{ET}	—	LC599331	LC599408	LC599449	LC599588	Present study
<i>Ps. amelanchieris</i>	MAFF 237782 = MUCC885 ^T	—	KX462583	KX462550	KX462669	KX462616	Nakashima <i>et al.</i> (2016)
<i>Ps. ampelopsis</i>	CBS 131583 = CPC 11680 ^T	GU253846	GU269830	GU320534	GU384542	—	Crous <i>et al.</i> (2013a)
<i>Ps. angiopteridis</i>	CBS 147385 ^{ET}	—	LC599332	LC599409	LC599450	LC599589	Present study
<i>Ps. angolensis</i>	CBS 149.53 ^T	JQ324941	JQ324975	JQ325011	JQ324988	—	Silva <i>et al.</i> (2016)
<i>Ps. angularis</i>	COAD 2073 ^T	—	KX793125	KX793124	—	—	Crous <i>et al.</i> (2017a)
<i>Ps. araliae</i>	MUCC 873 ^{ET}	GU253702	GU269653	GU320361	GU384371	KX462617	Crous <i>et al.</i> (2013a), Nakashima <i>et al.</i> (2016)

Table 16. (Continued).

Species	Isolates ¹	GenBank accession numbers ²					References
		LSU	ITS	<i>actA</i>	<i>tef1</i>	<i>rpb2</i>	
<i>Ps. arecaeum</i>	CBS 118406 ^T	GU253704	GU269655	GU320363	GU384373	—	Crous <i>et al.</i> (2013a)
<i>Ps. assamensis</i>	CBS 122467 ^T	GU253705	GU269656	GU320364	GU384374	—	Crous <i>et al.</i> (2013a)
<i>Ps. avicenniae</i>	CBS 146479 ^T	—	GU188047	LC599410	LC599451	LC599590	Shivas <i>et al.</i> (2009a)
<i>Ps. basiramifera</i>	CBS 111072 = CPC 1266 ^T	GU253709	GU269661	GU320368	DQ211677	—	Crous <i>et al.</i> (2013a)
<i>Ps. basitruncata</i>	CBS 114664 = CPC 1202 ^{ET}	GU253710/ DQ204759	DQ267600/ GU269662	DQ147622	DQ211675	—	Crous <i>et al.</i> (2013a)
<i>Ps. biophyti</i>	CPC 20020	—	LC599333	LC599411	LC599452	LC599591	Present study
<i>Ps. bixae</i>	CPC 25244 = COAD 1563 ^{ET}	KT290180	KT290153	KT313508	KT290207	—	Silva <i>et al.</i> (2016)
<i>Ps. brackenicola</i>	CPC 24695 = COAD 1991 ^T	KT037565	KT037524	KT037606	KT037484	—	Guatimosim <i>et al.</i> (2016)
<i>Ps. breonadiae</i>	CBS 143489 = CPC 30153 ^T	MH107959	MH107913	MH107985	MH108026	MH108006	Crous <i>et al.</i> (2018b)
<i>Ps. bruceae</i>	MUCC 2875 ^T	—	LC599334	LC599412	LC599453	—	Present study
<i>Ps. casuarinae</i>	CBS 128218 ^T	HQ599604	HQ599603	LC599413	LC599454	—	Crous <i>et al.</i> (2010b)
<i>Ps. ceratoniae</i>	CBS 147386 ^{ET}	—	LC599335	LC599414	LC599455	LC599592	Present study
<i>Ps. cercidicola</i>	MAFF 237791 = MUCC 896 ^T	GU253719	GU269671	GU320377	GU384388	KX462618	Crous <i>et al.</i> (2013a), Nakashima <i>et al.</i> (2016)
<i>Ps. cercidis-chinensis</i>	CBS 132109 = CPC 14481 ^{ET}	GU253718	GU269670	GU320376	GU384387/ LC599456	LC599593	Crous <i>et al.</i> (2013a)
<i>Ps. chamaecristae</i>	CPC 25228 = COAD 1973 ^{ET}	KT290174	KT290147	KT313502	KT290201	—	Silva <i>et al.</i> (2016)
<i>Ps. Chiangmaiensis</i>	CBS 123244 ^T	MH863288	EU882113	EU882147	KF903544	—	Cheewangkoon <i>et al.</i> (2008), Vu <i>et al.</i> (2019)
<i>Ps. chibaensis</i>	MUCC1670 ^{ET}	—	KX462584	KX462551	KX462670	KX462619	Nakashima <i>et al.</i> (2016)
<i>Ps. chionanthi-retusi</i>	TUA50 = NCHUPP L1605 ^{ET}	—	KX462585	KX462552	KX462671	KX462620	Nakashima <i>et al.</i> (2016)
<i>Ps. cladrastidis</i>	MUCC1494 ^{ET}	—	LC599336	LC599415	LC599457	LC599594	Present study
<i>Ps. convoluta</i>	CBS 113377 = MJM 1533 = C488 ^T	MF951226	DQ676519	—	—	MF951617/ LC599595	Videira <i>et al.</i> (2017)
<i>Ps. coprosmae</i>	CBS 114639 ^{ET}	JQ324946	GU269680	GU384397	GU320386	—	Present study
<i>Ps. cordiana</i>	CBS 114685 = CPC 2552 ^T	GU214472	AF362054/ GU269681	GU320387	GU384398	—	Crous <i>et al.</i> (2013a)
<i>Ps. corylopsidis</i>	MAFF 237795 = MUCC 908 ^{ET}	—	GU269684	GU320390	GU384401	KX462621	Nakashima <i>et al.</i> (2016)
<i>Ps. cotini</i>	MAFF410088 = MUCC1415 ^T	—	LC599337	LC599416	LC599458	LC599596	Present study
<i>Ps. cotoneastri</i>	MAFF 410089 = MUCC1416 ^T	—	KX462586	KX462553	KX462672	KX462622	Nakashima <i>et al.</i> (2016)
<i>Ps. cratevicola</i>	MUCC1088 ^{ET}	MF951233	MF951372	LC599417	LC599459	LC599597	Present study
<i>Ps. crispans</i>	CBS 125999 = CPC 14883 ^T	GU253825	GU269807	GU320510	GU384518	KX462623	Crous <i>et al.</i> (2013a), Nakashima <i>et al.</i> (2016)
<i>Ps. crocea</i>	CBS 126004 = CPC 11668 ^T	JQ324947	GU269792	GU320493	GU384502	—	Crous <i>et al.</i> (2013a)
<i>Ps. crousii</i>	CBS 119487	GU253729	GU269686	GU384403	GU320392	—	Crous <i>et al.</i> (2013a)

Table 16. (Continued).

Species	Isolates ¹	GenBank accession numbers ²					References
		LSU	ITS	<i>actA</i>	<i>tef1</i>	<i>rpb2</i>	
<i>Ps. cryptomericola</i>	MAFF240073 = NBRC 102150 ^{ET}	—	LC599338	LC599418	LC599460	LC599598	Present study
<i>Ps. curcunicola</i>	MUCC733 ^T	—	LC599339	LC599419	LC599461	LC599599	Present study
<i>Ps. cyathicola</i>	CBS 129520 = CPC 17047 ^T	JF951159	JF951139	KX462554	KX462673	KX462624	Guatimosim <i>et al.</i> (2016), Nakashima <i>et al.</i> (2016)
<i>Ps. cymbidiicola</i>	CBS 115132 ^{ET}	GU253733	GU269692	GU320397	GU384408	—	Crous <i>et al.</i> (2013a)
<i>Ps. dalbergiae</i>	TUA55 ^{ET}	—	LC599340	LC599420	LC599462	LC599600	Present study
<i>Ps. daphniphylli</i>	MAFF 410009 = MUCC1399 ^T	—	KX462587	KX462555	KX462674	KX462625	Nakashima <i>et al.</i> (2016)
<i>Ps. davidiicola</i>	MAFF 240281 = MUCC296 ^T	GU253734	GU269693	GU320398	GU384409	KX462626	Nakashima <i>et al.</i> (2016)
<i>Ps. delonicicola</i>	MUCC2869 ^T	—	LC599341	LC599421	LC599463	LC599601	Present study
<i>Ps. dingleyae</i>	CBS 114645 ^{ET}	KX286997	KX287299	—	—	KX288454	Videira <i>et al.</i> (2017)
<i>Ps. diospyriphila</i>	KACC47650 ^T	—	GU512009	LC515790	LC512003	—	Braun <i>et al.</i> (2020)
<i>Ps. diplosodonii</i>	CPC 25179 = COAD 1476 ^T	KT290162	KT290135	KT313490	KT290189	—	Silva <i>et al.</i> (2016)
<i>Ps. dodonaeae</i>	CBS 114647 ^{ET}	JQ324948	GU269697	JQ325013	GU384413	—	Crous <i>et al.</i> (2013a)
<i>Ps. dovyalidis</i>	CBS 126002 = CPC 13771 ^{ET}	GU253818	GU269800	GU320503	GU384513	—	Crous <i>et al.</i> (2013a)
<i>Ps. ebulicola</i>	CBS 147387 ^{ET}	—	LC599342	LC599422	—	LC599602	Present study
<i>Ps. elaeocarpicola</i>	MAFF 237189 = MUCC1236 ^T	—	KX462588	KX462556	KX462675	KX462627	Nakashima <i>et al.</i> (2016)
<i>Ps. emmoticola</i>	CPC 25187 = COAD 1491 ^T	KT290163	KT290136	KT313491	KT290190	—	Silva <i>et al.</i> (2016)
<i>Ps. eriobotryae</i>	MUCC 1007 ^{ET}	—	KX462589	KX462557	KX462676	KX462628	Nakashima <i>et al.</i> (2016)
<i>Ps. eriobotryicola</i>	TUA12 = NCHUPPL1601 ^{ET}	—	KX462590	KX462558	KX462677	KX462629	Nakashima <i>et al.</i> (2016)
<i>Ps. ershadii</i>	CBS 136114 = CCTU 1206 ^T	KP717032	KM452867	KM452844	KM452889	MN786459	Bakhshi <i>et al.</i> (2014), Braun <i>et al.</i> (2020)
<i>Ps. eucalyptorum</i>	CBS 114866 = CPC 11 ^T	JQ739817	KF901720	KF903474	KF903195	MF951618	Videira <i>et al.</i> (2017)
<i>Ps. eumusae</i>	CBS 114824 ^{ET}	—	EU514238	LFZN0100053	LFZN0100037	—	Crous <i>et al.</i> (2020)
<i>Ps. euonymi-japonici</i>	CGMCC 3.18576 ^T	—	MH255812	MH392525	—	MH392531	Wang <i>et al.</i> (2019)
<i>Ps. eupatoriella</i>	CBS 113372 ^T	GU253743	GU269704	GU320408	GU384420	MH392531	Crous <i>et al.</i> (2013a)
<i>Ps. eupatorii-formosani</i>	TUA59 = NCHUPPL1606 ^{ET}	—	KX462591	KX462559	KX462678	KX462630	Nakashima <i>et al.</i> (2016)
<i>Ps. euphorbiacearum</i>	COAD 1537 ^{ET}	KT290172	KT290145	KT313500	KT290199	—	Silva <i>et al.</i> (2016)
<i>Ps. exilis</i>	CPC 25193 = COAD 1501 ^{ET}	KT290166	KT290139	KT313494	KT290193	—	Silva <i>et al.</i> (2016)
<i>Ps. farfugii</i>	MUCC978 ^T	—	LC599343	LC599423	LC599464	LC599603	Present study
<i>Ps. fijiensis</i>	CBS 120258 = CIRAD 86 ^{ET}	JQ324952	EU514248	NW006921533	NW006921532	NW006921535	Crous <i>et al.</i> (2013a)
<i>Ps. flavomarginata</i>	CBS 126001 ^T	GU253822	GU269804	GU320507	GU384515 / LC599465	LC599604	Crous <i>et al.</i> (2013a)
<i>Ps. fori</i>	CBS 113285 ^T	DQ204748	AF468869	DQ147618	DQ211664	KT356874	Crous <i>et al.</i> (2013a), Ismail <i>et al.</i> (2016)
<i>Ps. formosana</i>	MUCC2612 ^{ET}	—	LC599344	LC599424	LC599466	LC599605	Present study
<i>Ps. forsythiae</i>	MAFF 410087 = MUCC1414 ^T	—	LC599345	LC599425	LC599467	—	Present study

Table 16. (Continued).

Species	Isolates ¹	GenBank accession numbers ²					References
		LSU	ITS	<i>actA</i>	<i>tef1</i>	<i>rpb2</i>	
<i>Ps. fukuii</i>	MAFF238121 = MUCC1297 ^{ET}	—	LC599347	LC599427	LC599469	LC599607	Present study
<i>Ps. fukuokaensis</i>	MAFF 237768 = MUCC 887 ^{ET}	GU253751	GU269714	GU320418	GU384430	KX462632	Nakashima <i>et al.</i> (2016)
<i>Ps. ginkgoana</i>	R. Kirschner 3563 (TNM) ^T	—	JX134048	—	—	—	Kirschner & Okuda (2013)
<i>Ps. glochidionis</i>	MAFF 237000; MUCC1211 ^{ET}	—	LC599348	LC599428	LC599470	LC599608	Present study
<i>Ps. gracilis</i>	CBS 242.94 ^T	DQ204750	DQ267582	DQ147616	DQ211666	—	Crous <i>et al.</i> (2013a)
<i>Ps. griseola f. griseola</i>	CBS 119906 ^{ET}	—	DQ289812	DQ289879	—	—	Crous <i>et al.</i> (2006b)
<i>Ps. griseola f. mesoamericana</i>	CBS 119113 ^{ET}	—	DQ289824	DQ289891	—	—	Crous <i>et al.</i> (2006b)
<i>Ps. hachijokibushii</i>	MAFF 238479 ^T	—	KX462593	KX462561	KX462680	KX462633	Nakashima <i>et al.</i> (2016)
<i>Ps. haiweiensis</i>	CBS 131584 = CPC 14084 ^T	GU253821	GU269803	GU320506	GU384514	KX462634	Crous <i>et al.</i> (2013a), Nakashima <i>et al.</i> (2016)
<i>Ps. hardenbergiae</i>	CBS 147381 ^T	—	LC599349	LC599429	LC599471	LC599609	Present study
<i>Ps. heteropyxidicola</i>	CBS 146082 = CPC 38030 ^T	MN567658	MN562151	MN556791	—	—	Crous <i>et al.</i> (2019e)
<i>Ps. hiratsukana</i>	MAFF 238300 = MUCC1105 ^{ET}	—	KX462594	KX462562	KX462681	KX462635	Nakashima <i>et al.</i> (2016)
<i>Ps. houttuyniae</i>	MAFF 238071 = MUCC1289 ^{ET}	—	KX462595	KX462563	KX462682	KX462636	Nakashima <i>et al.</i> (2016)
<i>Ps. humuli</i>	MUCC 742 ^{ET}	GU253758	GU269725	GU320428	GU384439	KX462637	Crous <i>et al.</i> (2013a), Nakashima <i>et al.</i> (2016)
<i>Ps. humulicola</i>	CBS 131585 ^T	JQ324956	GU269723	GU320427	GU384438	—	Crous <i>et al.</i> (2013a)
<i>Ps. imazekii</i>	MUCC 1668 ^{ET}	—	KX462596	KX462564	KX462683	KX462638	Nakashima <i>et al.</i> (2016)
<i>Ps. indonesiana</i>	CBS 122473 ^T	GU253765	GU269735	GU320437 EU514340	GU384448	—	Crous <i>et al.</i> (2013a)
<i>Ps. iwakiensis</i>	MUCC 1736 ^T	—	KX462607	KX462574	KX462693	KX462657	Nakashima <i>et al.</i> (2016)
<i>Ps. ixoriana</i>	MUCC2608 ^{ET}	—	LC599350	LC599430	LC599472	LC599610	Present study
<i>Ps. izuohshimense</i>	MAFF 238478 = MUCC1336 ^T	—	KX462597	KX462565	KX462684	KX462639	Nakashima <i>et al.</i> (2016)
<i>Ps. jagerae</i>	BRIP 58549 ^T	KM055435	KM055431	—	KM055438	—	Shivas <i>et al.</i> (2015)
<i>Ps. kadsurae</i>	MUCC 752 ^{ET}	—	KX462598	KX462566	KX462685	KX462640	Nakashima <i>et al.</i> (2016)
<i>Ps. kaki</i>	MAFF 238214 ^{ET}	—	LC512001	LC512007	LC515783	LC515794	Braun <i>et al.</i> (2020)
<i>Ps. kakiicola</i>	MAFF 238238 = MUCC 900 ^T	GU253761	GU269729	GU320431	GU384442	LC515786	Crous <i>et al.</i> (2013a), Braun <i>et al.</i> (2020)
<i>Ps. kenyirana</i>	MUCC 2873 ^T	—	LC599351	LC599431	LC599473	—	Present study
<i>Ps. kiggelariae</i>	CBS 132016 = CPC 11853 ^{NT}	GU253762	GU269730	GU320432	GU384443	—	Crous <i>et al.</i> (2013a)
<i>Ps. kobayashiana</i>	MAFF 236999 ^T	—	LC511998	LC512004	LC515780	LC515791	Braun <i>et al.</i> (2020)
<i>Ps. leandrae-fragilis</i>	COAD 1977 ^T	KY574287	KY574288	—	—	—	Crous <i>et al.</i> (2017a)
<i>Ps. leucadendri</i>	CPC 1869 ^{ET}	GU214480	GU269842	GU320545	GU384555	—	Crous <i>et al.</i> (2013a)
<i>Ps. liquidambaricola</i>	MAFF410455 ^{ET}	—	LC599352	LC599432	LC599474	LC599611	Present study
<i>Ps. longispora</i>	CBS 122470 ^T	GU253764	GU269734	GU320436 EU514342	GU384447	—	Crous <i>et al.</i> (2013a)

Table 16. (Continued).

Species	Isolates ¹	GenBank accession numbers ²					References
		LSU	ITS	<i>actA</i>	<i>tef1</i>	<i>rpb2</i>	
<i>Ps. lonicericola</i>	MUCC 889 = MAFF 237785 ^{ET}	GU253766	GU269736	GU320438	JQ324999	KX462641	Crous <i>et al.</i> (2013a), Nakashima <i>et al.</i> (2016)
<i>Ps. luzardii</i>	CPC 25196 = COAD 1505 ^{ET}	KT290167	KT290140	KT313495	KT290194	—	Silva <i>et al.</i> (2016)
<i>Ps. lyoniae</i>	MAFF 237775 = MUCC 910 ^{ET}	GU253768	GU269739	GU320441	GU384451	KX462642	Crous <i>et al.</i> (2013a), Nakashima <i>et al.</i> (2016)
<i>Ps. lythri</i>	CBS 132115 = CPC 14588 ^{ET}	GU253771	GU269742	GU320444	GU384454/ LC599475	LC599612	Crous <i>et al.</i> (2013a)
<i>Ps. macadamiae</i>	CBS 133432 ^{ET}	KX286998	KX287300	KU878551	KU878504	KX288455	Ong <i>et al.</i> (2017), Videira <i>et al.</i> (2017)
<i>Ps. macrospora</i>	CBS 114696 = CPC 2553 ^{ET}	GU214478	AF362055/ GU269745	GU320447	GU384457	—	Crous <i>et al.</i> (2013a)
<i>Ps. madagascariensis</i>	CBS 124155 ^T	—	GQ852767	KF253625	KF253265	KX462643	Nakashima <i>et al.</i> (2016)
<i>Ps. maetaengensis</i>	MFLUCC 14-0411 ^T	MN648328	MN648323	—	—	—	Hyde <i>et al.</i> (2020)
<i>Ps. mangifericola</i>	BRIP 52776b ^T	—	GU188048	—	—	—	Shivas <i>et al.</i> (2009b)
<i>Ps. manihotis</i>	CPC 25219 = COAD 1534 ^T	KT290171	KT290144	KT313499	KT290198	—	Silva <i>et al.</i> (2016)
<i>Ps. mapelanensis</i>	CMW40581 ^T	KM203121	KM203118	KM203127	KM203124	—	Osorio <i>et al.</i> (2015)
<i>Ps. marginalis</i>	CBS 131582 = CPC 12497 ^T	GU253812	GU269794	GU320495	GU384504	—	Crous <i>et al.</i> (2013a)
<i>Ps. mazandaranensis</i>	CCTU 1102 = CBS 136115 ^T	KP717020	KM452854	KM452831	KM452876	LC599613	Bakhshi <i>et al.</i> (2014)
<i>Ps. melicyti</i>	CBS 115023 ^T	JQ324968	GU269769	GU320472	GU384481	—	Crous <i>et al.</i> (2013a)
<i>Ps. metrosideri</i>	CBS 114294 ^{ET}	KX286999	KX287301	—	—	KX288456	Videira <i>et al.</i> (2017)
<i>Ps. microlepieae</i>	BCRC FU30353 ^T	—	KR348740	—	—	—	Kirschner & Wang (2015)
<i>Ps. musae</i>	CBS 116634 ^{ET}	GU253775	GU269747	GU320449	GU384459	LFZ001000453	Crous <i>et al.</i> (2013, 2020)
<i>Ps. naitoi</i>	MAFF 237906 = MUCC1072 ^{ET}	—	KX462599	KX462567	KX462686	KX462644	Nakashima <i>et al.</i> (2016)
<i>Ps. nandinae</i>	MAFF 237633 = MUCC1260 ^{ET}	—	KX462600	KX462568	KX462687	KX462645	Nakashima <i>et al.</i> (2016)
<i>Ps. natalensis</i>	CBS 111069 = CPC 1263 ^T	DQ267576	DQ303077	DQ147620	JQ325000	—	Crous <i>et al.</i> (2013a)
<i>Ps. nelumbonicola</i>	BCRC FU30367 ^T	—	KY304492	—	—	LC199940	Chen & Kirschner (2017)
<i>Ps. neriicola</i>	CBS 138010 = CPC 23765 ^T	KJ869222	KJ869165	KJ869231	KJ869240	KX462647	Crous <i>et al.</i> (2014c), Nakashima <i>et al.</i> (2016)
<i>Ps. nodosa</i>	CBS 554.71 ^T	MF951227	MF951367	—	—	MF951620	Videira <i>et al.</i> (2017)
<i>Ps. norchiensis</i>	CBS 120738 = CPC 13049 ^T	GU253780	EF394859	GU320455	GU384464	KX462648	Crous <i>et al.</i> (2013a), Nakashima <i>et al.</i> (2016)
<i>Ps. ocimi-basilici</i>	CPC 10283 ^T	GU214678	GU269754	GU320456	GU384465	—	Crous <i>et al.</i> (2013a)
<i>Ps. paederiae</i>	MAFF 239161	—	KX462603	KX462570	KX462689	KX462651	Nakashima <i>et al.</i> (2016)
<i>Ps. paleobrunnea</i>	CBS 124771 = CPC 13387 ^T	GQ303319	GQ303288	GU320500	GU384509	KX462652	Crous <i>et al.</i> (2013a), Nakashima <i>et al.</i> (2016)

Table 16. (Continued).

Species	Isolates ¹	GenBank accession numbers ²					References
		LSU	ITS	<i>actA</i>	<i>tef1</i>	<i>rpb2</i>	
<i>Ps. pancratii</i>	CBS 137.94 ^{ET}	GU253784	GU269759	GU320460	GU384470	—	Crous <i>et al.</i> (2013a)
<i>Ps. paraeosporioides</i>	MAFF237788 ^{ET}	GU253746	GU269707	GU320411	GU384423	—	Crous <i>et al.</i> (2013a)
<i>Ps. paranaensis</i>	CPC 24680 = COAD 1987 ^T	KT037563	KT037522	KT037604	KT037482	—	Guatimosim <i>et al.</i> (2016)
<i>Ps. parapseudarthriae</i>	CBS 137996 = CPC 23449 ^T	KJ869208	KJ869151	KJ869229	KJ869238	—	Crous <i>et al.</i> (2014c), Guatimosim <i>et al.</i> (2016)
<i>Ps. perae</i>	CPC 25171 = COAD 1465 ^T	KT290159	KT290132	KT313487	KT290186	—	Silva <i>et al.</i> (2016)
<i>Ps. perrottetiae</i>	CBS 147382 ^T	—	LC599353	LC599433	LC599477	LC599614	Present study
<i>Ps. photiniae</i>	MUCC 1661 ^{NT}	—	KX462604	KX462571	KX462690	KX462653	Nakashima <i>et al.</i> (2016)
<i>Ps. pini-densiflorae</i>	MUCC 1714 ^{ET}	—	LC599354	LC599434	LC599478	LC599615	Crous <i>et al.</i> (2013a)
<i>Ps. piperis</i>	COAD 1111	JX875063	JX875062	—	JX896123	—	Rocha <i>et al.</i> (2013)
<i>Ps. planaltinensis</i>	CPC 25189 = COAD 1495 ^T	KT290164	KT290137	KT313492	KT290191	—	Silva <i>et al.</i> (2016)
<i>Ps. platycericicola</i>	MUCC2876 ^T	—	LC599355	LC599435	LC599479	LC599616	Present study
<i>Ps. plectranthi</i>	CBS 131586 = CPC 11462 ^T	JQ324962	GU269791	GU320492	GU384501	—	Crous <i>et al.</i> (2013a)
<i>Ps. plumeriifolii</i>	CPC 25191 = COAD 1498 ^{ET}	KT290165	KT290138	KT313493	KT290192	—	Silva <i>et al.</i> (2016)
<i>Ps. pothomorphes</i>	CPC 25166 = COAD 1450 ^T	KT290158	KT290131	KT313486	KT290185	—	Silva <i>et al.</i> (2016)
<i>Ps. profusa</i>	CBS 132306 = CPC 10055 ^{ET}	GU253787	GU269762	GU320463	GU384473	—	Crous <i>et al.</i> (2013a)
<i>Ps. proiphydis</i>	BRIP 58545 ^T	KM055434	KM055430	—	KM055437	—	Shivas <i>et al.</i> (2015)
<i>Ps. proteae</i>	CBS 131587 = CPC 15217 ^T	GU253826	GU269808	GU320511	GU384519/ LC599480	LC599617	Crous <i>et al.</i> (2013a)
<i>Ps. pruni-grayanae</i> <i>comb.nov.</i>	MUCC 1715 ^{ET}	—	LC599356	—	LC599481	LC599618	Present study
<i>Ps. pseudomusae</i>	CBS 147147 ^T	—	MW063423	MW070772	MW071091	MW070919	Crous <i>et al.</i> (2020)
<i>Ps. pseudomyrticola</i>	CBS 145554 = CPC 35448 ^T	MK876446	MK876405	MK876461	MK876499	MK876490	Crous <i>et al.</i> (2019a)
<i>Ps. pseudostigminaplantani</i>	CBS 131588 = CPC 11726 ^T	JQ324963	GU269857	GU320560	GU384568	—	Crous <i>et al.</i> (2013a)
<i>Ps. punctata</i>	CBS 132116 = CPC 14734 ^{ET}	GU253791	GU269765	GU320468	GU384477	MF951622	Crous <i>et al.</i> (2013a), Videira <i>et al.</i> (2017)
<i>Ps. punicae</i>	MAFF236998 = MUCC 1209	—	KX462606	KX462573	KX462692	KX462655	Nakashima <i>et al.</i> (2016)
<i>Ps. pyracanthae</i>	MAFF237140 = MUCC 1226 ^{ET}	GU253792	GU269767	GU320470	GU384479/ LC599482	LC599619	Crous <i>et al.</i> (2013a)
<i>Ps. pyracanthigena</i>	CBS 131589 = CPC 10808 ^T	—	GU269766	GU320469	GU384478	—	Crous <i>et al.</i> (2013a)
<i>Ps. ravenalicola</i>	CBS 122468 ^T	GU253828	GU269810	GU320513	GU384521	—	Crous <i>et al.</i> (2013a)
<i>Ps. rhabdothamni</i>	CBS 114872 ^T	JQ324964	GU269768	GU320471	GU384480	—	Crous <i>et al.</i> (2013a)
<i>Ps. rhamnellae</i>	CBS 131590 = CPC 12500 ^T	GU253813	GU269795	GU320496	GU384505	—	Crous <i>et al.</i> (2013a)
<i>Ps. rhapsicola</i>	MAFF305042 = MUCC1484 ^T	—	LC599357	LC599436	LC599483	LC599620	Present study
<i>Ps. rhododendri-indici</i>	CBS 131591 = CPC 10822 ^T	JQ324965	GU269722	GU320426	—	—	Crous <i>et al.</i> (2013a)

Table 16. (Continued).

Species	Isolates ¹	GenBank accession numbers ²					References
		LSU	ITS	<i>actA</i>	<i>tef1</i>	<i>rpb2</i>	
<i>Ps. riachueli</i> var. <i>horiana</i>	MUCC2141 ^{ET}	—	LC599358	LC599437	LC599484	LC599621	Present study
<i>Ps. richardsoniicola</i>	CPC 25248 = COAD 1568 ^{ET}	KT290181	KT290154	KT313509	KT290208	—	Silva <i>et al.</i> (2016)
<i>Ps. rigidae</i>	CPC 25175 = COAD 1472 ^{ET}	KT290161	KT290134	KT313489	KT290188	—	Silva <i>et al.</i> (2016)
<i>Ps. robusta</i>	CBS 111175 = CPC 1269 = CMW 5151 ^T	DQ204767	AY309597	DQ147617	DQ211683	KX462656	Crous <i>et al.</i> (2013a), Nakashima <i>et al.</i> 2016
<i>Ps. rosae</i>	MFLUCC 14-0408 ^T	MG829063	MG828952	—	—	—	Wanasinghe <i>et al.</i> (2018b)
<i>Ps. sambucigena</i>	CBS 126000 ^{ET}	GU253809	GU269788	GU320508	GU384498	—	Crous <i>et al.</i> (2013a)
<i>Ps. sawadae</i>	MAFF 239714		LC599359	LC599438	LC599485	LC599622	Present study
<i>Ps. schizolobii</i>	CBS 120029 = CPC 12962 ^T	KF251826	KF251322	KF253628	KF253269	—	Guatimosim <i>et al.</i> (2016)
<i>Ps. sennae-multijugae</i>	CPC 25206 = COAD 1519 ^T	KT290169	KT290142	KT313497	KT290196	—	Silva <i>et al.</i> (2016)
<i>Ps. serpocaulonicola</i>	CPC 25077 = COAD 1866 ^T	KT037566	KT037525	KT037607	KT037485	—	Guatimosim <i>et al.</i> (2016)
<i>Ps. solani-pseudocapsicicola</i>	CPC 25229 = COAD 1974 ^T	KT290175	KT290148	KT313503	KT290202	—	Silva <i>et al.</i> (2016)
<i>Ps. sophoricola</i>	CCTU 1037 = CBS 136020 ^T	KP717027	KM452861	KM452838	KM452883	LC599486	Bakhshi <i>et al.</i> (2014)
<i>Ps. sphaerulinae</i>	CBS 112621 ^T	GQ852652	KF901625	—	KF903215	—	Crous <i>et al.</i> (2009b), Quaedvlieg <i>et al.</i> (2014)
<i>Ps. stemonicola</i>	MUCC2874 ^T	—	LC599360	LC599439	LC599487	—	Present study
<i>Ps. stephanandrae</i>	MAFF237799 = MUCC914 ^{ET}	GU253831	GU269814	GU320516	GU384526	KX462658	Silva <i>et al.</i> (2016), Nakashima <i>et al.</i> (2016)
<i>Ps. stranvaesia</i>	MAFF410090 = MUCC1417 ^T	—	LC599361	LC599440	LC599488	LC599623	Present study
<i>Ps. struthanthi</i>	CPC 25199 = COAD 1512 ^{ET}	KT290168	KT290141	KT313496	KT290195	—	Silva <i>et al.</i> (2016)
<i>Ps. styracina</i>	COAD 2369 ^T	MH480643	MH397664	MH480641	MH480642	—	Crous <i>et al.</i> (2018a)
<i>Ps. symploci</i>	NCHUPP L1685 = CBS142471 ^{ET}	—	LC599362	LC599441	LC599489	LC599624	Present study
<i>Ps. tabernaemontanae</i>	CPC 19198 ^{ET}	—	LC599363	LC599442	—	LC599625	Present study
<i>Ps. tereticornis</i>	CBS 125214 = CPC 13299 ^T	—	GQ852770	GU320499	GU384508	KX462659	Nakashima <i>et al.</i> (2016)
<i>Ps. terengganuensis</i>	MUCC2871 ^T	—	LC599364	LC599443	LC599490	—	Present study
<i>Ps. tineae</i>	TUA40 = NCHUPP L1603 ^{ET}	—	KX462608	KX462577	KX462696	KX462660	Nakashima <i>et al.</i> (2016)
<i>Ps. togashiana</i>	MAFF410006 ^T (<i>Mycosphaerella togashiana</i>)	—	LC599365	LC599444	LC599491	LC599626	Present study
<i>Ps. trichogena</i>	CPC 24664 = COAD 1087 ^T	KT037560	KT037519	KT037601	KT037479	—	Guatimosim <i>et al.</i> (2016)
<i>Ps. trinidadensis</i>	COAD 1756 ^{ET}	KT290184	KT290157	—	KT290210	—	Present study
<i>Ps. tumulosa</i>	CBS 121158 ^T	—	DQ530217	—	—	—	Crous <i>et al.</i> (2019d)
<i>Ps. vassobiae</i>	CPC 25251 = COAD 1572 ^T	KT290182	KT290155	KT313510	—	—	Silva <i>et al.</i> (2016)
<i>Ps. viburnigena</i>	CBS 125998 = CPC 15249 ^{ET}	GU253827	GU269809	GU384520	GU320512	—	Crous <i>et al.</i> (2013a)

Table 16. (Continued).

Species	Isolates ¹	GenBank accession numbers ²					References
		LSU	ITS	<i>actA</i>	<i>tef1</i>	<i>rpb2</i>	
<i>Ps. violamaculans</i>	MUCC 1660 ^{NT}	—	KX462610	KX462579	KX462698	KX462662	Nakashima <i>et al.</i> (2016)
<i>Ps. vitis</i>	CBS 132012 = CPC 11595	GU214483	GU269829	GU320533	GU384541	KX462663	Crous <i>et al.</i> (2013a), Nakashima <i>et al.</i> (2016)
<i>Ps. wulfiae</i>	MUCC2361	—	LC599366	LC599445	LC599492	LC599627	Present study
	CPC 25232 = COAD 1976 ^T	KT290177	KT290150	KT313505	KT290204	—	Silva <i>et al.</i> (2016)
<i>Ps. xanthocercidis</i>	CBS 131593 = CPC 11665 ^{ISO} ^T	JQ324971	JQ324983	JQ325026	JQ325005	—	Crous <i>et al.</i> (2013a)
<i>Ps. xenopunicae</i>	CBS 147384 ^T	—	LC599367	LC599446	LC599493	LC599628	Present study
<i>Ps. xenosyzygiicola</i>	MAFF237986 = MUCC1481 ^{ET}	—	KX462611	KX462580	KX462699	KX462664	Nakashima <i>et al.</i> (2016)
<i>Ps. xylophiae</i>	CPC 25173 = COAD 1469 ^T	KT290160	KT290133	KT313488	KT290187	—	Silva <i>et al.</i> (2016)
<i>Ps. yakushimensis</i>	MAFF237025 = MUCC1214 ^{ET}	—	LC599368	LC599447	LC599494	LC599629	Present study
<i>Ps. zambiae</i>	CBS 136423 = CPC 22686 ^T	KF777228	KF777175	—	—	MF951630	Videira <i>et al.</i> (2017)
<i>Ps. zelkova</i>	MAFF 238237 = MUCC872 ^{NT}	—	GU269835	GU320537	GU384547	KX462665	Nakashima <i>et al.</i> (2016)

¹ BCRC: Bioresource Collection and Research Center, Food Industry Research and Development Institute, Hsinchu, Taiwan; CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CCTU: Culture Collection of Tabriz University, Tabriz, Iran; COAD: Coleção Octávio de Almeida Drumond, Universidade Federal de Viçosa, Brazil; CPC: Culture collection of Pedro Crous, housed at the Westerdijk Fungal Biodiversity Institute; MAFF: Genebank Project, NARO, Tsukuba, Ibaraki, Japan; MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; MUCC: Culture Collection, Laboratory of Plant Pathology, Mie University, Tsu, Mie Prefecture, Japan; NBRC: Biological Resource Center, National Institute of Technology and Evaluation, Chiba, Japan; NCHUPP: the herbarium, Department of National Chung Hsing University, Taichung, Taiwan. ^{T, ET, ISO} and ^{NT} indicate ex-type, ex-epitype, ex-isotype and ex-neotype strains, respectively.

² ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial 28S large subunit nrRNA gene; *actA*: partial actin gene; *tef1*: partial translation elongation factor 1- α gene; *rpb2*: partial RNA polymerase II second largest subunit gene.

Pseudocercospora abeliae (Katsuki) Nishij. *et al.*, Mycoscience 40: 269. 1999. Fig. 64A–C.

Basionym: *Cercospora abeliae* Katsuki, Ann. Phytopathol. Soc. Japan 20: 71. 1955.

Leaf spots amphigenous, angular to irregular, subcircular, blackish brown to dark brown, often greyish white at the centre, 2–5 mm. **Caespituli** amphigenous, visible as dark olivaceous grey masses composed of superficial hyphae and conidia. **Mycelium** internal. **Stromata** amphigenous, substomatal, epidermal, erumpent, 20–50 μ m diam, pale olivaceous brown to pale brown. **Conidiophores** densely to loosely fasciculate, arising from the upper part of stromata, rarely branched from superficial hyphae, straight to sinuous-geniculate, subcylindrical, unbranched, 25–65 \times 2–3.8 μ m, 0–2-septate, pale olivaceous brown to pale brown, paler toward the apex, smooth. **Conidiogenous cells** integrated, terminal, proliferating sympodially, rounded at the apex, with unthickened loci, 2 μ m diam. **Conidia** solitary, holoblastic, cylindrical to obclavate, 25–55 \times 2.5–5 μ m, 3–6-septate, hyaline, or pale olivaceous, smooth to rough, subacute to rounded at the apex, obconically truncated and unthickened at the base, not darkened, 2 μ m diam (adapted from Nakashima *et al.* 1999).

Typus: **Japan**, Fukuoka, Fukuoka, on *Abelia chinensis* (Caprifoliaceae), 15 Sep. 1954, S. Katsuki (**holotype**, in the Katsuki collection, TNS-F); Toyama, Kureha, Family Park, 25 Sep. 1998, T. Kobayashi & E. Imaizumi (**epitype** designated here TSU-MUMH11438, MBT 10005049, dried culture, culture ex-epitype TSU-MUCC1674).

Additional materials examined: **Japan**, on *Abelia glandiflora*, Tochigi, Sano, 4 Sep. 1998, T. Kobayashi; Ibaraki, Oarai, on *Abelia glandiflora*, 24 Sep. 1979, T. Kobayashi, TFM: FPH-5007; Ibaraki, Inashiki, Kukisaki, FFPRI, on *Abelia glandiflora*, 15 Oct. 1981, T. Kobayashi, TFM: FPH-5472; Ibaraki, Tsukuba, Tsukuba Medical Plant Research Station, on *Abelia glandiflora*, 9 Oct. 1997, T. Kobayashi & C. Nakashima; Ibaraki, Iwai, on *Abelia glandiflora*, 10 Sep. 1998, T. & Y. Kobayashi; Chiba, Kisaradzu, Fukuda, on *Abelia glandiflora*, 20 Sep. 1974, T. Kobayashi, TFM: FPH-4243; Tokyo, Chofu, Jindaiji, on *Abelia glandiflora*, 25 Sep. 1974, T. Kobayashi, TFM: FPH-4346; Tokyo, Setagaya, Tokyo University of Agriculture, on *Abelia glandiflora*, 6 Oct. 1998, C. Nakashima; Shizuoka, Hamamtsu, Fruit Park, on *Abelia glandiflora*, 1 Nov. 1996, T. Kobayashi, C. Nakashima & T. Nishijima; Fukuoka, Yame, Kuroki, Fukuoka For. Exp. Stn., on *Abelia glandiflora*, 20 Sep. 1974, S. Ogawa, TFM: FPH-4191; on *Abelia tetrasepala*, Tokyo, Jindaiji, Jindai Bot. Park, 7 Nov. 1998, C. Nakashima & E. Imaizumi, TSU-MUMH CNS504.

Illustrations: Nakashima *et al.* (1999).



Fig. 63. Symptoms caused by *Pseudocercospora* spp. and cultural characteristics. **A, B.** Black Sigatoka disease of *Musa* spp. caused by *Pseudocercospora fijiensis*. **C.** Early defoliation of *Cryptomeria japonica* caused by *Pseudocercospora cryptomeriicola*. **D.** Shot hole of *Prunus* sp. caused by *Pseudocercospora prunicola*. **E.** Sooty spot of *Actinidia deliciosa* caused by *Pseudocercospora actinidiae*. **F.** Angular leaf spot of *Diospyros kaki* caused by *Pseudocercospora kaki*. **G.** Obscure leaf spot of *Nerium oleander* var. *indicum* caused by *Pseudocercospora kurimensis*. **H.** Upper surface of colony on MEA (*Pseudocercospora fuligena* TSU-MUCC460). **I.** Under surface of colony on MEA (*Pseudocercospora actinidiae* TSU-MUCC1454). **J–M.** Various colony morphologies on MEA. **J, K.** *Pseudocercospora actinidiae* (culture TSU-MUCC1454). **L.** *Pseudocercospora farfugii* (ex-type culture TSU-MUCC978). **M.** *Pseudocercospora fuligena* (culture TSU-MUCC460).

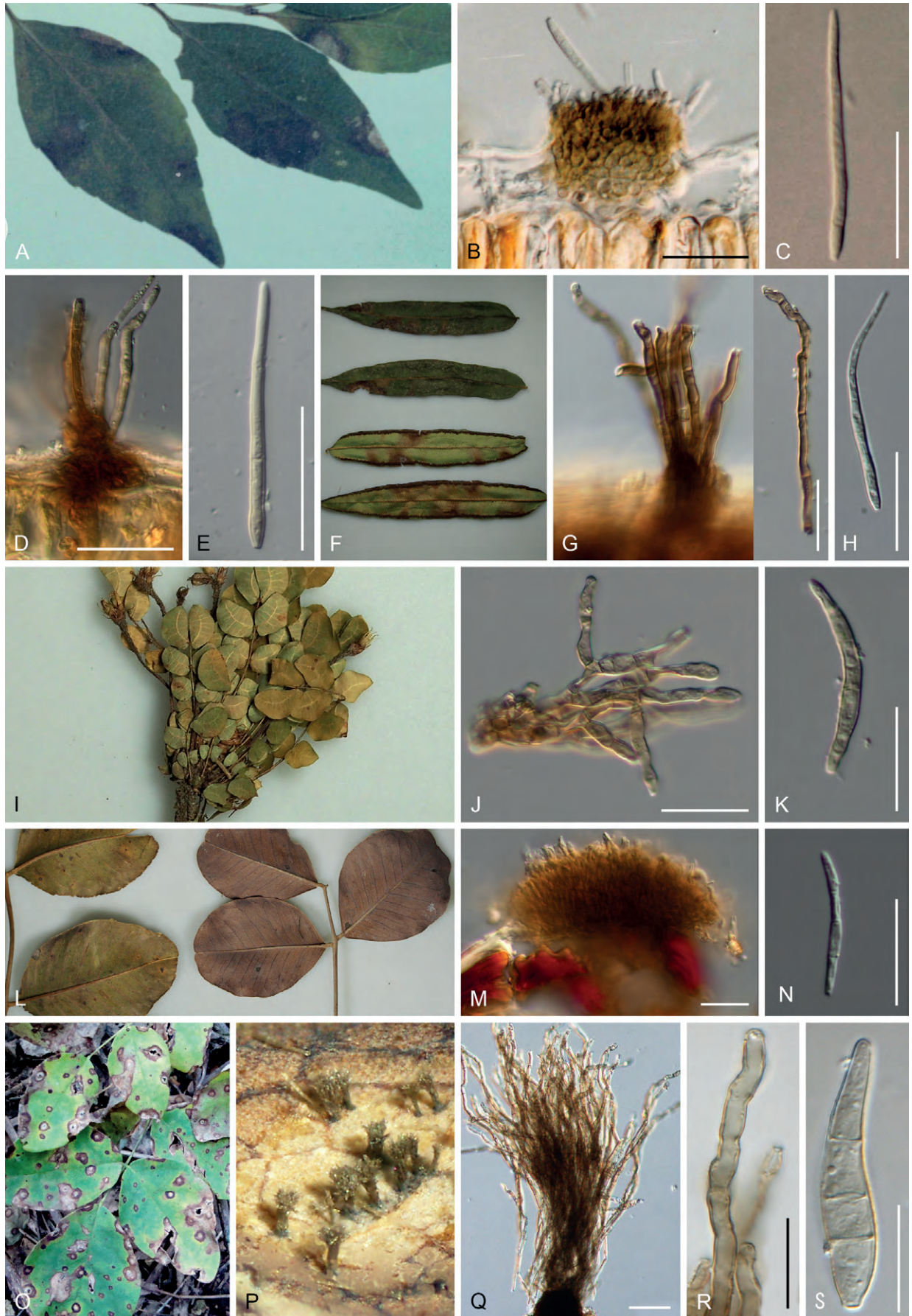


Fig. 64. *Pseudocercospora* spp. plate 1. **A–C.** *Pseudocercospora abeliae* (epitype TSU-MUMH11438). **A.** Disease symptoms on *Abelia grandiflora*. **B.** Stroma and conidiophores. **C.** Conidium. **D, E.** *Pseudocercospora aleuritidis* (neotype TSU-MUMH1934). **D.** Stroma and conidiophores. **E.** Conidium. **F–H.** *Pseudocercospora angiopteridis* (epitype CBS H-24676). **F.** Disease symptoms on *Angiopteris evecta*. **G.** Stroma and conidiophores. **H.** Conidium. **I–K.** *Pseudocercospora biophyti* (epitype KRAM F-49038). **I.** Disease symptoms on *Biophytum petersianum*. **J.** Conidiophores. **K.** Conidium. **L–N.** *Pseudocercospora ceratoniae* (epitype CBS H-24677). **L.** Disease symptoms on *Ceratonia siliqua*. **M.** Stroma and conidiophores. **N.** Conidium. **O–S.** *Pseudocercospora cladrastidis* (epitype HHUF30085). **O.** Disease symptoms on *Cladrastis amurensis*. **P.** Synnematous conidiophores on the leaf spot. **Q.** Conidiophores. **R.** Conidiogenous cell on conidiophore. **S.** Conidium. Scale bars = 20 μ m. Pictures O–S were taken from Sasaki *et al.* (2012).

Note: Holotype material was examined, and an epitype selected for further molecular phylogenetic studies.

Pseudocercospora aleuritis (I. Miyake) Deighton, Mycol. Pap. 140: 138. 1976. Fig. 64D, E.

Basionym: *Cercospora aleuritis* I. Miyake [as '*aleuritidis*'], Bot. Mag. (Tokyo) 26: 66. 1912.

Leaf spots amphigenous, circular to subcircular, blackish on upper leaf surface, yellowish brown at the centre with dark brown margin on hypophyllous leaf surface, 6–10 mm (*vide* Miyake 1912). *Caespituli* amphigenous. *Mycelium* internal, pale brown. *Stromata* amphigenous, mainly epiphyllous, substomatal, epidermal, erumpent, 38–65 µm diam, brown to dark brown, without superficial hyphae. *Conidiophores* densely to loosely fasciculate, emerging from the upper part of stromata, simple, rarely branched, straight to sinuous-geniculate, cylindrical, 20–65 × 2.5–3.8 µm, 0–4-septate, pale brown to brown, smooth. *Conidiogenous cells* integrated, terminal, proliferating sympodially or percurrently, with unthickened loci, 2.5 µm diam. *Conidia* solitary, holoblastic, cylindrical to obclavate, 25–76 × 3.8–5 µm, 0–3-septate, hyaline or pale brown, smooth to rough, thick-walled, subacute to rounded at the apex, obconically truncated and unthickened at the base, not darkened, 2.5 µm diam.

Typus: **Japan**, Okinawa, Okinawa Is., Kunigami, Yona Field centre, Univ. of Ryukyu, on *Aleurites montanus* (= *Vernicia montana*) (*Euphorbiaceae*), Nov. 1994, T. Kobayashi (**neotype** designated here TSU-MUMH1934, MBT 10005050, culture ex-neotype MAFF237174 = MUCC1230).

Additional materials examined: **Japan**, Nagasaki, Omura, on *Aleurites fordii* (= *Vernicia fordii*), 15 Oct. 1951, E. Kurosawa, MUMH-CNS362; Okayama, on *Aleurites cordatus*, 20 Nov. 1960, H. Tanaka, TFM: FPH-3243; Kobe, Hyogo, 21 Nov. 1960, S. Akai, TFM: FPH-3244.

Notes: The herbarium where the holotype specimen (on *Aleurites cordatus* = *V. montana*, China, Hynan, Pron. Sangteh, 12 Oct. 1908, I. Miyake.) has been deposited is unknown, and the specimen could not be located. A neotype was selected from Japanese specimens based on the similarity of the morphological description.

Pseudocercospora angiopteridis Goh & W.H. Hsieh, Trans. Mycol. Soc. Republ. China 4: 27. 1989. Fig. 64F–H.

Leaf spots amphigenous, water-soaked, with indefinite margin, pale brown with dark brown and indefinite border, 10–30 mm. *Caespituli* epiphyllous, visible as black and loose fascicles. *Mycelium* internal, brown to pale brown. *Stromata* small to well developed, epiphyllous, submerged, erumpent, 20–50 µm diam, dark brown. *Conidiophores* arising from upper part of stromata, straight at the basal part, sinuous-geniculate to geniculate at the upper part, subcylindrical, loosely fasciculate in 2–10, simple, 20–140 × 3.8–5 µm, 3–7-septate, brown, pale brown at the apex, smooth. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially or percurrently, conically truncated at the apex, with unthickened, sometimes rim-like, and slightly convexed conidial loci at shoulder or at the apex caused by sympodial proliferation, 2.5–3.5 µm. *Conidia* solitary, holoblastic, variable in shape, cylindrical to obclavate, acicular, 52–82 × 2–5 µm, 6–9-septate, hyaline, or very pale coloured, smooth to rough, straight to curved, rounded to subacute at the apex, long obconically truncated and unthickened at the base, not darkened, 2–3.5 µm diam.

Typus: **Taiwan Island**, Hwalien Hsieh, Taluke, on *Angiopteris lygodifolia* (*Marattiaceae*), 1 Feb. 1985, T.K. Goh (**holotype** NCHUPP-148a; **isotype** K(M) IMI 312070). **Thailand**, on *Angiopteris evecta*, Chiang Mai, Chiang Mai Botanical Garden, 2 Nov. 2012, P.W. Crous (**epitype** designated here CBS H-24676, MBT 10005051, culture ex-epitype CBS 147385 = CPC 21666).

Notes: The epitype chosen from the specimens on the same host genus in Asia closely corresponds with the morphology of the holotype. The tabular key to *Pseudocercospora* species on ferns based on the morphology is provided in Braun *et al.* (2013). No DNA data are available from the holotype.

Pseudocercospora basitruncata Crous, Mycol. Mem. 21: 123. 1998.

Description and illustrations: Crous (1998).

Typus: **Colombia**, Astorga, Nemocon, Cundinamarca, on *Eucalyptus* sp. (*Myrtaceae*), 5 Jan. 1942, J. Orjuela-Navarrete (**holotype** BPI 436146; **isotypes** Herbario de Fitopatología Dept. de Agric. Bogota 00990; BPI 436141, 436142, Herbario de Fitopatología Dept. de Agric. Bogota 00993, 00999); on *Eucalyptus* sp., 11 Jan. 1972, E. Feliu, BPI 436195, 436196; on *Eucalyptus grandis*, Sinai, May 1995, M.J. Wingfield (**epitype** designated here PREM 54408, MBT 10005052, cultures ex-epitype CPC 1202–1204 = CBS 114664).

Notes: The epitype was chosen from specimens collected in Colombia, the type locality. It closely corresponds with the morphology of the holotype. No DNA data are available from the holotype.

Pseudocercospora biophyti (Syd. & P. Syd.) Deighton, Mycol. Pap. 140: 140. 1976. Fig. 64I–K.

Basionym: *Cercospora biophyti* Syd. & P. Syd., Philipp. J. Sci., C, Bot. 8: 284. 1913.

Leaf spots indistinct. *Caespituli* mainly hypophyllous, visible as dark olivaceous grey to brown mycelial mat composed of superficial hyphae and conidia, or as a sooty mold. *Mycelium* internal and external, developed at the leaf surface. *Stromata* lacking to small, hypophyllous, substomatal, epidermal, erumpent, up to 25 µm diam, pale brown to brown, with superficial hyphae. *Conidiophores* densely to loosely fasciculate, arising from the upper part of stromata or branched from superficial hyphae, straight to sinuous-geniculate, creeping on the surface of leaf, subcylindrical, branched, tangled, 10–80 × 2.5–5 µm, multi-septate, pale brown to brown, smooth to rough. *Conidiogenous cells* integrated, terminal, proliferating sympodially or percurrently, rounded at the apex, with unthickened or small rim-like loci, 1.5–2 µm. *Conidia* solitary, holoblastic, cylindrical to obclavate, 25–55 × 2.5–5 µm, 3–6-septate, hyaline or pale brown, smooth to rough, subacute to rounded at the apex, long obconically truncated and unthickened at the base, not darkened, 1.5–2 µm diam.

Typus: **Philippines**, Los Banos, on *Biophytum sensitivum* (*Oxalidaceae*), 7 Jan. 1913, H. Sydow (**isotype** CUP-039199).

Material examined: **Benin**, Collines, on *Biophytum petersianum*, 22 Oct. 2011, M. Piatek & N. Yourou (**reference strain** designated here KRAM F-49038, culture CPC 20020).

Notes: The type material of *Ps. biophyti* was collected from the Philippines and has not been examined in this study. The symptoms and morphology of the specimen from Benin were identical to that described for *Ps. biophyti*. In this study, we propose a reference strain to facilitate further studies.

Pseudocercospora boehmeriigena U. Braun, Trudy Bot. Inst. Komarova 20: 42. 1997.

Descriptions and illustrations: Braun & Melnik (1997), Silva *et al.* (2016).

Typus: **USA**, New York, Saratoga, South Ballston, on *Boehmeria cylindrica*, Sep., C.H. Peck (**holotype** NYS f494). **Brazil**, Minas Gerais, Viçosa, Universidade Federal de Viçosa, on *Boehmeria nivea* (*Urticaceae*), 21 May 2013, R.W. Barreto (**epitype** designated here CBS H-22170, MBT 10005053, culture ex-epitype COAD 41562 = CPC 25243).

Notes: *Pseudocercospora boehmeriigena* was recently described by Braun & Melnik (1997). Although the species was treated by Silva *et al.* (2016), they did not designate an epitype. The host plant of this species, *Boehmeria cylindrica*, is widely distributed in North and South America. Based on the distribution of this fungus, and its morphology, we designate an epitype for the species.

Pseudocercospora ceratoniae (Pat. & Trab.) Deighton, Mycol. Pap. 140: 141. 1976. Fig. 64L–N.

Basionym: *Cercospora ceratoniae* Pat. & Trab., Bull. Soc. Mycol. France 19(3): 260. 1903.

Leaf spots amphigenous, scattered, angular to irregular, vein limited, 2–5 mm, greyish at the centre, blackish brown. *Caespituli* amphigenous. *Mycelium* internal and external, hyaline to pale brown. *Stromata* amphigenous, substomatal, epidermal, erumpent, well-developed, 22.5–97.5 µm diam, pale to dark brown, with superficial hyphae. *Conidiophores* well-developed, dense, arising from the upper part of stromata, short, straight to curved, subcylindrical, unbranched, rarely branched at the basal part, 12–20 × 2–3.8 µm, septate, pale brown to brown, paler towards the tip, smooth. *Conidiogenous cells* integrated, terminal, proliferating percurrently, conically truncated at the apex, with unthickened and truncated conidial loci, 1–1.5 µm. *Conidia* solitary, holoblastic, cylindrical to filamentous, obclavate, 12–60 × 2–2.5 µm, 1–6-septate, hyaline, straight to sinuous, smooth, acute at the apex, obconically truncated and unthickened at the base, not darkened, 1–1.5 µm wide.

Typus: **Algeria**, Algier, on *Ceratonia siliqua* (*Fabaceae*), 1901, Par N. Patouillard (**holotype** FH 7806). **Italy**, on *Ceratonia siliqua*, Nov. 2011, G. Polizzi (**epitype** designated here CBS H-24677, MBT 10005054, culture ex-epitype CPC 19998 = CBS 147386).

Notes: The epitype was selected from the same host based on the similarity of morphological characters to that of the holotype. The disease symptoms and morphological characters are similar to that observed on a specimen from Taiwan island (See Hsieh & Goh 1990).

Pseudocercospora cladrastidis (Jacq.) J.K. Bai & M.Y. Cheng, Acta Mycol. Sin. 11: 121, 1992. Fig. 64O–S.

Basionym: *Cercospora cladrastidis* Jacq., in Jaczewski *et al.*, Fungi Ross. Exs. no. 350. 1899.

Leaf spots amphigenous, circular, scattered, pale brown to brown with reddish brown margin, 1–5 mm diam. *Caespituli* hypophyllous, synnematosus with blackish brown conidiophores. *Mycelium* internal, hyaline to brown. *Stromata* hypophyllous, substomatal, epidermal, erumpent, well-developed, subglobose to globose, dark brown to blackish, 31–60 µm diam. *Conidiophores* well-developed, densely fasciculate, synnematosus, or loosely fasciculate, arising from the upper part of stromata, straight at the base, sometimes curved,

cylindrical, unbranched, geniculated at the upper part, 78–170(–450) × 1.6–5 µm, multi-septate, pale to dark brown, paler towards the tip, smooth to rough. *Conidiogenous cells* integrated, terminal, proliferating sympodially or percurrently, conically truncated at the apex, with unthickened and truncated conidial loci, 1–2 µm diam. *Conidia* solitary, holoblastic, obclavate, 24–49 × 2–7 µm, 4–5-septate, hyaline, or slightly pigmented, straight to curved, smooth, rounded at the apex, obconically truncated and unthickened at the base, not darkened, 1–2 µm diam.

Typus: **Japan**, Aomori, Nishimeya, Shirakami, on *Maackia amurensis* (*Fabaceae*), 28 Aug. 2010, K. Tanaka, K. Hirayama, & K. Honda (**epitype** designated here HHUF30085, MBT 10005056, culture ex-epitype TSU-MUCC1494). **Russia**, Amurskaja Oblast, Khabarovsk Krai, Primorskij Krai, 1895, on *Maackia amurensis* (**lectotype** LE40382).

Additional materials examined: **Japan**, Aomori, Nishimeya, Shirakami, on *Maackia amurensis*, 29 Aug. 2010, K. Tanaka & K. Honda, HHUF30086, culture TSU-MUCC1495; *ibid.*, on *Maackia amurensis*, 17 Sep. 2010, K. Tanaka, A. Hashimoto & K. Honda, HHUF30087, culture TSU-MUCC1496; *ibid.*, on *Maackia amurensis*, 8 Jul. 2014, C. Nakashima, K. Shibayama & K. Motohashi, TSU-MUMH11492, culture TSU-MUCC1722.

Notes: Braun & Melnik (1997) examined the lectotype (LE 40382) of the present species. In addition, some *exsiccatae* specimens have been deposited (BPI 976394, BPI 976395, and WIS-F-0012808). The epitype for further molecular studies was selected from Japanese materials based on the similarity of morphological characters to the lectotype description by Braun & Melnik (1997).

Pseudocercospora coprosmae U. Braun & C.F. Hill, Australas. Pl. Pathol. 32: 88. 2003.

Description and illustrations: Braun *et al.* (2003).

Typus: **New Zealand**, Auckland, Grey Lynn, Western Springs Park, on *Coprosma robusta* (*Rubiaceae*), 29 Apr. 2001, C.F. Hill 404 (**holotype** HAL 1731); Auckland, Grey Lynn, Western Springs Park, on *Coprosma robusta*, 21 Dec. 2003, C.F. Hill (**epitype** designated here PDD 89282, MBT 10005058, **iso-epitypes** U. Braun: Fungi selecti exsiccati 57 & Hill 957 in CBS H, culture ex-epitype ICMP 15279 = CBS 114639).

Notes: To fix the phylogenetic application of the name, an epitype was selected from topotypic material.

Pseudocercospora cratevicola C. Nakash. & U. Braun, IMA Fungus 4: 271. 2013. Fig. 65A, B.

Description: Braun *et al.* (2013).

Typus: **India**, Madras, Coimbatore, Government Farm, on *Crateva religiosa* (*Capparaceae*), 5 Feb. 1912, W. McRae (**holotype** S, F42112). **Japan**, Chiba, Tateyama, Fujiwara, on *Crateva religiosa*, 18 Sep. 1998, C. Nakashima & S. Uematsu (**epitype** designated here TSU-MUMH CNS462, MBT 10005059, culture ex-epitype TSU-MUCC1088).

Additional materials examined: **Japan**, Shizuoka, Ito, on *Crateva formosensis*, 29 Sep. 1999, T. Kobayashi & C. Nakashima (TSU-MUMH CNS797 and HAL 2597 F).

Notes: An epitype was selected for further molecular studies from the Japanese specimens on *C. religiosa*. Based on a morphological study of the type material, Japanese specimens on *Prathigada crataevae* were described as a new species (Braun *et al.* 2013).

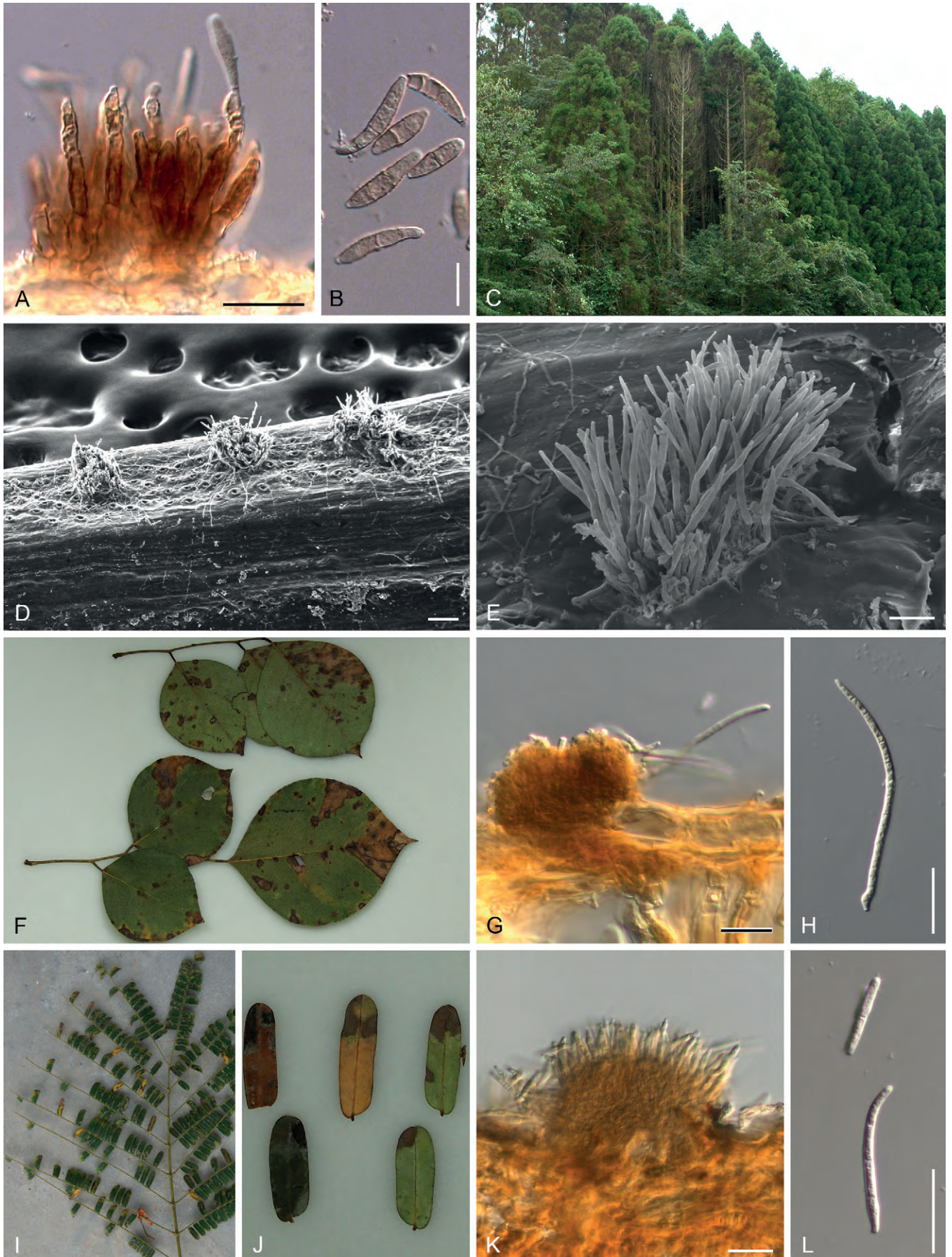


Fig. 65. *Pseudocercospora* spp. plate 2. **A, B.** *Pseudocercospora cratevicola* (epitype TSU-MUMH CNS462). **A.** Stroma and conidiophores on *Crateva formosensis*. **B.** Conidia. **C–E.** *Pseudocercospora cryptomericola* (epitype TFM: FPH-7851). **C.** Early defoliation of diseased leaves of *Cryptomeria japonica*. **D.** Caespituli on a leaf. **E.** Conidiophores and conidia bearing from stroma. **F–H.** *Pseudocercospora dalbergiae* (epitype TSU-MUMH TUA55). **F.** Disease symptoms on *Dalbergia sissoo*. **G.** Stroma and conidiophores. **H.** Conidium. **I–L.** *Pseudocercospora delonicicola* (holotype UMT201901). **I.** Disease symptoms on *Delonix* sp. **J.** Magnified symptoms. **K.** Stroma and conidiophores. **L.** Conidia. Scale bars = 20 μ m.

Pseudocercospora cryptomeriicola (Sawada) C. Nakash. *et al.*, *Mycoscience* 48: 254, 2007. Fig. 65C–E.

Basionym: *Cercospora cryptomeriicola* Sawada, *Bull. Gov. Forest Exp. Sta. Meguro* 45: 53. 1950.

Descriptions and illustrations: Nakashima *et al.* (2007), Braun *et al.* (2013).

Typus: **Japan**, Yamagata, Kamabuchi, on *Cryptomeria japonica* (*Cupressaceae*), 8 Aug. 1949, K. Sato (**holotype** IUM-FS 62); Kumamoto, Kikuchi, on *Cryptomeria japonica*, 7 Nov. 2005, C. Nakashima, K. Motohashi & T. Akashi (**epitype** designated here TFM: FPH-7851, MBT 10005060, culture ex-epitype MAFF 240073 = NBRC102150 = MUCC145).

Additional materials examined: **Japan**, Aichi, Shitara, Furiwake, on *Cr. japonica*, 16 Jun. 1954, I. Ando, TFM: FPH-1085; Kumamoto, Kikuchi, on *Cr. japonica*, 1 Jun. 2004, C. Nakashima, K. Motohashi & T. Akashi, TFM: FPH-7850, culture MAFF240072; Miyazaki, Shiiba, on *Cr. japonica*, 8 Jun. 2001, T. Sanui, culture TSU-MUCC170 = MAFF 238328 = MUCC1088.

Notes: *Pseudocercospora cryptomeriicola* is a pathogen of an endemic plant in Japan, *Cr. japonica*, and is only known from Japan. The epitype was selected based on the similarity of morphological characters to that of the holotype specimen on *Cr. japonica*.

Pseudocercospora cymbidiicola U. Braun & C.F. Hill, *Mycol. Prog.* 1: 23, 2002.

Description and illustrations: Braun & Hill (2002).

Typus: **New Zealand**, Auckland, Mt. Albert, on *Cymbidium* sp. (*Orchidaceae*), 24 Sep. 2000, C.F. Hill (**holotype** HAL 1585); Auckland, Mt. Albert, on *Cymbidium* sp., 25 Mar. 2004, C.F. Hill 1007 (**epitype** designated here PDD 81460, MBT 10005061, culture ex-epitype CBS 115132).

Note: The epitype was selected from topotypic material based on the similarity of morphological characters.

Pseudocercospora dalbergiae (S.H. Sun) J.M. Yen, *Bull. Trimestriell Soc. Mycol. France* 94: 386. 1979. Fig. 65F–H.

Basionym: *Cercospora dalbergiae* S.H. Sun, *J. Agric. Forest., Taiwan* 9: 43. 1955.

Leaf spots amphigenous, circular to irregular, scattered, dark brown with greyish brown centre, 1–10 mm diam, often enlarged and confluent. *Caespituli* amphigenous. *Mycelium* internal and external, hyaline, or pale brown. *Stromata* amphigenous, small to developed, substomatal, epidermal, erumpent, brown to pale brown, 24–55 µm diam. *Conidiophores* dense, arising from the upper part of stromata, or solitary, branched from superficial hyphae, straight or strongly geniculate, cylindrical, 5–25 × 2.5 µm, 0–2-septate, pale brown, smooth. *Conidiogenous cells* integrated, terminal, or intercalary, proliferating sympodially, conically truncated at the apex, with unthickened and truncated conidial loci, 1.5–2 µm. *Conidia* solitary, holoblastic, obclavate to filamentous, 28–80 × 1.5–2.5 µm, 3–6-septate, hyaline, straight to curved, smooth, rounded to subacute at the apex, truncated and unthickened at the base, not darkened, 1.5–2 µm diam.

Typus: **Taiwan Island**, Taichun, Taichun, on *Dalbergia sissoo* (*Fabaceae*), 17 Aug. 1955, S.H. Sun (**holotype** deposited in unknown fungarium); (line drawing, in Sun SH (1955) *Studies on the genus Cercospora found in Taiwan* (I). *Journal of Agriculture and Forestry Taiwan* 4: 141, fig. 3, **lectotype** designated here MBT 10005062); Taichun, Dakengdizhen Park,

on *Dalbergia sissoo*, 9 Oct. 2014, C. Nakashima, K. Motohashi, Y. Hattori & C.Y. Chen (**epitype** designated here TSU-MUMH TUA55, MBT 10005063, culture ex-epitype TSU-MUCC TUA55).

Notes: The location of the type material is unknown. A lectotype was therefore selected from the protologue. An epitype was selected from a newly collected topotypic specimen to facilitate further molecular studies.

Pseudocercospora delonicicola C. Nakash., L. Suhaizan & I. Nurul Faziha, *sp. nov.* MycoBank MB 838198. Fig. 65I–L.

Etymology: Derived from the name of host plant, *Delonix*.

Diseased leaves are easily defoliating. *Leaf spots* amphigenous, angular to irregular, 1–10 mm diam, dark brown to blackish brown, with black border at upper surface, often surrounded yellowish halo, brown to dark brown at lower surface. *Caespituli* amphigenous, punctiform, scattered, visible as olivaceous brown masses. *Mycelium* internal. *Stromata* amphigenous, substomatal to epidermal, erumpent, well developed, 25–75 µm diam, pale brown to olivaceous brown, without superficial hyphae. *Conidiophores* dense, short, arising from the upper part of stromata, straight to geniculate-sinuuous, subcylindrical, unbranched, 7.5–25 × 2–2.5 µm, 0–1-septate, pale brown to brown, paler towards the tip, smooth. *Conidiogenous cells* integrated, terminal, proliferating sympodially or percurrently, with unthickened conidial loci. *Conidia* solitary, irregular in shape, cylindrical to obclavate, 10–50 × 2–2.5 µm, 1–5-septate, hyaline, smooth, rounded at the apex, truncate and unthickened at the base, not darkened, 2–2.5 µm diam.

Typus: **Malaysia**, Terengganu, Universiti Malaysia Terengganu, on *Delonix* sp. (*Fabaceae*), 22 Jun. 2019, C. Nakashima & Y. Hattori (**holotype** UMT201901, isotype TSU-MUMH11874, culture ex-type TSU-MUCC2869).

Note: Present species differs from *Ps. delonicis* (on *Delonix regia*, Singapore) in having small stromata and well-developed superficial hyphae.

Pseudocercospora dodonaeae Boesew., *Trans. Brit. Mycol. Soc.* 77: 453, 1981.

Description and illustration: Crous & Braun (1996).

Typus: **New Zealand**, on *Dodonaea viscosa*, Auckland, H.J. Boesewinkel, Jul. 1978 (**holotype** PDD 41332); *ibid.*, Grey Lynn, Western Springs Park, on *Dodonaea viscosa*, 2 Dec. 2003, C.F. Hill 826-B (**epitype** designated here PDD 93500, MBT 10005064, culture ex-epitype CBS 114647 = ICMP 15283).

Notes: Three cercosporoid species on *Dodonaea* plants, *Passalora dodonaeae*, *Pseudocercospora dodonaeae*, and *Ps. mitteriana*, were examined by Crous & Braun (1996). The epitype of *Ps. dodonaeae* was selected from topotypic material for further phylogenetic studies.

Pseudocercospora ebulicola (W. Yamam.) Deighton, *Mycol. Pap.* 140: 143. 1976. Fig. 66A–C.

Basionym: *Cercospora ebulicola* W. Yamam., *Trans. Sapporo Nat. Hist. Soc.* 13: 139. 1934.

Leaf spots amphigenous, indistinct, vein limited, 1–10 mm, dark brown to pale brown. *Caespituli* mainly hypophyllous, visible as sooty or pale olivaceous brown mycelial mat. *Mycelium* internal and external, superficial hyphae creeping at lower leaf surface, brown to

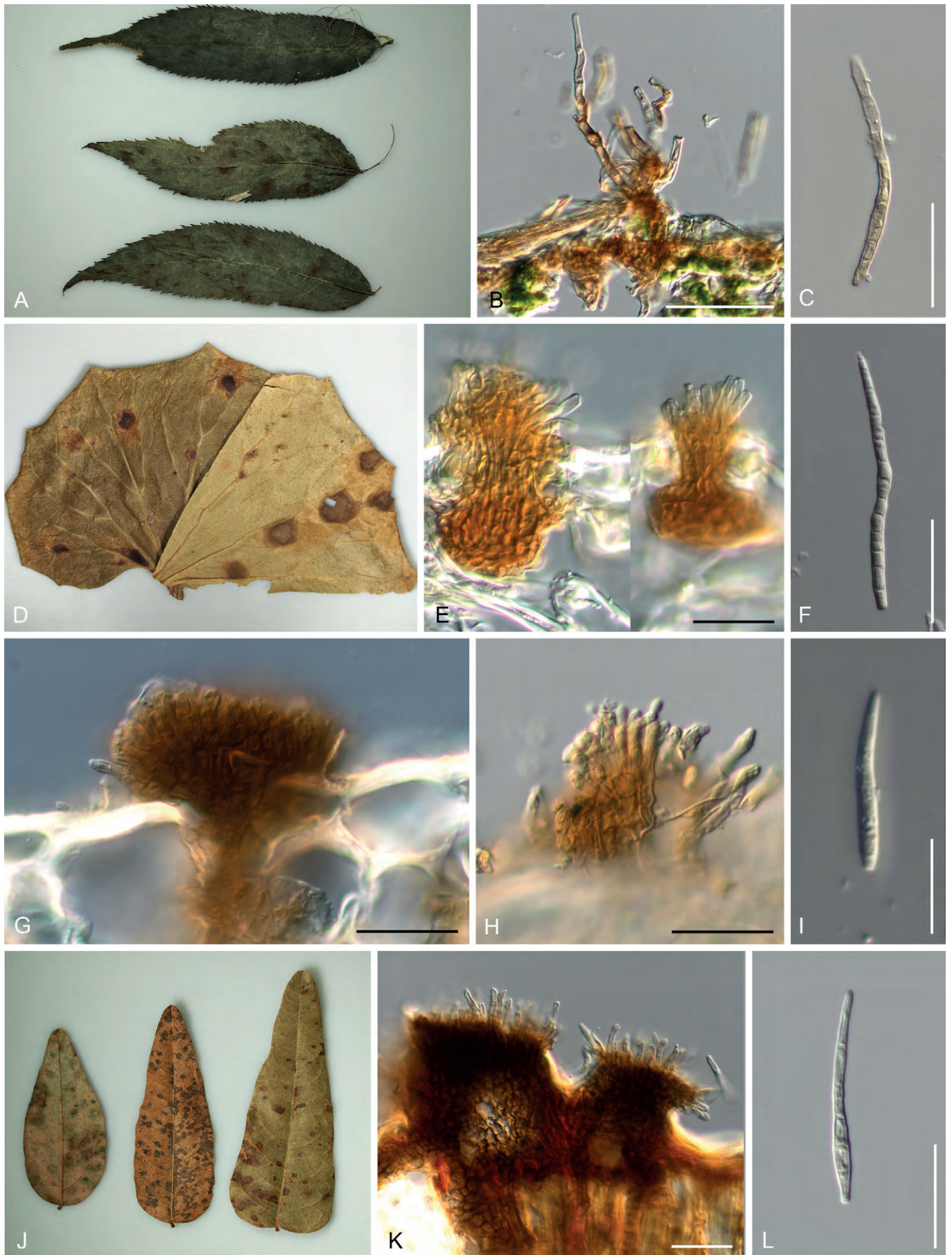


Fig. 66. *Pseudocercospora* spp. plate 3. **A–C.** *Pseudocercospora ebulicola* (epitype CBS H-24678). **A.** Disease symptoms on *Sambucus* sp. **B.** Stroma and conidiophores. **C.** Conidium. **D–F.** *Pseudocercospora farugii* (holotype TSU-MUMH11202). **D.** Disease symptoms on *Farugium japonicum*. **E.** Stroma and conidiophores. **F.** Conidium. **G–I.** *Pseudocercospora glochidionis* (epitype TSU-MUMH11940). **G, H.** Stroma and conidiophores. **I.** Conidium. **J–L.** *Pseudocercospora hardenbergiae* (holotype CBS H-24673). **J.** Disease symptoms on *Hardenbergia violacea*. **K.** Stroma and conidiophores. **L.** Conidium. Scale bars = 20 µm.

pale brown. *Stromata* lacking to developed, amphigenous, mainly hypophyllous, substomatal to epidermal, erumpent, globose, up to 47 µm diam, brown to dark brown, with superficial hyphae on lower leaf surface. *Conidiophores* loose to dense, emerging from the upper part of stromata, straight to sinuous, subcylindrical, simple or branched, irregular in width, 10–120 × 2–5 µm, multi-septate, hyaline to dark brown, irregular in width, smooth. *Conidiogenous cells* integrated, terminal or intercalary, proliferating sympodially, with unthickened and reflective conidial loci at shoulder caused by sympodial proliferation, 2–2.5 µm diam. *Conidia* solitary, variable in shape, acicular, cylindrical to obclavate, 38–100 × 2–5 µm, 3–8-septate, hyaline, or pale coloured, smooth, acute to rounded at the apex, obconically truncated and unthickened at the base, not darkened, 2–2.5 µm wide.

Typus: Taiwan Island, Sozan, on *Sambucus javanica* (*Adoxaceae*), 3 Dec. 1933, W. Yamamoto (**lectotype** CUP-039732, MBT 202795); on *Sambucus* sp., 18 Dec. 2011, P.W. Crous (**epitype** designated here CBS H-24678, MBT 10005065, culture ex-epitype CBS 147387 = CPC 20159).

Notes: Pseudocercospora ebulicola is a well-known species, and numerous collections are also maintained in Japanese fungaria. The epitype was selected from specimens collected on Taiwan Island based on the morphological similarity to that of the original description of lectotype, designated by Braun *et al.* (2015b).

Pseudocercospora euphorbiacearum U. Braun, *Biblioth. Lichenol.* 86: 89. 2003.

Description and illustration: Braun (2003).

Typus: Dominican Republic, Haina, on *Dalechampia scandens* (*Euphorbiaceae*), 26 Jan. 1926, R. Ciferri (**holotype** MA Ciferri 886[7669] B). **Brazil**, on *Dalechampia* sp., Minas Gerais, Viçosa, Reserva Floresta I Mata do Paraíso, 5 Aug. 2013, M. Silva (**epitype** designated here CBS H-22163, MBT 10005066, **iso-epitype** VIC 42797, culture ex-epitype COAD 1537 = CPC 25222).

Notes: The holotype material has not been examined. Silva *et al.* (2016) examined four *Pseudocercospora* species on *Euphorbiaceae* plants and indicated that species on different host genera clustered phylogenetically apart. The epitype was selected based on the similarity of morphological characters on the same host genus to that of the original description.

Pseudocercospora farfugii C. Nakash., I. Araki, & Ai Ito, **sp. nov.** MycoBank MB 838200. Fig. 66D–F.

Etymology: Derived from the name of host genus, *Farfugium*.

Leaf spots amphigenous, pale brown to dark brown on the upper leaf surface, pale brown to brown with dark brown border on the lower leaf surface, scattered, circular to orbicular, 10–20 mm diam, later enlarged, irregular. *Caespituli* amphigenous, scattered. *Mycelium* internal. *Stromata* amphigenous, small to developed, substomatal, epidermal, erumpent, subglobose, 20–70 µm diam, pale brown to brown. *Conidiophores* loose to densely fasciculate, arising from the upper part of stromata, straight to mildly geniculate, cylindrical, 10–30 × 2.5–3.8 µm, 0–1-septate, hyaline or pale brown, paler towards the apex, smooth. *Conidiogenous cells* integrated, terminal, proliferating sympodially or percurrently, rounded or truncated at the apex, with unthickened conidial loci, 2.5–3 µm diam. *Conidia* solitary, holoblastic, cylindrical to acicular, 60–180 × 2.5–5 µm, 6–14-septate,

hyaline, smooth, acute at the apex, truncate and unthickened at the base, 2.5–3 µm diam.

Typus: Japan, Mie, Tsu, Mie University, on *Farfugium japonicum* (*Asteraceae*), 28 Nov. 2008, I. Araki & A. Ito (**holotype** TSU-MUMH11202, culture ex-type TSU-MUCC978).

Additional material examined: Japan, Shizuoka, Kanzanji, on *Farfugium japonicum*, J. Nishikawa, TSU-MUMH11203, culture TSU-MUCC137.

Pseudocercospora formosana (W. Yamam.) Deighton, *Mycol. Pap.* 140: 144. 1976.

Basionym: Cercospora formosana W. Yamam., *J. Soc. Trop. Agric., Formosa* 6: 600. 1934.

Diseased leaves are easily defoliating. *Leaf spots* amphigenous, scattered, angular to irregular, vein limited, later enlarged, confluent, 1–3 mm diam, pale to dark brown. *Mycelium* internal and external. *Caespituli* amphigenous, mainly hypophyllous, visible as olivaceous brown masses composed of conidiophores and conidia. *Stromata* lacking or small, composed of a few brown cells, substomatal, erumpent, submerged. *Conidiophores* emerging from stromata, branched from creeping superficial hyphae, short, loose, straight to geniculate-sinuous, subcylindrical, 2–12.5 × 2–2.5 µm, 0–1-septate, pale brown to brown, paler towards the tip, smooth. *Conidiogenous cells* integrated, terminal or intercalary, proliferating sympodially, with unthickened conidial loci, 1.5–2 µm diam. *Conidia* solitary, holoblastic, cylindrical to obclavate, straight to curved, 30–40 × 2–2.5 µm, 2–4-septate, hyaline, smooth, acute at the apex, obconical truncate and unthickened at the base, not darkened, 1.5–2 µm diam.

Typus: Japan, Chiba, Tateyama, on *Lantana camara* (*Verbenaceae*), 4 Jun. 1997, C. Nakashima & S. Uematsu (**epitype** designated here TSU-MUMH11939, MBT 10005067, culture ex-epitype MAFF 238239). **Taiwan Island**, Taihoku, on *Lantana camara*, 20 Jan. 1934, W. Yamamoto (**lectotype** designated here NTU-PPE, hb. Sawada, MBT 10005893, **isotype** IMI 8570).

Additional materials examined: Japan, Okinawa, Kunigami, Onna, on *Lantana camara*, 17 Nov. 2007, C. Nakashima & T. Akashi, TSU-MUMH10957, culture TSU-MUCC855. **Malaysia**, Terengganu, Universiti Malaysia Terengganu, on *Lantana* sp., 22 Aug. 2018, C. Nakashima & Y. Hattori, culture TSU-MUCC2612.

Notes: Isotypes have been deposited in fungaria (IMI 8570 *vide* Crous & Braun 2003, and NTU-PPE). An isotype specimen preserved at NTU-PPT was selected as lectotype. Nishikawa *et al.* (2001) concluded that *Ps. formosana* was a synonym of *Ps. guianensis* on *Lantana* spp. based on the overlapping size of stromata and density of conidiophores on stromata. However, these morphological characters should be treated as distinguishing features for the two species. Furthermore, Crous *et al.* (2013a) showed that the Jamaican isolate of *Ps. guianensis* on *Lantana camara* (see *Ps. guianensis*) was located in a distinct clade from *Ps. formosana*. For Asian *Pseudocercospora* species on *Lantana* spp., *Ps. formosana* represents the most appropriate name.

Pseudocercospora fukuii (W. Yamam.) W.H. Hsieh & Goh, *Trans. Mycol. Soc. Rep. China* 2: 115. 1987.

Basionym: Cercospora fukuii W. Yamam. [as 'fukui'], *J. Soc. Trop. Agric., Formosa* 6: 601. 1934.

Description and illustrations: Goh & Hsieh (1987).

Typus: Japan, Tokyo, Akiruno, Itsukaichi, on *Boehmeria nivea* var. *concolor*

f. nipononivea (*Urticaceae*), May 1999, E. Imaizumi (**epitype** designated here TSU-MUMH11938, MBT 10005068, culture ex-epitype MAFF 238121). **Taiwan Island**, Taipei, on *Boehmeria cylindrica*, 20 Feb. 1934, W. Yamamoto (**lectotype** designated here CUP-039844, MBT 10005896, **isotype** IMI 8555).

Additional materials examined: **Japan**, Tokyo, Jindaiji, on *Boehmeria nivea* var. *concolor* f. *nipononivea*, 19 Jul. 1997, C. Nakashima, TSU-MUMH CNS200, culture MAFF238074; Okinawa, Okinawa Is, Nakijin, on *Boehmeria nivea* var. *concolor* f. *nipononivea*, 28 Mar. 2000, C. Nakashima, TSU-MUMH CNS902, culture MAFF238235.

Notes: The lectotype was selected from isotype materials preserved at fungaria. In addition, the epitype was selected from Japanese specimens. Morphological characters of the epitype were identical to the description and illustrations based on IMI 8555 in Goh & Hsieh (1987). Many fungarium specimens from Japan are maintained in TSU-MUMH and other fungaria.

Pseudocercospora glochidionis (Sawada) Goh & W.H. Hsieh, *Trans. Mycol. Soc. Rep. China* 2: 136. 1987. Fig. 66G–I.

Basionym: *Cercospora glochidionis* Sawada, *Rept. Dept. Agric. Res. Inst. Taiwan* 1: 670, 1919 [1920].

= *Gloeosporium glochidionis* Sawada, *Trans. Nat. Hist. Soc. Formosa* 24: 78, 1916.

Caespituli amphigenous. *Mycelium* internal or external, pale brown. *Stromata* small to well developed, amphigenous, mainly epiphyllous, substomatal, epidermal, erumpent, 20–110 µm diam, pale brown to brown. *Conidiophores* short, dense, emerging from the upper part of stromata, simple, straight to mildly sinuous, cylindrical, 17–25 × 2–2.5 µm, 0–4-septate, pale brown, smooth. *Conidiogenous cells* integrated, terminal, proliferating percurrently, conically truncated at the apex, with unthickened loci, 1–2 µm diam. *Conidia* solitary, holoblastic, obclavate, 32–55 × 2–2.5 µm, 0–4-septate, hyaline, smooth, subacute at the apex, obconically truncated and unthickened at the base, not darkened, 1.5–2 µm diam.

Typus: **Japan**, Kagoshima, Amami-Oshima Is, Tatsugo, on *Glochidion zeylanicum* (*Phyllanthaceae*), 10 Nov. 1993, T. Kobayashi & M. Muramoto (**epitype** designated here TSU-MUMH11940, MBT 10005069, culture ex-epitype MAFF237000). **Taiwan Island**, Taipei, on *Glochidion hongkongense*, 19 Feb. 1916, K. Sawada (**lectotype** designated here NTU-PPE, hb. Sawada, MBT 10005838); *ibid.*, 10 Mar. 1918 (**syntype**, NTU-PPE, hb. Sawada).

Notes: The lectotype material was selected from syntypes maintained at NTU-PPE, hb. Sawada. The specimen collected from Amami island, located in the same island arc, was selected as epitype based on the similarity of morphological characters to that of the original description.

Pseudocercospora hardenbergiae Crous & C. Nakash., **sp. nov.** MycoBank MB 838650. Fig. 66J–L.

Etymology: Derived from the name of host plant, *Hardenbergia*.

Leaf spots amphigenous, scattered, angular, vein limited, often enlarged and confluent, 1–3 mm diam, pale brown to brown. *Caespituli* amphigenous, visible as black conidial masses. *Mycelium* internal. *Stromata* amphigenous, small to well-developed, substomatal, epidermal, submerged, erumpent, dark blackish brown to pale brown, 22–150 µm diam. *Conidiophores* dense, arising from the upper part of stromata, straight to sinuous-geniculate, cylindrical,

unbranched, pale brown to brown, paler towards the apex, 2.5–15 × 2–2.5 µm, 0–2-septate, smooth. *Conidiogenous cells* integrated, terminal, proliferating percurrently or sympodially, with unthickened and truncated conidial loci, 2 µm diam. *Conidia* solitary, holoblastic, cylindrical to obclavate, 25–68 × 2.5–3 µm, 1–7-septate, hyaline to pale coloured, smooth, acute at the apex, obconically truncated, unthickened and not darkened at the base, 2 µm diam.

Typus: **Australia**, Queensland, on *Hardenbergia violacea* (*Fabaceae*), 16 Jul. 2009, P.W. Crous (**holotype** CBS H-24673, culture ex-type CBS 147381 = CPC 17177).

Notes: *Pseudocercospora hardenbergiae* is proposed as a new taxon, occurring on *Hardenbergia violacea*, which is endemic to Australia, ranging from Queensland to Tasmania.

Pseudocercospora ixorana (J.M. Yen & Lim) U. Braun & Crous [as '*ixoriana*'], *Mycosphaerella* and its anamorphs: 1. Names published in *Cercospora* and *Passalora*: 230. 2003. Fig. 67A–C.

Basionym: *Cercospora ixorana* J.M. Yen & Lim [as '*ixoriana*'], *Bull. Trimestiel Soc. Mycol. France* 85(4): 471. 1969 (1970).

Leaf spots large, amphigenous, circular to subcircular, 8–10 mm diam, dark brown, greyish white at the centre, irregular at marginal area, dark brown upper, often enlarged, up to 30 mm diam. *Caespituli* hypophyllous, punctiform, scattered, visible as olivaceous brown masses composed of conidiophores and conidia. *Mycelium* internal and external. *Stromata* hypophyllous, small, composed of few brown cells or up to 30 µm diam, substomatal to epidermal, erumpent. *Conidiophores* densely fasciculate, arising from the upper part of stromata or solitary from superficial hyphae, straight to geniculate-sinuous, subcylindrical, 5–30 × 2–3 µm, 0–1-septate, dark brown to pale blackish, paler towards the tip, smooth. *Conidiogenous cells* integrated, terminal, proliferating sympodially, with unthickened conidial loci, 2–3 µm diam. *Conidia* solitary, holoblastic, obclavate, 40–50 × 2–3 µm, 3–4-septate, hyaline to pale brown, smooth, rounded at the apex, obconically truncate and unthickened at the base, 2 µm diam.

Typus: **Malaysia**, Terengganu, Universiti Malaysia Terengganu, on *Ixora chinensis* (*Rubiaceae*), 22 Aug. 2018, C. Nakashima & Y. Hattori (**epitype** designated here UMT201801KL, MBT 10005070, **iso-epitype** TSU-MUMH11942, cultures ex-epitype TSU-MUCC2608–2609). **Singapore**, on *Ixora chinensis*, 2 Aug. 1969, G. Lim (**holotype** PC).

Notes: The holotype material has not been examined. Symptoms and morphological characters of the epitype selected in this study are similar to that of the protologue. Although conidial length was slightly shorter than in the description (36–109 µm; Yen & Lim 1970), the line drawings (fig. 6; Yen & Lim 1970), depicted two classes of conidia, namely longer and shorter conidia. The shorter conidia are comparable to those observed in this study.

Pseudocercospora kenyirana C. Nakash., L. Suhaizan & I. Nurul Faziha, **sp. nov.** MycoBank MB 838201. Fig. 67D–F.

Etymology: Derived from the collection site in Malaysia.

Leaf spots amphigenous, scattered, angular to irregular, vein limited, enlarged and confluent, 2–10 mm diam, pale brown, surrounded by dark brown coloured vein. *Caespituli* amphigenous. *Mycelium* internal and external. *Stromata* amphigenous, well-developed on the upper leaf surface,

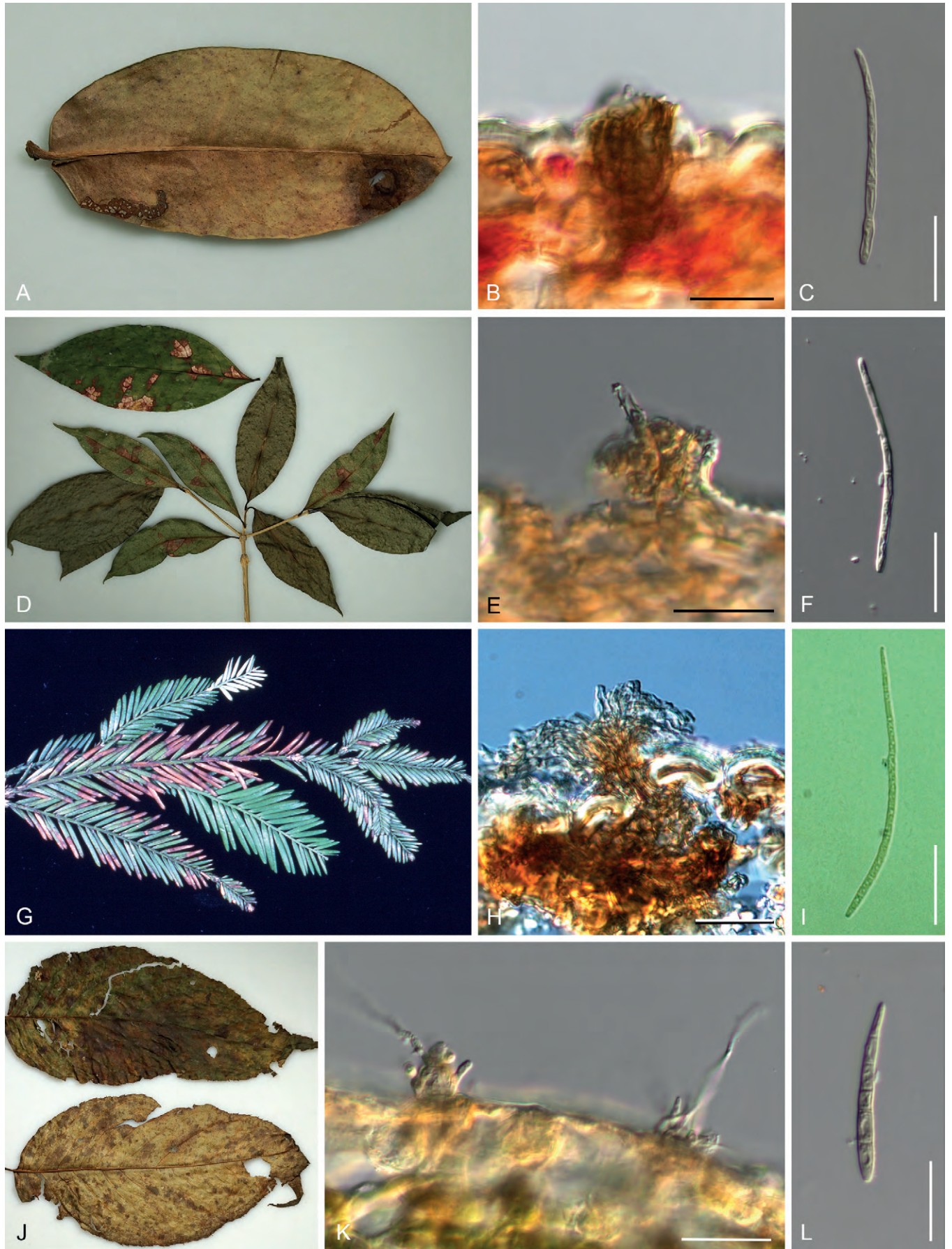


Fig. 67. *Pseudocercospora* spp. plate 4. **A–C.** *Pseudocercospora ixoriana* (epitype UMT201801KL). **A.** Disease symptoms on *Ixora chinensis*. **B.** Stroma and conidiophores. **C.** Conidium. **D–F.** *Pseudocercospora kenyirana* (holotype UMT201916KL). **D.** Disease symptoms on *Trigoniastrium* sp. **E.** Stroma and conidiophores. **F.** Conidium. **G–I.** *Pseudocercospora paraexosporioides* (epitype TSU-MUMH CNS448). **G.** Disease symptoms on *Sequoia sempervirens*. **H.** Stroma and conidiophores. **I.** Conidium. **J–L.** *Pseudocercospora perrottetiae* (holotype CBS H-24674). **J.** Disease symptoms on *Perrottetia arisanensis*. **K.** Stromata and conidiophores. **L.** Conidium. Scale bars = 20 μ m.

epidermal, erumpent, subglobose, brown to dark brown, 25–30 µm diam, lacking or small on the lower leaf surface, brown, substomatal, up to 30 µm diam. *Conidiophores* short, arising from the upper part of stromata or branched from superficial hyphae, straight to slightly curved, cylindrical, unbranched, pale brown to brown, paler towards the apex, 2.5–15 × 2–2.5 µm, 0–1-septate, smooth. *Conidiogenous cells* integrated, terminal, proliferating percurrently, with unthickened and truncated conidial loci, 2–2.5 µm diam. *Conidia* solitary, holoblastic, cylindrical to obclavate, 35–55 × 2–2.5 µm, 1–8-septate, hyaline, smooth, acute at the apex, obconical truncate and unthickened, not darkened, at the base, 2–2.5 µm diam.

Typus: **Malaysia**, Terengganu, Hulu Terengganu, Kenyir Lake, on *Trigoniastrum* sp. (*Polygalaceae*), 23 Jun. 2019, C. Nakashima, Y. Hattori, L. Suhaizan & I. Nurul Faziha Faziha (**holotype** UMT201916KL, isotype TSU-MUMH11878, culture ex-type TSU-MUCC2873).

Note: No cercosporoid species are known from *Trigoniastrum*, which is an endemic plant to Malaysia and Indonesia.

Pseudocercospora liquidambaricola (J.M. Yen) U. Braun, *Schlechtendalia* 5: 44. 2000.

Basionym: *Cercospora liquidambaricola* J.M. Yen, *Bull. Trimestiel Soc. Mycol. France* 94(1): 54. 1978.

Descriptions and illustrations: Kobayashi *et al.* (2002), Braun *et al.* (2015b).

Typus: **Japan**, Okinawa, Ishigaki Island, Ishigaki, Maesato, on *Liquidambar formosana* (*Altingiaceae*), 18 Nov. 1988, T. Kobayashi & M. Tsurumachi (**epitype** designated here TFM: FPH-7026, MBT 10005071, culture ex-epitype MAFF 410455). **Taiwan Island**, Taichung, on *Liquidambar formosana*, 29 Oct. 1971, J.M. Yen (**holotype** PC Yen 71255); Taipei, on *Liquidambar formosana*, 14 Oct. 1928, K. Sawada (**neotype** NTU-PPE, hb. Sawada, *vide* Braun *et al.* 2015b).

Additional material examined: **Japan**, Okinawa, Ishigaki Island, Ishigaki, Maesato, on *Liquidambar formosana*, Nov. 1988, T. Kobayashi & M. Tsurumachi, TFM: FPH-7027.

Notes: Braun *et al.* (2015b) designated a neotype for this species because holotype material could not be traced in PC or UC. In this study, an epitype was selected to facilitate further molecular studies from the specimens collected in the same archipelago as the type locality.

Pseudocercospora metrosideri U. Braun, *Fungal Diversity* 8: 44. 2001.

Description and illustrations: Braun (2001a).

Typus: **New Zealand**, North Island, New Plymouth, on *Metrosideros parkinsonii* (*Myrtaceae*), 16 Dec. 1965, G.F. Laundon (**holotype** IMI 116995); Auckland, Blockhouse Bay, Boundary Road, on *Metrosideros excelsa*, 17 Oct. 2003 (**epitype** designated here HAL C.F. Hill 929, MBT 10005077, culture ex-epitype CBS 114294 = ICMP 15227).

Notes: The holotype material has not been examined. An epitype was selected based on the similarity of morphological characters to the original description and illustrations.

Pseudocercospora pancratii (Ellis & Everh.) U. Braun & R.F. Castañeda, *Cryptog. Bot.* 2: 294. 1991.

Basionym: *Cercospora pancratii* Ellis & Everh., *J. Mycol.* 3(2): 15. 1887.

Description and illustrations: Braun & Castañeda (1991), Braun *et al.* (2014).

Typus: **Cuba**, Guisa, Hranma, on *Hippeastrum equestre* (*Amaryllidaceae*), 8 Nov. 1988, R.F. Castañeda (**epitype** designated here as metabolically inactive culture, CBS 137.94, MBT 10005078, culture ex-epitype CBS 137.94). **USA**, Louisiana, Plaquemines Parish, on *Pancreatium coronarium*, 4 Jun. 1886, A.B. Langlois (**holotype** NY 00838178, **isotype** BPI 457098).

Notes: The holotype material has not been examined, and the epitype is based on similarity to published descriptions and illustrations. See also *Ps. terengganuensis*.

Pseudocercospora paraexosporioides C. Nakash. & U. Braun, *IMA Fungus* 4: 336. 2013. Fig. 67G–I.

Description: Braun *et al.* (2013).

Typus: **Japan**, Tokushima, on *Sequoia sempervirens* (*Cupressaceae*), 4 Sep. 1959, K. Ito (**holotype** TFM: FPH-551); *ibid.*, Ibaraki, Tsukuba, 11 Sep. 1998, T. Kobayashi & C. Nakashima (**epitype** designated here TSU-MUMH CNS448, MBT 10005079, culture ex-epitype MAFF237788).

Additional material examined: **Japan**, Fukuoka, Tanushimaru, on *Sequoia sempervirens*, 20 Jun. 2000, T. Kobayashi & Y. Ono, TSU-MUCNS 970.

Notes: *Pseudocercospora paraexosporioides* was separated from *Ps. exosporioides* occurring in European countries. It differs from *Ps. paraexosporioides* in having much larger stromata, up to 300 µm diam, large sporodochial conidiomata, and much shorter, usually subcylindrical conidia with few septa (Braun *et al.* 2013). To facilitate further phylogenetic studies, an epitype was selected based on the similarity of morphological characters to that of the holotype specimen.

Pseudocercospora perrottetiae Crous, C. Nakash. & C.Y. Chen, *sp. nov.* MycoBank MB838651. Fig. 67J–L.

Etymology: Derived from the host plant, *Perrottetia*.

Leaf spots amphigenous, angular to irregular with distinct border, 5–10 mm, dark brown on the upper leaf surface, somewhat paler and indistinct on the lower surface, often confluent. *Caespituli* amphigenous, mainly hypogenous. *Mycelium* internal, pale brown, rarely external. *Stromata* hypogenous, small to developed, substomatal to intraepidermal, erumpent, subglobose, up to 32 µm diam. *Conidiophores* emerging from upper part of stromata, mildly sinuous, cylindrical, unbranched, smooth, 10–15 × 2.5–3 µm, 0–1-septate, hyaline to pale brown, paler towards the apex. *Conidiogenous cells* integrated, terminal, proliferating sympodially, rounded at the apex, with unthickened conidial loci, 2 µm diam. *Conidia* solitary, holoblastic, obclavate, straight to slightly curved, 32–50 × 2.5–3 µm, 3–4-septate, hyaline to pale olivaceous brown, smooth to rough, obconically truncated and unthickened at the base, 2 µm diam, subacute at the apex.

Typus: **Taiwan Island**, on *Perrottetia arisanensis* (*Streptaxidae*), 18 Dec. 2011, P.W. Crous (**holotype** CBS H-24674, cultures ex-type CBS 147382 = CPC 20074, CBS 147383 = CPC 20066).

Notes: No cercosporoid taxa are known from *Perrottetia*, and therefore the present collection is described as new.

Pseudocercospora pini-densiflorae (Hori & Nambu) Deighton, *Trans. Brit. Mycol. Soc.* 88: 390. 1987.

Basionym: *Cercospora pini-densiflorae* Hori & Nambu, *J. Pl. Prot., Tokyo* 4: 353. 1917.

Description and illustrations: Braun *et al.* (2013).

Typus: **Japan**, Kagoshima, Magome, on *Pinus densiflora* (*Pinaceae*), 20 Sep. 1915 (**holotype** not preserved); Kagoshima, Magome, on *Pinus densiflora*, 1 Oct. 1915, K. Hara (**neotype** NIAES C-511, MBT 176152, topotypic material of type); Aichi, Nagoya, Chikusa, Higashiyama Botanical Garden, on *Pinus strobus*, 1 Sep. 2012, K. Motohashi & S. Ukita (**epitype** designated here TSU-MUMH11935, MBT 10005080, culture ex-epitype TSU-MUCC1714).

Notes: The holotype specimen could not be traced and a neotype was selected from topotypic specimens (Braun *et al.* 2013). Although *Ps. pini-densiflora* is a plant quarantine targeted species in European countries and Japan, the ex-type isolate for reference has not been preserved. An epitype was designated based on the similarity of morphological characters to that of the protologue to facilitate molecular examination and further studies.

Pseudocercospora platyceriicola C. Nakash., Y. Hatt, L. Suhaizan & I. Nurul Faziha, **sp. nov.** MycoBank MB 838202. Fig. 68A–D.

Etymology: Derived from the host genus, *Platycerium* sp.

Leaf spots amphigenous, subcircular to fusiform, water soaked, indefinite border, 3–18 mm diam, brown to reddish brown, scattered, later enlarged and confluent. *Caespituli* hypophyllous, punctiform, scattered, visible as blackish conidial masses. *Mycelium* internal and external. *Stromata* lacking or small, substomatal to intraepidermal, composed of a few dark brown cells, 10–20 µm diam, with dark brown external hyphae. *Conidiophores* emerging loosely from small stromata or solitary from external hyphae, straight to distinctly geniculate, subcylindrical, irregular in width, unbranched, smooth to rough, 2.5–45 × 2.5–3 µm, 0–3-septate, hyaline to dark brown, paler towards the apex. *Conidiogenous cells* integrated, terminal, proliferating sympodially or percurrently, with unthickened conidial loci, 2–2.5 µm diam. *Conidia* solitary, cylindrical to obclavate, straight to slightly curved, 25–50 × 2–2.5 µm, 2–6-septate, hyaline to pale blackish brown, smooth to rough, obconically truncated and unthickened at the base, 2–2.5 µm diam, rounded or acute at the apex.

Typus: **Malaysia**, Terengganu, Hulu Terengganu, Kenyir Lake, on *Platycerium* sp. (*Polypodiaceae*), 23 Jun. 2019, C. Nakashima, Y. Hattori, L. Suhaizan & I. Nurul Faziha (**holotype** UMT201939KL, **isotype** TSU-MUMH11881, culture ex-type TSU-MUCC2876).

Notes: *Pseudocercospora platyceriicola* differs from *Cercospora platycerii* (also on *Platycerium*), as the latter has hyaline, acicular conidia.

Pseudocercospora profusa (Syd. & P. Syd.) Deighton, *Trans. Brit. Mycol. Soc.* 88: 388. 1987.

Basionym: *Cercospora profusa* Syd. & P. Syd., *Ann. Mycol.* 7(2): 175. 1909.

Description and illustrations: Shin & Kim (2001), Crous *et al.* (2013a).

Typus: **Japan**, Tosa, Hoki-ga-mine, on *Acalypha australis* (*Euphorbiaceae*), 17 Oct. 1908, T. Yoshinaga (**lectotype** designated here S, hb. Sydow F37710, MBT 100005719). **South Korea**, Seoul, on *Acalypha australis*, 17 Sep. 2003, H.D. Shin (**epitype** designated here CBS H-20882, MBT 10005081, cultures ex-epitype CPC 10713–10715).

Additional materials examined: **Japan**, Tosa, Hoki-ga-mine, on *Acalypha australis* (*Euphorbiaceae*), 17 Oct. 1908, T. Yoshinaga (syntype NIAES C-267). **South Korea**, Wonju, on *Acalypha australis*, 18 Oct. 2002, H.D. Shin, CBS H-20881, culture CPC 10055.

Notes: Many specimens of this taxon are preserved in Japanese fungaria, although they are not linked to cultures. To facilitate molecular phylogenetic studies, an epitype was selected from South Korean specimens based on the similarity of morphological characters to the original description.

Pseudocercospora pruni-grayanae (Sawada) C. Nakash. & Motohashi., **comb. nov.** MycoBank MB 838210. Fig. 61AB, AC, 68E–H.

Basionym: *Phaeoisariopsis pruni-grayanae* Sawada, *Bull. Gov. Forest Exp. Sta. Meguro* 105: 113. 1958.

Leaf spots amphigenous, scattered, angular to irregular, enlarged and confluent, 3–8 mm, dark brown to brown. *Caespituli* amphigenous, mainly hypophyllous, scattered, visible as synnematus fascicles. *Mycelium* internal, pale brown. *Stromata* amphigenous, mainly hypophyllous, small, epidermal, erumpent, substomatal, brown to dark brown, 20–25 µm diam. *Conidiophores* densely fasciculate, synnematus to divergent, arising from the upper part of stromata, straight, divergent or geniculate at the upper part, cylindrical, unbranched, blackish brown to olivaceous brown, paler towards the apex, 50–120 × 3.5–5 µm, 1–4-septate, smooth to rough. *Conidiogenous cells* integrated, terminal, proliferating sympodially, with unthickened or rim-like and refractive loci, 2.5–3.8 µm diam. *Conidia* solitary, holoblastic, obclavate, 30–65 × 5–7.5 µm, 3–5-septate, hyaline, or pale brown at central part, smooth to rough, rounded to subacute at the apex, obconical truncate and unthickened or rim-like, not darkened, at the base, 2.5–3.5 µm diam.

Typus: **Japan**, Iwate, Morioka, Sakurayama, on *Padus grayana* (*Rosaceae*), 7 Sep. 1947, K. Sawada (**lectotype** designated here IUM-FS424, MBT 10005840); *ibid.*, Koma, on *Padus grayana*, 27 Aug. 1948, K. Sawada (**syntype** IUM-FS425); *ibid.*, 10 Sep. 2013, C. Nakashima & K. Motohashi (**epitype** designated here TSU-MUMH 11475, MBT 10005082, culture ex-epitype TSU-MUCC1715).

Notes: The lectotype specimen designated here is maintained in the IUM fungarium. The topotypic material with similar morphological characters, characterised by synnematus conidiophores and beak-like basal ends of conidia was selected as epitype for further molecular phylogenetic studies.

Pseudocercospora punctata (Wakef.) B. Sutton, *Mycol. Res.* 97: 125. 1993.

Basionym: *Septogloeum punctatum* Wakef., *Bull. Misc. Inf., Kew*: 204. 1931.

Description and illustrations: Crous (1999).

Typus: **South Africa**, Kwazulu-Natal Province, Durban, P.A. van der Bijl 323, on *Eugenia cordata* (= *Syzygium cordatum*) (*Myrtaceae*), 1922 (**holotype** in K, IMI 352712); Limpopo Province, Gundani, on living leaves of *Syzygium cordatum* 18 Dec. 2015, J. Roux (**epitype** designated here, CBS H-24919, MBT 10005841, culture ex-epitype CPC 39344).

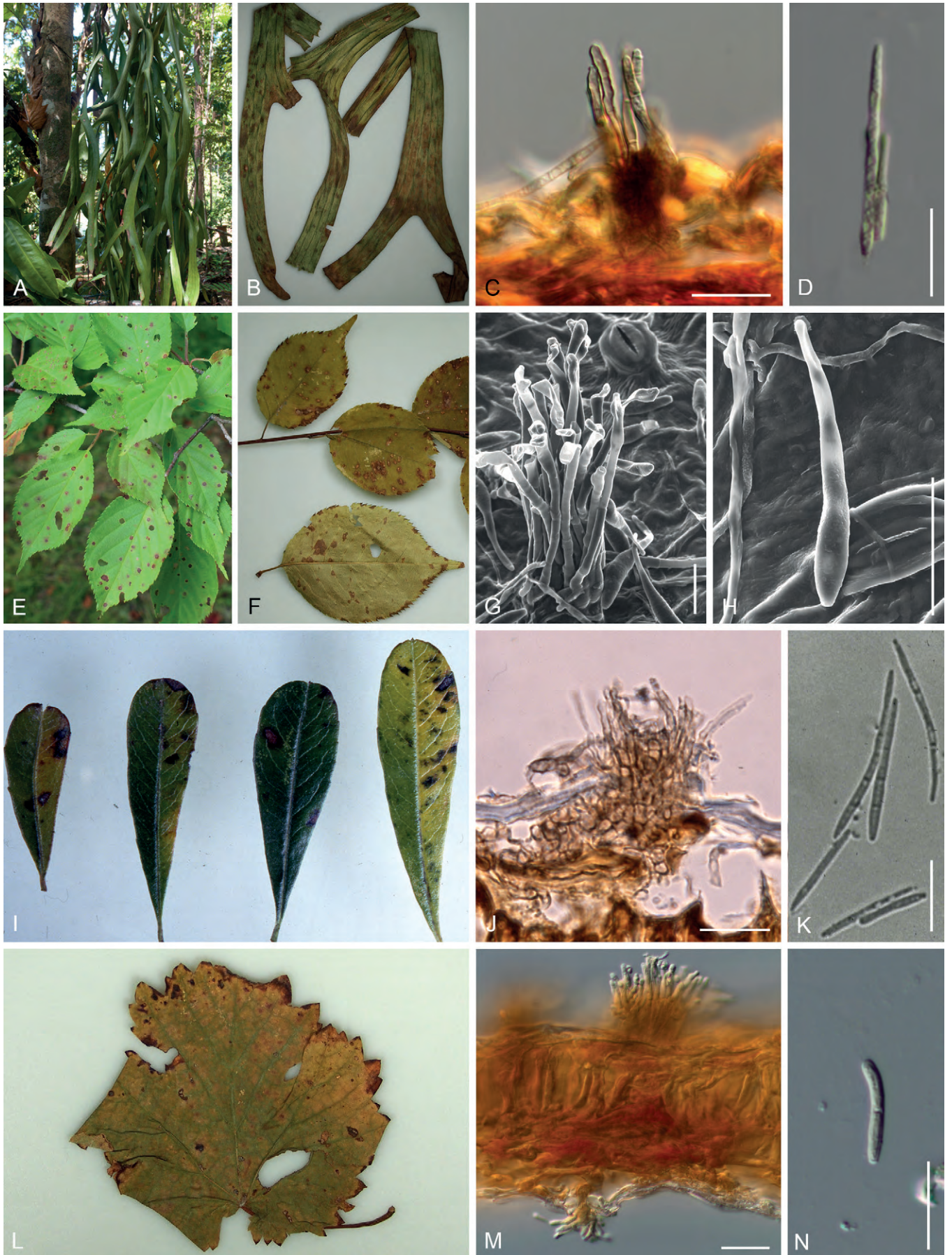


Fig. 68. *Pseudocercospora* spp. plate 5. **A–D.** *Pseudocercospora platycericola* (holotype UMT201939KL). **A.** Disease symptoms on *Platycerium* sp. **B.** Magnified symptoms. **C.** Stroma and conidiophores. **D.** Conidium. **E–H.** *Pseudocercospora pruni-grayanae* (epitype TSU-MUMH 11475). **E.** Disease symptoms on *Padus grayana*. **F.** Magnified symptoms. **G.** Conidiophores. **H.** Conidium. **I–K.** *Pseudocercospora pyracanthae* (epitype TSU-MUMH11941). **I.** Disease symptoms on *Pyracantha angustifolia*. **J.** Stroma and conidiophores. **K.** Conidia. **L–N.** *Pseudocercospora riachueli* var. *horiana* (epitype TSU-MUMH11544). **L.** Disease symptoms on *Vitis* sp. **M.** Stromata and conidiophores. **N.** Conidium. Scale bars = 20 µm.

Additional materials examined: Madagascar, on *Syzygium* sp., 25 Oct. 2007, P.W. Crous, cultures CPC 14734 = CBS 132116, CPC 14737, CPC 14740. **South Africa** near Mozambique border, *Syzygium cordatum*, 19 Oct. 2020, M.J. Wingfield, HPC 3498, culture CPC 40081; Kwazulu-Natal Province, on *Syzygium cordatum*, M.J. Wingfield, culture CBS 113315.

Note: The epitype was selected based on the similarity of morphological characters to those of the holotype specimen (Crous 1999). *Pseudocercospora punctata* is a common foliar pathogen on leaves of *Syzygium cordatum* in South Africa.

Pseudocercospora pyracanthae (Katsuki) C. Nakash. & Tak. Kobay., Ann. Phytopathol. Soc. Japan 63: 313, 1997. Fig. 68I–K.

Basionym: *Cercospora pyracanthae* Katsuki [as '*pyracanthae*'], Bull. Agric. Impr. Sect. Econ. Dept. Fukuoka Prefecture Japan 1: 19. 1949.

Description: Nakashima & Kobayashi (1997).

Typus: Japan, Fukuoka, Kurume, on *Pyracantha angustifolia* (Rosaceae), 6 Nov. 1947, S. Katsuki (**holotype** TNS-F-243829); Ibaraki, Tsukuba, Nov. 1994, T. Nishijima (**epitype** designated here TSU-MUMH11941, MBT 10005083, culture ex-epitype MAFF 237140).

Additional materials examined: Japan, Chiba, Sanmu, Oct., on *Pyracantha angustifolia*, 1976, E. Ishizawa, TFM: FPH-4432; Okayama, Okayama, on *Pyracantha angustifolia*, 20 Nov. 1960, H. Tanaka, TFM: FPH-3247; Ibaraki, Tsukuba, on *Pyracantha angustifolia*, 15 Apr. 1995, T. Kobayashi & C. Nakashima, TSU-MUMH CNS446, culture TSU-MUCC892; Kumamoto, on *Pyracantha crenulata*, 1973, T. Kobayashi, culture MAFF 410022.

Notes: Many specimens of *Ps. pyracanthae* are maintained in fungaria in Japan. The epitype was selected based on the similarity of morphological characters to that of the examined holotype specimen.

Pseudocercospora riachueli* var. *horiana (Togashi & Katsuki) U. Braun & Crous, *Mycosphaerella* and its anamorphs: 1. Names published in *Cercospora* and *Passalora*: 354. 2003. Fig. 68L–N.

Basionym: *Cercospora horiana* Togashi & Katsuki, Sci. Rep. Yokohama Natl. Univ., Sect. 2 1: 4. 1952.

Caespituli amphigenous. **Mycelium** internal, pale brown. **Stromata** small to developed, amphigenous, substomatal, epidermal, erumpent, 15–43 µm diam, brown, without superficial hyphae. **Conidiophores** dense, emerging from the upper part of stromata, simple, straight, cylindrical, short, 10–28 × 2–2.5 µm, 0–1-septate, pale brown, paler towards apex, smooth. **Conidiogenous cells** integrated, terminal, proliferating percurrently, rounded at the apex, with unthickened loci, 2 µm diam. **Conidia** solitary, holoblastic, cylindrical to obclavate, 22–30 × 2.5 µm, 0–2-septate, hyaline or pale brown, smooth, subacute to rounded at the apex, truncated and unthickened at the base, not darkened, 2 µm diam.

Typus: Japan, Tokyo, Minamitama, Nanao, on *Parthenocissus tricuspidata* (Vitaceae), 7 Oct. 1951, E. Kurosawa (**holotype** TNS-F 243957); Mie, Tsu, on *Vitis* sp., 27 Aug. 2016, C. Nakashima (**epitype** designated here TSU-MUMH11544, MBT 10005084, culture ex-epitype MUCC2141).

Notes: Although the host plant of the holotype is *Parthenocissus tricuspidata* (Vitaceae), the morphological characters of the specimen on *Vitis*, the host plant of the epitype designated in this study, are identical.

Pseudocercospora stemnicola C. Nakash., Y. Hatt., L. Suhaizan & I. Nurul Faziha, **sp. nov.** MycoBank MB 838203. Fig. 69A–C.

Etymology: Derived from the host genus, *Stemona*.

Leaf spots amphigenous, angular, vein limited, distinct, greyish brown to brown, surrounded by blackish brown border, later enlarged and confluent, 3–15 mm diam, often holed. **Caespituli** amphigenous. **Mycelium** internal. **Stromata** epidermal, substomatal, erumpent, subglobose, 25–73 µm diam. **Conidiophores** emerging from upper part of stromata, unbranched, straight to sinuous-geniculate, cylindrical, irregular in width, unbranched, smooth to rough, conically truncated at the apex, 12–40 × 2.5–5 µm, 0–2-septate, blackish brown, paler towards the apex. **Conidiogenous cells** integrated, terminal, terminal, proliferating sympodially or percurrently, with unthickened conidial loci, 2 µm diam. **Conidia** solitary, holoblastic, acicular, cylindrical, or obclavate, straight to curved, subhyaline, smooth to rough, 20–75 × 2–2.5 µm, 1–6-septate, obconically truncated and unthickened at the base, 2–2.5 µm diam, acute at the apex.

Typus: Malaysia, Terengganu, Hulu Terengganu, Kenyir Lake, on *Stemona tuberosa* (Stemonaceae), 23 Jun. 2019, C. Nakashima, Y. Hattori, L. Suhaizan & I. Nurul Faziha (**holotype** UMT201923KL, **isotype** TSU-MUMH11879, culture ex-type MUCC2874).

Notes: *Pseudocercospora stemonae*, which also occurs on this host (Braun 2001b), is distinct in having larger and olivaceous brown conidia (60–150 × 3–3.5 µm, 5–14-septate).

Pseudocercospora symploci Katsuki & Tak. Kobay. ex U. Braun & Crous, *Mycosphaerella* and its anamorphs: 1. Names published in *Cercospora* and *Passalora*: 394. 2003. Fig. 69D, E.

Leaf spots subcircular to irregular, 5–20 mm diam, on the upper leaf surface, at first a purplish brown speck, later frequently extending to the edge of the leaf, becoming tan to dark brown with a purplish margin, on the hypophyllous surface greyish brown (*vide* Katsuki & Kobayashi 1975). **Caespituli** amphigenous. **Mycelium** internal. **Stromata** amphigenous, small to well-developed, epidermal, erumpent, brown to pale brown, 20–75 µm diam. **Conidiophores** short, dense, arising from the upper part of stromata, straight to mildly geniculate, cylindrical, unbranched, hyaline or pale brown, paler towards the apex, 5–15 × 2–2.5 µm, 0–1-septate, smooth. **Conidiogenous cells** integrated, terminal, proliferating sympodially or percurrently, with unthickened and truncated conidial loci at the apex, 2–2.5 µm diam. **Conidia** solitary, holoblastic, long obclavate to acicular, 38–70 × 2.5–3 µm, 4–8-septate, hyaline, or pale olivaceous brown, smooth to rough, subacute at the apex, truncate and unthickened at the base, 2–2.5 µm diam.

Typus: Taiwan Island, Hsinchu, on *Symplocos crataegoides* var. *chinensis* (Symplocaceae), 27 Apr. 1930, K. Sawada (**lectotype** designated here NTU-PPE, hb. Sawada, MBT 10005897, **isotype** TNS-F220525); Taichung, Chisui, on *Symplocos crataegoides* var. *chinensis*, 25 Jul. 1931, K. Sawada (**syntype**); Taichung City, Heping Dist., Mt. Dashueshan, on *Symplocos paniculata*, 9 Oct. 2014, C. Nakashima, K. Motohashi, Y. Hattori & C.Y. Chen (**epitype** designated here NCHUPP 3352, MBT 10005085, culture ex-epitype NCHUPP L1685 = CBS 142471).

Notes: In this study, a lectotype was selected from syntype specimens. The morphological characteristics of the isotype (TNS-F220525) were examined. The chosen epitype specimen (NCHUPP 3352) is morphologically similar to the isotype.

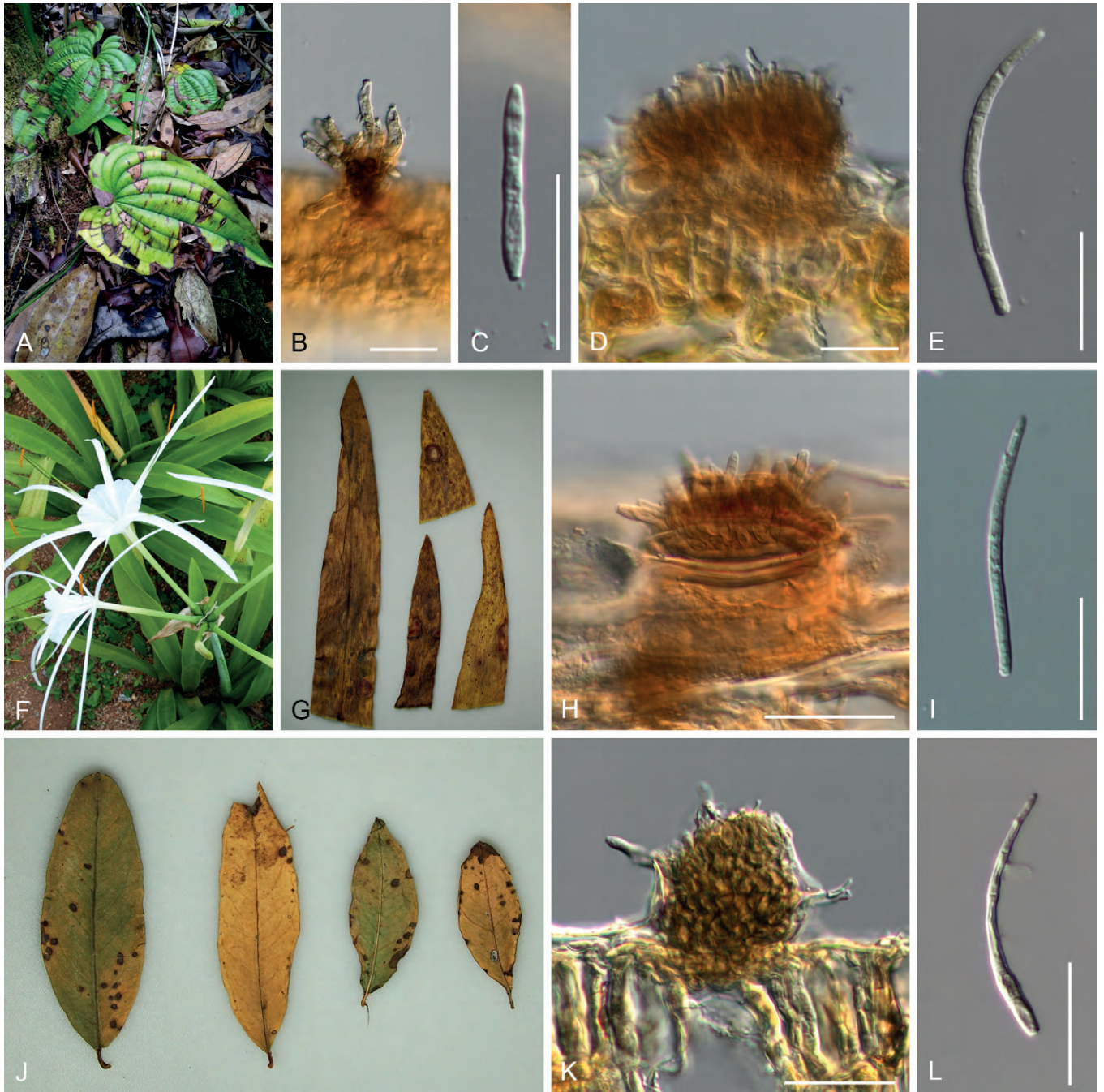


Fig. 69. *Pseudocercospora* spp. plate 6. **A–C.** *Pseudocercospora stemonicola* (holotype UMT201923KL). **A.** Disease symptoms on *Stemona tuberosa*. **B.** Stroma and conidiophores. **C.** Conidium. **D, E.** *Pseudocercospora symploci* (epitype NCHUPP3352). **D.** Stroma and conidiophores on *Symplocos paniculata*. **E.** Conidium. **F–I.** *Pseudocercospora terengganuensis* (holotype UMT201909). **F, G.** Disease symptoms on *Hymenocallis speciosa*. **H.** Stroma and conidiophores. **I.** Conidium. **J–L.** *Pseudocercospora xenopunicae* (holotype CBS H-24675). **J.** Disease symptoms on *Punica granatum*. **K.** Stroma and conidiophores. **L.** Conidium. Scale bars = 20 µm.

Pseudocercospora tabernaemontanae (Syd. & P. Syd.) Deighton, Mycol. Pap. 140: 154. 1976.

Basionym: *Cercospora tabernaemontanae* Syd. & P. Syd., Philipp. J. Sci., C, 8(5): 507. 1913.

Description and illustrations: Hsieh & Goh (1990).

Typus: Laos, Vientiane Capital, Xaythany District, Xay Village, on *Tabernaemontana coronaria* (Apocynaceae), 25 Jul. 2006, P. Phengsintham (epitype designated here HAL P107, MBT 10005086, culture ex-epitype CPC 19198). **Philippines**, Los Banos, P.I., on *Tabernaemontana pandacaqui*, 20 Apr. 1913, M.B. Raimundo (holotype S F37811).

Notes: The holotype material has not been examined, but the present collection from Laos is a good fit for the species (Phengsintham *et al.* 2010).

Pseudocercospora terengganuensis C. Nakash., Y. Hatt., L. Suhaizan & I. Nurul Faziha, *sp. nov.* MycoBank MB 838267. Fig. 69F–I.

Etymology: Derived from the collection site in Malaysia.

Leaf spots amphigenous, circular to subcircular, 3–10 mm diam, brown, reddish brown at centre, blackish brown, with definite border. *Caespituli* amphigenous, punctiform, scattered. *Mycelium* internal

and external; internal hyphae hyaline to pale brown, external hyphae brown to reddish brown. *Stromata* amphigenous, substomatal to epidermal, erumpent, 35–50 µm diam, brown to reddish brown, with superficial hyphae. *Conidiophores* dense, emerging from upper part of stromata, or solitary from superficial hyphae, short, straight to geniculate-sinuous, cylindrical, unbranched, 2.5–30 × 2.5–3 µm, 0–1-septate, pale brown, paler towards the apex, smooth. *Conidiogenous cells* integrated, terminal, proliferating percurrently, rarely sympodially, with conically truncate and unthickened conidial loci. *Conidia* solitary, acicular to narrowly obclavate, 26–75 × 2–2.5 µm, 3–7-septate, hyaline or pale coloured, smooth, acute to rounded at the apex, truncate and unthickened at the base, not darkened, 2–2.5 µm wide.

Typus: **Malaysia**, Terengganu, University of Malaysia Terengganu, on *Hymenocallis speciosa* (*Amaryllidaceae*), 22 Jun. 2019, C. Nakashima, Y. Hattori, L. Suhaizan, & I. Nurul Faziha (**holotype** UMT201909, **isotype** TSU-MUMH11876, culture ex-type TSU-MUCC 2871).

Notes: *Pseudocercospora pancratii* is also known on *Hymenocallis*, and has been reported from Middle and North America, India, Japan, Kenya and Myanmar (see *Ps. pancratii*). Morphologically, *Ps. terengganunensis* is distinct in having hyaline to very pale coloured conidia that form on stromata and superficial hyphae, and somewhat smaller stromata with superficial hyphae. Moreover, their phylogenetic relationships indicate that these are two different species on the same host plant.

Pseudocercospora togashiana (K. Ito & Tak. Kobay.) C. Nakash. & Tak. Kobay., **comb. nov.** MycoBank MB 838225.

Basionym: *Mycosphaerella togashiana* K. Ito & Tak. Kobay. Bull. Gov. Forest Exp. Sta.: 23. 1953.

Typus: **Japan**, Tokyo, Meguro, Forest Experimental Station, on *Populus simonii* (*Salicaceae*), 24 Jul. 1951, T. Kobayashi (**holotype** of *Mycosphaerella togashiana* TFM: FPH 3703, culture ex-type MAFF410006, **isotype** TFM: FPH-3563).

Additional materials examined: **Japan**, Tokyo, Meguro, Forest Experimental Station, on *Populus alba*, 20 Oct. 1948, K. Ito, TFM: FPH-38; Tokyo, Meguro, Forest Experimental Station, on *Populus maximowiczii* (= *Populus suaveolens*), 19 Oct. 1948, K. Ito, TFM: FPH-36; Tokyo, Meguro, Forest Experimental Station, on *Populus monilifera* (= *Populus deltoides* subsp. *monilifera*), 19 Oct. 1948, K. Ito, TFM: FPH-37; *ibid.*, 15 Sep. 1950, T. Kobayashi, TFM: FPH-166.

Illustrations: Ito & Kobayashi (1953).

Notes: Eleven “mycosphaerella-like” species have been described from *Populus* and *Salix*. However, the relationships of asexual and sexual morphs remain unclear, except for *M. togashiana*, and its *Pseudocercospora* asexual morph. In this study, we propose the new combination in *Pseudocercospora* based on *M. togashiana* (Deighton 1976).

Pseudocercospora trinidadensis (F. Stevens & Solheim) Crous *et al.*, Mycotaxon 72: 179. 1999.

Basionym: *Cercospora trinidadensis* F. Stevens & Solheim, Mycologia 23(5): 376. 1931.

Description and illustrations: Crous *et al.* (1999), Silva *et al.* (2016).

Typus: **Brazil**, Rio de Janeiro, Nova Friburgo, Fazenda Barreto II, on *Croton urucurana*, 1 Jun. 2014, R.W. Barreto (**epitype** designated here VIC 42851,

MBT 10005842, culture ex-epitype COAD 1756 = CPC 26082). **Trinidad and Tobago**, St. Augustine, Trinidad, on *Croton gossypifolius* (*Euphorbiaceae*), 13 Aug. 1922, F.L. Stevens (No.839) (**holotype** BPI 442019).

Notes: Crous *et al.* (1999) recognised the present species as separate from *Cercospora tigllii*, and proposed a new combination under the genus *Pseudocercospora*. The specimen examined by Silva *et al.* (2016) is selected as the epitype based on the similarity of morphological characters to the holotype specimen.

Pseudocercospora xenopunicae Crous & C. Nakash., **sp. nov.** MycoBank MB838652. Fig. 69J–L.

Etymology: Derived from the host genus, *Punica*, with prefix “xeno-”.

Leaf spots amphigenous, circular to subcircular, 2–3 mm diam, dark brown, pale brown at the centre. *Caespituli* amphigenous. *Mycelium* internal and external, hyaline to pale olivaceous brown. *Stromata* amphigenous, substomatal to epidermal, erumpent, submerged, globose, olivaceous brown to brown, 12.5–42 µm diam, with superficial hyphae. *Conidiophores* dense, emerging from upper part of stromata, or solitary from superficial hyphae, straight to sinuous-geniculate, cylindrical, unbranched, 2.5–30 × 2–2.5 µm, 0–2-septate, pale brown, paler towards the apex, smooth, conically truncated at the apex. *Conidiogenous cells* integrated, terminal, proliferating sympodially, with truncated and unthickened conidial loci, 2–2.5 µm. *Conidia* solitary, cylindrical to obclavate, straight to curved, 25–55 × 2–2.5 µm, 1–4-septate, hyaline to olivaceous brown, smooth, acute at the apex, obconical truncated and unthickened at the base, not darkened, 2–2.5 µm diam.

Typus: **South Africa**, Limpopo Province, Westfalia, Tzaneen, on *Punica granatum* (*Lythraceae*), 8 Jul. 2011, P.W. Crous (**holotype** CBS H-24675, culture ex-type CBS 147384 = CPC 19712).

Notes: *Pseudocercospora punicae* is a well-known species on *Punica*. *Pseudocercospora xenopunicae* is distinct in that it has amphigenous caespituli, superficial hyphae with branching conidiophores, and narrower conidia than that of *Ps. punicae*. Moreover, the phylogenetic position of *Ps. xenopunicae* is quite removed from that of *Ps. punicae*. According to the USDA Fungal Databases (Farr & Rossman 2022), *Ps. punicae* has been reported worldwide from 45 countries. More detailed studies using phylogeny and morphology will be required to elucidate the species diversity of *Pseudocercospora* on *Punica*.

Genome sequenced strain: *Pseudocercospora vitis*. **Japan**, Mie, Iga, on *Vitis vinifera*, 31 Jul. 2017, H. Kondo, culture HUCC 2361. This Whole Genome Shotgun project has been deposited at GenBank under the accession JALRML000000000 (BioProject: PRJNA827019, BioSample: SAMN27594420; present study)

Authors: C. Nakashima, M. Bakhshi, R. Cheewangkoon, L. Suhaizan, I. Nurul Faziha, J.Z. Groenewald & P.W. Crous

Pteridopassalora C. Nakash. & Crous, **gen. nov.** MycoBank MB 841508.

Etymology: Derived from *Passalora* and *pteridophyte*.

Classification: *Dothideomycetes*, *Dothideomycetidae*, *Mycosphaerellales*, *Mycosphaerellaceae*.

Stromata small to well-developed. *Conidiophores* emerging from stromata or superficial hyphae, cylindrical, smooth to rough. *Conidiogenous cells* integrated to terminal on conidiophore, with unthickened or slightly thickened loci. *Conidia* solitary, variable in shape, cylindrical, filamentous to narrowly-obclavate, multi-septate, truncate and unthickened hilum at the base. *Sexual morph* not observed.

Cultural characteristics: Colonies growing slowly; on PDA surface smoke grey with patches of grey olivaceous, iron grey in reverse; on MEA pale olivaceous grey (surface), iron grey in reverse; on OA olivaceous grey with patches of pale olivaceous grey.

Type species: *Pteridopassalora nephrolepidicola* (Crous & R.G. Shivas) C. Nakash. & Crous. Holotype and ex-type culture: CBS H-20492, CBS 128211 = CPC 17049, CPC 17050.

DNA barcodes (genus): LSU and *rpb2*.

DNA barcodes (species): LSU, ITS and *rpb2*. Table 17. Fig. 70.

Optimal media and cultivation conditions: on CMA, sporulation of the asexual morph as *in situ* are observed (Kirschner & Wang 2015).

Distribution: Australia, mainland China and Taiwan Island.

Hosts: Known only from the pteridophytes, *Nephrolepis falcata* and *Lygodium japonicum*.

Disease symptoms: Leaf spots and leaf blight.

Notes: The unthickened or slightly thickened conidiogenous loci of *Pteridopassalora* are also seen in *Passalora s. lat.* and *Pseudocercospora*. The unresolved taxonomic position of the basionym *Pseudocercospora nephrolepidicola* has been discussed before (Kirschner & Wang 2015, Nakashima *et al.* 2016). Phylogenetic analysis using the combined matrix composed of LSU+ITS+*RPB2* regions, which are barcodes for *Passalora s. lat.* (Vieira *et al.* 2017), showed *Pseudocercospora nephrolepidicola* warranted transfer to a new genus, *Pteridopassalora*. Many species of *Passalora* and *Pseudocercospora* that have been reported on ferns in recent years (Crous *et al.* 2010, Braun *et al.* 2013, Kirschner & Liu 2014, Kirschner & Wang 2015, Guatimosim *et al.* 2016, Nakashima *et al.* 2016), have morphological characteristics that resembling those of *Pteridopassalora*. Further studies are required to clarify their molecular phylogeny.

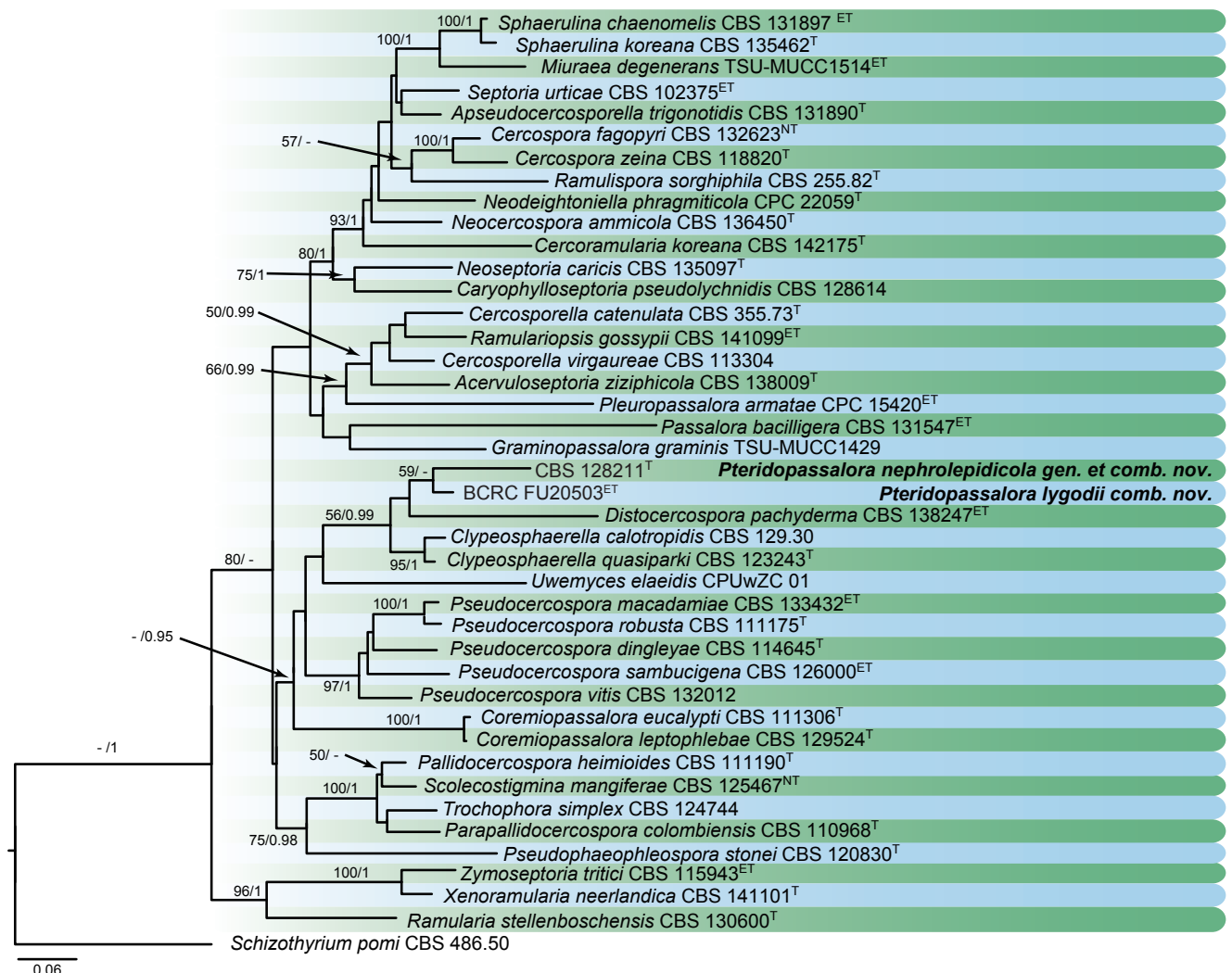


Fig. 70. Maximum Likelihood (ML) phylogram constructed from LSU (750 bp), ITS (583 bp), and *rpb2* (766 bp) sequences of *Pteridopassalora* spp. within *Passalora s. lat.* Maximum Likelihood bootstrap support values (> 50 %) and Bayesian posterior probability scores (> 0.95) are shown at the nodes. The novel taxa are printed in **bold**. The phylogenetic tree was rooted to *Schizothyrium pomi* CBS 486.50. GenBank accession numbers are indicated in Table 17. ^T and ^{NT} indicate ex-type, ex-epitype, and ex-neotype strains, respectively. TreeBASE: S28912.

Table 17. DNA barcodes of accepted *Pteridopassalora* spp.

Species	Isolates ¹	GenBank accession numbers ²			References
		LSU	ITS	<i>rpb2</i>	
<i>Pteridopassalora lygodii</i>	BCRC FU30503 ^{ET}	—	KR527201	—	Kirschner & Wang (2015)
<i>Pt. nephrolepidicola</i>	CBS 128211 = CPC 17049 ^T	HQ599591	HQ599590	KX462646	Crous <i>et al.</i> (2010), Nakashima <i>et al.</i> (2016)

¹ BCRC: Bioresource Collection and Research Center, Food Industry Research and Development Institute, Hsinchu, Taiwan; CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CPC: Culture collection of Pedro Crous, housed at CBS. ^T and ^{ET} indicate ex-type and ex-epitype strains, respectively.

² LSU: partial 28S large subunit nrRNA gene; ITS: internal transcribed spacers and intervening 5.8S nrDNA; *rpb2*: partial RNA polymerase II second largest subunit gene.

References: Crous *et al.* 1998 (morphology); Kirschner & Wang 2015 (morphology); Nakashima *et al.* 2016 (phylogeny); Videira *et al.* 2017 (phylogeny and DNA barcodes).

Pteridopassalora nephrolepidicola (Crous & R.G. Shivas) C. Nakash. & Crous, **comb. nov.** MycoBank MB 841683.

Basionym: *Pseudocercospora nephrolepidicola* Crous & R.G. Shivas, *Persoonia* 25: 139. 2010.

Description and illustrations: Crous *et al.* (2010a).

Typus: **Australia**, Queensland, Brisbane Botanical Garden, on fronds of *Nephrolepis falcata* (*Nephrolepidaceae*), 14 Jul. 2009, P.W. Crous & R.G. Shivas (**holotype** CBS H-20492, cultures ex-type CBS 128211 = CPC 17049, CPC 17050).

Pteridopassalora lygodii (Goh & W.H. Hsieh) C. Nakash. & Crous, **comb. nov.** MycoBank MB 841767.

Basionym: *Pseudocercospora lygodii* Goh & W.H. Hsieh, *Trans. Mycol. Soc. Rep. China* 2 (2): 131. 1987.

Description and illustrations: Kirschner & Wang (2015).

Typus: **Taiwan Island**, Hsinchu County, Hsinpu, on pinnules of *Lygoium japonicum* (*Lygoiaceae*), 2 May 1920, E. Kurosawa (**holotype** PPMH); Taipei City, Tianmu Trail, on pinnules of *Lygoium japonicum*, 4 Apr. 2015 (**epitype** designated here TNM R. Kirschner 4182, MBT 10003650, culture ex-epitype BCRC FU30503).

Notes: An epitype collected on the same host from Taiwan island is proposed based on morphological similarity to that of the holotype.

Authors: C. Nakashima & P.W. Crous

Zymoseptoria Quaedvlieg & Crous, *Persoonia* 26: 64. 2011. Fig 71.

Classification: *Dothideomycetes*, *Dothideomycetidae*, *Mycosphaerellales*, *Mycosphaerellaceae*.

Type species: *Zymoseptoria tritici* (Desm.) Quaedvlieg & Crous, *basionym:* *Septoria tritici* Desm., *Ann. Sci. Nat., Bot., sér. 2*, 17: 107. 1842. *Holotype:* France, on *Triticum* sp., PC. *Epitype* and *ex-type* strain designated by Quaedvlieg *et al.* (2011); CBS H-20545, CBS 115943 = IPO 323.

DNA barcodes (genus): ITS, LSU.

DNA barcodes (species): *rpb2*, *tef1*. Table 18. Fig. 72.

Ascomata pseudothecial, globose, subepidermal, substomatal, brown, produced in older pale grey lesions; pseudothecia with central periphysate ostiole; wall of 2–3 layers of brown *textura angularis*. *Hamathecium* tissues absent. *Asci* stipitate, bitunicate, hyaline, smooth, obovoid to fusoid-ellipsoid, 8-spored, with apical chamber. *Ascospores* multiseriate, hyaline, smooth, fusoid-ellipsoid, medianly 1-septate, with bipolar, heterothallic mating

Table 18. DNA barcodes of accepted *Zymoseptoria* spp.

Species	Isolates ¹	GenBank accession numbers ²				References
		ITS	LSU	<i>tef1</i>	<i>rpb2</i>	
<i>Zymoseptoria ardabiliae</i>	CBS 130977 ^T	JQ739806	JQ739846	JQ739790	JN982483	Quaedvlieg <i>et al.</i> (2011), Stukenbrock <i>et al.</i> (2012)
<i>Z. brevis</i>	CBS 128853 ^T	JF700867	JQ739833	JQ739777	JF700799	Quaedvlieg <i>et al.</i> (2011), Stukenbrock <i>et al.</i> (2012)
<i>Z. crescenta</i>	CBS 144410 ^T	MH259304	MH267287	MH271694	MH271695	Crous <i>et al.</i> (2018c)
<i>Z. halophila</i>	CBS 128854 ^T	JF700876	JQ739842	JQ739786	JF700808	Quaedvlieg <i>et al.</i> (2011), Stukenbrock <i>et al.</i> (2012)
<i>Z. passerinii</i>	CBS 120382 ^{ET}	JF700877	JQ739843	JQ739787	JF700809	Quaedvlieg <i>et al.</i> (2011), Stukenbrock <i>et al.</i> (2012)
<i>Z. pseudotritici</i>	CBS 130976 ^T	JN982480	JQ739828	JQ739772	JN982482	Quaedvlieg <i>et al.</i> (2011), Stukenbrock <i>et al.</i> (2012)
<i>Z. tritici</i>	CBS 115943 ^{ET}	AF181692	GU214436	—	KX348112	Stukenbrock <i>et al.</i> (2012), Videira <i>et al.</i> (2016)
<i>Z. verkleyi</i>	CBS 133618 ^T	KC005781	KC005802	—	—	Crous <i>et al.</i> (2012a)

¹ CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands. ^T and ^{ET} indicate ex-type and ex-epitype strains, respectively.

² ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial 28S large subunit nrRNA gene; *tef1*: partial translation elongation factor 1- α gene; *rpb2*: partial RNA polymerase II second largest subunit gene.

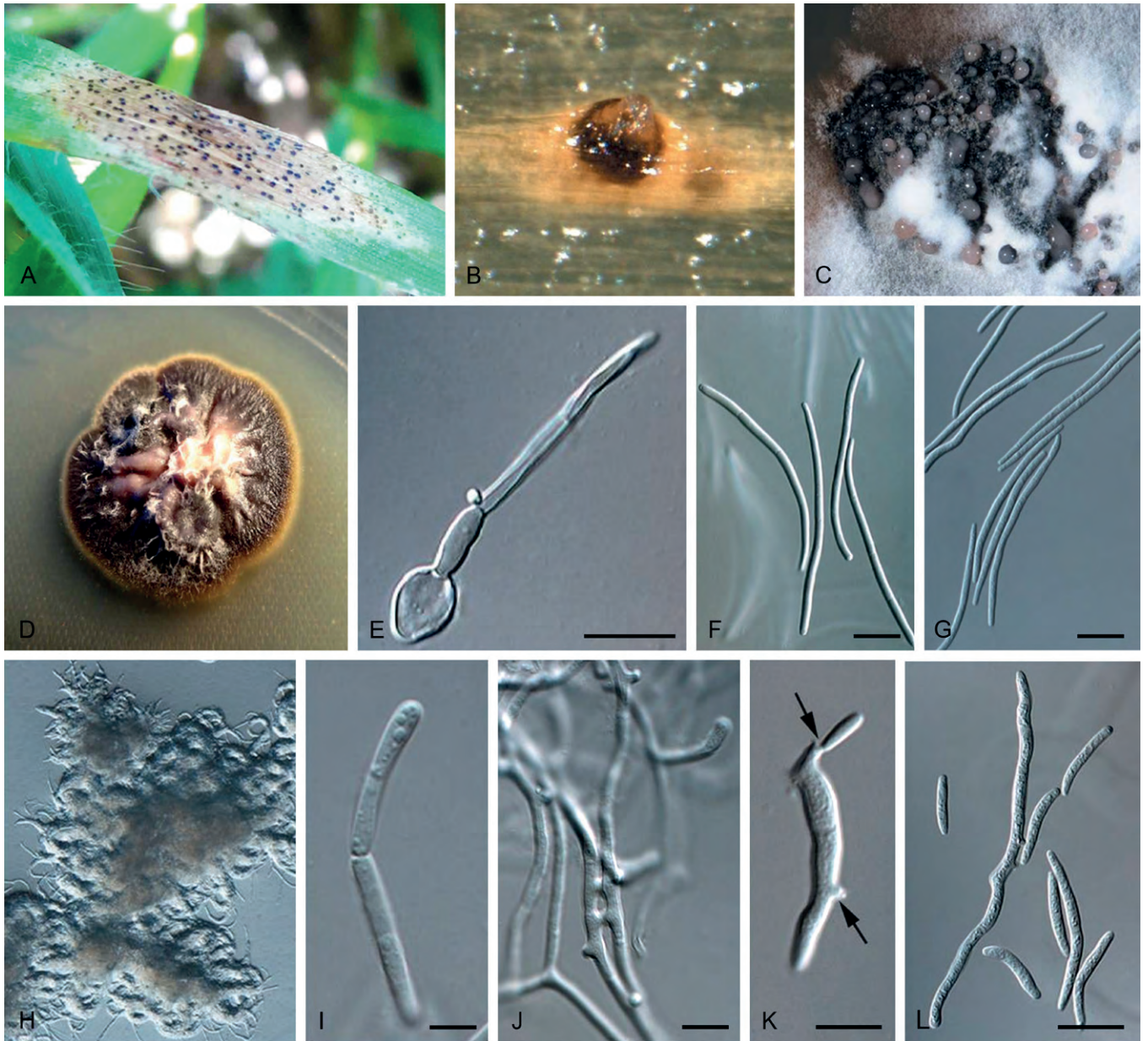


Fig. 71. *Zymoseptoria* spp. **A, B.** Disease symptoms. **A.** *Zymoseptoria crescent* (ex-type CBS 144410) on living leaves of *Aegilops triuncialis*. **B.** *Zymoseptoria brevis* (ex-type CBS 128853) forming a pycnidium on leaves of *Hordeum vulgare*. **C, D.** Colony sporulation on PDA. **C.** *Zymoseptoria brevis* (ex-type CBS 128853) colony with yeast-like growth on synthetic nutrient-poor agar. **D.** *Zymoseptoria crescenta* (ex-type CBS 144410) colony with yeast-like growth on synthetic nutrient-poor agar. **E.** Conidiogenous cell of *Zymoseptoria passerinii* (ex-epitype CBS 120382) formed inside pycnidium. **F, G.** Conidia (Type I). **F.** *Zymoseptoria tritici* (ex-epitype CBS 115943). **G.** *Zymoseptoria halophila* (ex-type CBS 128854). **H.** *Zymoseptoria halophila* (ex-type CBS 128854) colony with yeast-like growth on synthetic nutrient-poor agar. **I, J.** Conidia (Type II) of *Zymoseptoria halophila* (ex-type CBS 128854) formed as phragmospores in aerial hyphae. **K, L.** Conidia (Type III). **K.** *Zymoseptoria brevis* (ex-type CBS 128853) formed via microcyclic conidiation (arrows indicate Type III). **L.** *Zymoseptoria tritici* (ex-epitype CBS 115943). Scale bars = 10 µm. Pictures A, D taken from Crous *et al.* (2018c); B, C, E–L from Quaedvlieg *et al.* (2011).

system. *Conidiomata* pycnidial, dark brown to black, semi-immersed to erumpent, subglobose, with an ostiole. *Conidiomata* wall multi-layer, comprised of *textura angularis*. *Conidiophores* smooth, hyaline, septate, or reduced to conidiogenous cells. *Conidiogenous cells* aggregated, subcylindrical, ampulliform to doliiform, phialidic with periclinal thickening, or inconspicuous, percurrent proliferation at apex. *Hilum* not thickened nor darkened. *Type I conidia* hyaline, solitary, guttulate, smooth, cylindrical to subulate, tapering towards rounded apex with rounded to truncate base. *Type II conidia* disarticulate from aerial hyphae into phragmospores via microcyclic conidiation. *Type III conidia* microcyclic conidiation with yeast-like growth. *Sexual morph* unknown (adapted from Quaedvlieg *et al.* 2011, Stukenbrock *et al.* 2012).

Cultural characteristics: Colonies on PDA flat, with moderate aerial mycelium, surface pale olivaceous grey to olivaceous grey, iron grey from reverse. Colonies on MEA erumpent, with less mycelium, surface iron grey with patches or without patches, greenish black to black from reverse. Colonies on OA filamentous, with sparse aerial mycelium, somewhat erumpent, with patches.

Optimal media and cultivation conditions: OA, PDA or SNA at 25 °C under nuv-light to induce sporulation.

Distribution: Worldwide.

Hosts: Pathogens or saprobes on a variety of grass hosts including *Aegilops triuncialis*, *Dactylis* sp., *Elymus* sp., *Hordeum vulgare*,

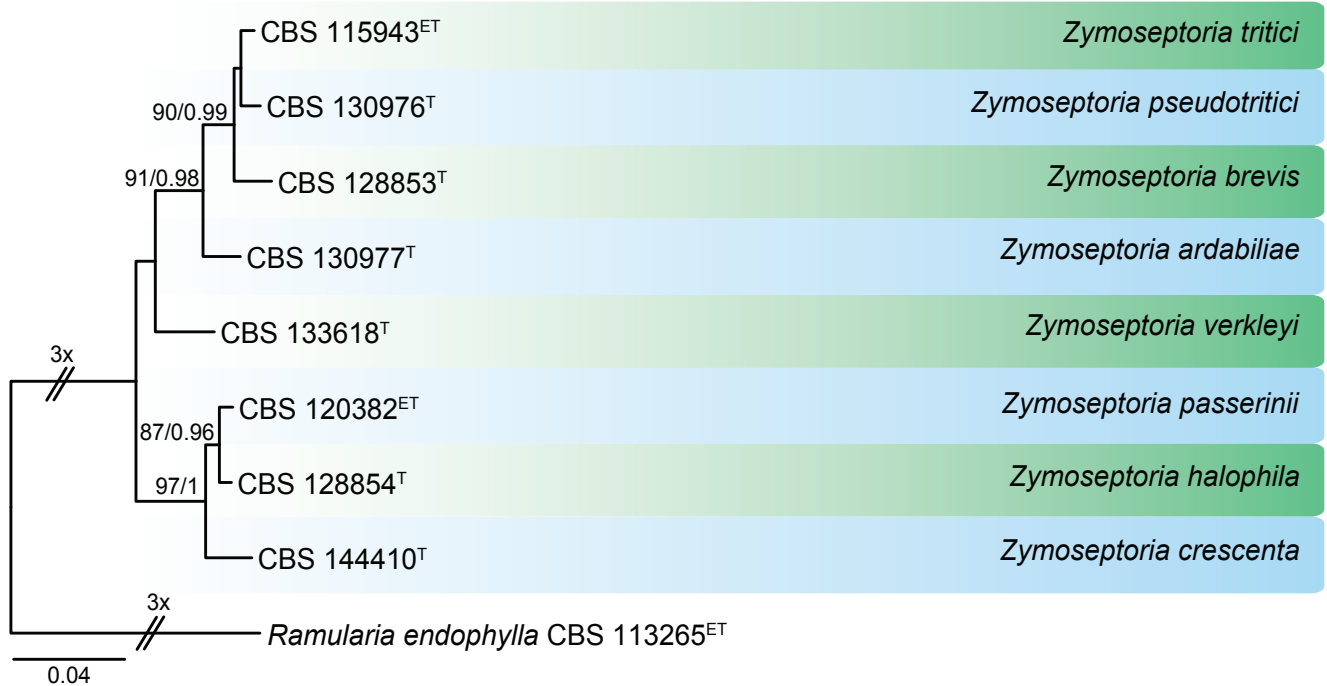


Fig. 72. RAxML phylogram constructed from ITS (471 bp), LSU (728 bp), *tef1* (270 bp) and *rpb2* (293) sequences of all accepted species of *Zymoseptoria*. Maximum likelihood bootstrap support values (> 70 %) and Bayesian posterior probability scores (> 0.95) are indicated on the branches. The phylogenetic tree was rooted to *Ramularia endophylla* CBS 113265. GenBank accession numbers are indicated in Table 18. ^T and ^{ET} indicate ex-type and ex-epitype strains, respectively. TreeBASE: S26192.

Lolium sp., *Poa annua* and *Triticum eastivum* (*Poaceae*).

Disease symptoms: Leaf spots or leaf blotch.

Notes: *Zymoseptoria* was introduced by Quaedvlieg *et al.* (2011) to accommodate septoria-like species pathogenic to grass hosts. Species of *Zymoseptoria* mostly have phialides with periclinal thickening, or percurrent proliferation at the apex of conidiogenous cells. Presently, this genus contains eight accepted species, which exhibit a yeast-like growth on artificial media and produces up to three types of conidia (Type I, pycnidial conidia; Type II, phragmospores on aerial hyphae; Type III, yeast-like growth proliferating via microcyclic conidiation) typical for the genus (Quaedvlieg *et al.* 2011, Stukenbrock *et al.* 2012).

References: Quaedvlieg *et al.* 2011, Stukenbrock *et al.* 2012, Crous *et al.* 2012a, 2018c (morphology and phylogeny).

Genome sequenced strain: *Zymoseptoria crescenta*. Iran, East Azarbaijan Province, Kaleybar, on living leaves of *Aegilops triuncialis*, May 2012, M. Abrinbana, culture ex-type CBS 144410. This Whole Genome Shotgun project has been deposited at GenBank under the accession JALRMM000000000 (BioProject: PRJNA827019, BioSample: SAMN27594421; present study).

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DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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