



One stop shop IV: taxonomic update with molecular phylogeny for important phytopathogenic genera: 76–100 (2020)

Ruvishika S. Jayawardena^{1,2,7} · Kevin D. Hyde^{1,2,3,18} · Yi Jyun Chen^{2,7} · Viktor Papp⁴ · Balázs Palla⁴ · Dávid Papp^{5,6} · Chitrabhanu S. Bhunjun^{2,7} · Vedprakash G. Hurdeal^{2,7} · Chanokned Senwanna^{2,8} · Ishara S. Manawasinghe^{2,9,18} · Dulanjalee L. Harischandra^{2,7,9} · Ajay Kumar Gautam¹⁰ · Shubhi Avasthi¹¹ · Boontiya Chuankid^{2,7} · Ishani D. Goonasekara^{2,7} · Sinang Hongsanan¹² · XiangYu Zeng^{2,7,19} · Kapila K. Liyanage^{2,17,20} · NingGuo Liu² · Anuruddha Karunarathna^{2,8} · Kalani K. Hapuarachchi² · Thatsanee Luangharn^{2,3} · Olivier Raspé^{2,7} · Rashika Brahmanage^{2,7,9} · Mingkwan Doilom^{3,16,17} · Hyang B. Lee¹³ · Liu Mei⁹ · Rajesh Jeewon¹⁴ · Naruemon Huanraluek² · Napalai Chaiwan^{2,7} · Marc Stadler¹⁵ · Yong Wang¹

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Abstract

This is a continuation of a series focused on providing a stable platform for the taxonomy of phytopathogenic fungi and fungus-like organisms. This paper focuses on one family: *Erysiphaceae* and 24 phytopathogenic genera: *Armillaria*, *Barriopsis*, *Cercospora*, *Cladosporium*, *Clinoconidium*, *Colletotrichum*, *Cylindrocladiella*, *Dothidotthia*, *Fomitopsis*, *Ganoderma*, *Golovinomyces*, *Heterobasidium*, *Meliola*, *Mucor*, *Neoerysiphe*, *Nothophoma*, *Phellinus*, *Phytophthora*, *Pseudoseptoria*, *Pythium*, *Rhizopus*, *Stemphylium*, *Thyrostroma* and *Wojnowiciella*. Each genus is provided with a taxonomic background, distribution, hosts, disease symptoms, and updated backbone trees. Species confirmed with pathogenicity studies are denoted when data are available. Six of the genera are updated from previous entries as many new species have been described.

Keywords Disease · Plant pathology · Phylogeny · Taxonomy · Symptoms

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✉ Yong Wang
yongwangbis@aliyun.com

Extended author information available on the last page of the article

Introduction

This is the fourth paper in the *One Stop Shop* series focusing on providing a stable platform for the taxonomy of plant pathogenic fungi and fungus-like organisms. Genera included in this series are associated with plant diseases, and when the data are available we discuss the species that have been established as pathogens using Koch's postulates. Some genera, however, are not well-known plant pathogens and some may be emerging pathogens, and need further studies to confirm their pathogenicity. Hyde et al. (2014) launched this series and stated its specific aims.

Three issues of *One Stop Shop* (OSS) have been published treating 73 genera and two families of plant pathogenic fungi and fungus-like organisms (Hyde et al. 2014; Jayawardena et al. 2019a, b, Table 1). In this fourth contribution, a further 24 genera and one family are treated, providing clarification of their taxonomy and classification. Six of the entries are updates from previous entries as many changes have occurred in these genera. For each entry, the background of the genus, disease symptoms, host distribution, pathogen biology and epidemiology, morphological

based identification, molecular-based identification, updated phylogeny and recommended genetic markers are provided and discussed. All contributed entries will be placed in the database, <http://www.onestopshopfungi.org>. The main outcome of this series is to enhance the current understanding of plant pathogens and gain better insights into the current classification, providing a stable taxonomy and phylogeny for plant pathogens. This will provide a definitive classification for mycologists and plant pathologists to accurately identify causal agents of disease and to implement accurate control strategies.

Materials and methods

Photo plates of the symptoms of the disease and morphological characters are given, when available. Classification follows Wijayawardene et al. (2020).

For the treated taxa, all species that have been published until 30 March 2020 are included in the phylogenetic analyses. Sequence data from ex-type, ex-epitype or authentic or reference/voucher strains for each species were retrieved from GenBank. Sequence data from single gene regions

Table 1 All entries treated in One stop shop (OSS) series

OSS1 (Hyde et al. 2014)	OSS2 (Jayawardena et al. 2019a)	OSS3 (Jayawardena et al. 2019b)	OSS4 (This paper)
<i>Bipolaris</i>	<i>Alternaria</i>	<i>Alternaria</i> (update)	<i>Armillaria</i>
<i>Botryosphaeriaceae</i>	<i>Bipolaris</i> (update)	<i>Capnodium</i>	<i>Barriopsis</i>
<i>Botryosphaeria</i>	<i>Boeremia</i>	<i>Chaetothyria</i>	<i>Cercospora</i>
<i>Botrytis</i>	<i>Botryosphaeria</i> (update)	<i>Cytospora</i>	<i>Cladosporium</i> (update)
<i>Choanephora</i>	<i>Calonectria</i>	<i>Cyphellophora</i>	<i>Clinoconidium</i>
<i>Colletotrichum</i>	<i>Coniella</i>	<i>Cyttaria</i>	<i>Colletotrichum</i> (update)
<i>Curvularia</i>	<i>Corticaceae</i>	<i>Dactylonectria</i>	<i>Cylindricladiella</i>
<i>Diaporthe</i>	<i>Curvularia</i> (update)	<i>Diplodia</i> (update)	<i>Dothidotthia</i>
<i>Diplodia</i>	<i>Elsinoë</i>	<i>Dothiorella</i> (update)	<i>Erysiphaceae</i>
<i>Dothiorella</i>	<i>Entyloma</i>	<i>Entoleuca</i>	<i>Fomitopsis</i>
<i>Fusarium</i>	<i>Erythrimum</i>	<i>Eutiarosporella</i>	<i>Ganoderma</i>
<i>Gilbertella</i>	<i>Fomitiporia</i>	<i>Fusarium</i> (update)	<i>Golovinomyces</i>
<i>Lasiodiplodia</i>	<i>Fulviformes</i>	<i>Ilyonectria</i>	<i>Heterobasidium</i>
<i>Mucor</i>	<i>Laetisaria</i>	<i>Lasiodiplodia</i> (update)	<i>Meliola</i>
<i>Neofusicoccum</i>	<i>Limonomyces</i>	<i>Macrophomina</i>	<i>Mucor</i> (update)
<i>Pestalotiopsis</i>	<i>Neofabraea</i>	<i>Medeolaria</i>	<i>Neoerysiphe</i>
<i>Phyllosticta</i>	<i>Neofusicoccum</i> (update)	<i>Neonectria</i>	<i>Nothophoma</i>
<i>Phytophthora</i>	<i>Phaeoacremonium</i>	<i>Neopestalotiopsis</i>	<i>Phellinus</i>
<i>Puccinia</i>	<i>Phellinotus</i>	<i>Pestalotiopsis</i> (update)	<i>Phytophthora</i> (update)
<i>Pyrenophora</i>	<i>Phyllosticta</i> (update)	<i>Plasmopara</i>	<i>Pseudoseptoria</i>
<i>Pythium</i>	<i>Plenodomus</i>	<i>Pseudopestalotiopsis</i>	<i>Pythium</i> (update)
<i>Rhizopus</i>	<i>Pseudopyricularia</i>	<i>Rosellinia</i>	<i>Rhizopus</i> (update)
<i>Stagonosporopsis</i>	<i>Tilletia</i>	<i>Sphaeropsis</i>	<i>Stemphylium</i>
<i>Ustilago</i>	<i>Venturia</i>	<i>Stagonosporopsis</i> (update)	<i>Thyrostroma</i>
<i>Verticillium</i>	<i>Waitea</i>	<i>Verticillium</i> (update)	<i>Wojnowiciella</i>

were aligned using Clustal Xv.1.81 (Thompson et al. 1997) and further alignment of the sequences carried out using the default settings of MAFFT v.7 (Kato and Toh 2008; <http://mafft.cbrc.jp/alignment/server/>), and manual adjustment was conducted using BioEdit where necessary. Gene regions were also combined using BioEdit v.7.0.9.0 (Hall 1999). Primers for each gene locus can be found in the bibliography related to the phylogeny presented in each genus. Phylogenetic analyses consisted of maximum likelihood (ML), maximum parsimony (MP) and Bayesian posterior probability (BYPP). Maximum parsimony analysis was performed using PAUP (Phylogenetic Analysis Using Parsimony) v. 4.0b10 (Swofford 2002) to obtain the most parsimonious trees. Maximum likelihood analyses were also performed in raxmlGUIv.0.9b2 (Silvestro and Michalak 2010) or RAxML-HPC2 on XSEDE (8.2.8) on the CIPRES science gateway platform (<http://www.phylo.org>; Miller et al. 2010). Bayesian inference was conducted using MrBayes v. 3.2.6 on the CIPRES science gateway platform (<http://www.phylo.org>; Miller et al. 2010) or stand-alone MrBayes v.3.1.2 (Ronquist and Huelsenbeck 2003). MrModeltest v. 2.3 (Nylander 2004) or jModeltest v. 2.1.4 (Darriba et al. 2012) was used for the statistical selection of the best-fit model of nucleotide substitution to parametrize the analyses.

Results

76. *Armillaria* (Fr.) Staude, Schwämme Mitteldeutschl. 28: xxviii, 130 (1857)

Background

Armillaria is a plant pathogenic genus in the phylum Basidiomycota, family Physalacriaceae (He et al. 2019), collectively referred to as shoestring root-rot fungi or honey mushrooms. *Armillaria* can cause root-rot disease in a wide variety of woody hosts worldwide. *Armillaria* has undergone significant revision in the past 20 years. The genus once accommodated any white-spored agaric with broadly attached gills and an annulus (Volk et al. 1996). *Armillaria mellea* is the type species. Most *Armillaria* species have the potential to infect healthy and stressed trees, they differ in their pathogenicity to their hosts and under certain circumstances, they behave as obligate saprobes. Most *Armillaria* species are facultative necrotrophs causing root and butt rot on a broad range of woody plants affecting a variety of forest, shade, ornamental and orchard trees and shrubs. Some *Armillaria* species cause significant economic losses to forest trees and in nursery plantations. *Armillaria* root disease is found in many temperate and tropical forests throughout the world. This fungus spreads mainly through the interaction of tree roots. As saprotrophs, *Armillaria* species are important wood decomposers that contribute to nutrient

cycling in forest ecosystems. As pathogens, they infect and eventually kill susceptible trees, which impacts forest structure, composition and succession. Trees that are used for fibre or lumber production, as well as trees located in recreation sites, are affected by these diseases. Such *Armillaria* infections may cause yield reduction and tree mortality in silvicultural and agricultural tree plantations and provoke economic losses.

Armillaria species are expected to become more aggressive during drought and thus enhance root rot (La Porta et al. 2008; Kolb et al. 2016; Kubiak et al. 2017). The incidence of *Armillaria* related root disease is likely to increase as temperatures increase and precipitation decreases due to climate change (Sturrock et al. 2011). Whilst the ability of the pathogen to sporulate, spread and infect is affected by temperature and moisture, factors that stress host trees directly may be just as critical to a successful invasion of host tissues. It seems likely that the disease will become more severe in the future, wherever *Armillaria* susceptible tree species are subjected to increased levels of climate stress (Klopfenstein et al. 2009). Currently, *Armillaria* root disease causes large growth/volume losses (e.g., 16–55%) in areas of western and North America (Filip and Goheen 1984; Cruickshank et al. 2011; Lockman and Kearns 2016). *Armillaria* root disease is typically more severe in trees that are maladapted to climate-induced stress (Ayres and Lombardero 2000; Kliejunas et al. 2009; Sturrock et al. 2011). Thus, it is likely that climate change will further exacerbate damage from *Armillaria* root disease, which can further predispose trees to beetle attack (e.g. Hertert et al. 1975; Tkacz and Schmitz 1986; Goheen and Hansen 1993).

Armillaria mellea is an edible species that has long been used as a Traditional Chinese Medicine. Some of *Armillaria* species are believed to be able to improve health and prevent various diseases, such as insomnia, pain, and neurasthenia. Extracts of *A. mellea* exhibit anti-oxidative, anti-inflammatory and immune-modulatory activities. *Armillaria mellea* can also induce maturation of human dendritic cells. The chemical constituents isolated from *A. mellea* include sesquiterpenoids, steroids, triterpenoids, adenosine and resin acids. Armillariol C is a furan-based natural product isolated from *Armillaria* species. A xylosyl 1,3-galactofucan (AMPS-III) was isolated and identified as a novel anti-inflammatory agent from this species.

Classification—Basidiomycota, Agaricomycotina, Agaricomycetes, Agaricomycetidae, Agaricales, Physalacriaceae (He et al. 2019)

Type species—*Armillaria mellea* (Vahl) P. Kumm.

Distribution—Worldwide, mostly in temperate areas (northern and southern hemisphere) and some in tropical areas.

Disease symptoms—*Armillaria* root disease, shoestring root rot

Symptoms caused by this fungus can be categorized into two categories:

Crown symptoms—branch dieback, crown thinning, chlorosis, reddening of foliage or heavier than normal production of cones.

Basal symptoms—the fungus can grow up from the roots in the inner bark in some tree species and causes basal cankers above the infected roots. Resinosis (exudation of resin) can be observed in resinous conifers. In some plants, decayed roots or decay in the inner wood of stem bases can be observed. Species cause a white rot of wood. In white rot, wood often has a bleached, whitish appearance and are spongy or stringy, and maybe wet. Black lines called “zone lines” are usually seen in the decayed wood. These lines are curved planes in the wood, sometimes called “pseudo-sclerotial plates”, composed of thickened, dark fungal cells. They may play a role in the protection of *Armillaria* from unfavourable conditions or other fungi that attempt to invade its territory, including other individuals of the same species. Actively decaying wood may be luminescent, producing a faint glow in the dark (Baumgartner and Rizzo 2002; Worrall 2004; Klopfenstein 2009).

There are three major signs of *Armillaria* root disease in the field.

Mycelial fans can always be seen in infected and recently killed trees. These are white mats of fungal mycelium between the inner bark and wood that are generally substantial and have a mushroom odour.

Rhizomorphs are commonly associated with infection and are often attached to infected roots, but they may also be attached to the surface of uninfected roots. Depending on the species these may be few, small, fragile, hard to find or abundant and robust. Rhizomorphs can be cylindrical in soil or flattened under bark, reddish-brown to black branched and have a cream-coloured tip when actively growing (Guil-laumin and Legrand 2013).

Mushrooms that have honey-brown caps can be seen in clusters near or on the base of trees.

Hosts—Many angiosperms and gymnosperms (especially conifers) in native, planted forests, orchards and vineyards (Farr and Rossman 2020).

Pathogen biology, disease cycle and epidemiology

Sexual reproduction results in the diploid mycelium. Such a mycelium is the dominant phase that is found growing in wood, growing through the soil as rhizomorphs, and killing trees. *Armillaria* species can be dispersed through airborne sexual basidiospores which will establish a new infection center. These taxa do not reproduce asexually but disperse by growing mycelium which is the most common source of infection, through root contacts or root grafts or by growing through the soil as rhizomorphs. Mycelium in colonized roots and the rhizomorphs produced serve as the

most common mode of infection and may survive for up to 50 years or more in stumps, depending on the climate, size of the stump, and other factors (Baumgartner and Rizzo 2002; Worrall 2004; Klopfenstein 2009).

Morphology-based identification and diversity

Armillaria has included only white-spored wood-inhabiting agarics with broadly attached to decurrent gills and macroscopic black to reddish-brown rhizomorphs. *Armillaria* basidiomes are easily recognized by their caespitose habit, annulus and honey colour. It is, however, extremely difficult to identify some species due to the lack of morphological apomorphies (Watling et al. 1991; Pegler 2000). Besides, basidiomata are often not available to differentiate species, which further complicates the taxonomy of *Armillaria* (Harrington and Wingfield 1995). In this regard, *Armillaria* provides a clear example of where a phylogenetic approach can contribute significantly to its taxonomy. Until the late 1970s, *Armillaria mellea* was considered by most researchers to be a polymorphic species with a wide host range and distribution. Herink (1973), among others, suspected that this single species might be a species complex. However, since the morphology of basidiomata is difficult to study because of overlapping and inconsistent traditionally used morphological characters, other avenues of research were pursued. Hintikka (1973) developed a technique that allowed the determination of mating types in *Armillaria*. Using a modification of this method, Korhonen (1978a) was able to distinguish five European biological species. The cumbersome nature of the mating-type method of species identification prompted a search for other techniques for identifying collections. They were able to separate all North American species (NABS) of *Armillaria* except for *A. calvescens* and *A. gallica*, which are apparently very closely related (Anderson and Stasovski 1992). Ten species of *Armillaria* in North America have been confirmed from multiple studies utilizing a combination of morphological, biological and phylogenetic species concepts (Anderson and Ullrich 1979; Anderson and Stasovski 1992; Burdsall and Volk 1993; Kim et al. 2006; Ross-Davis et al. 2012). Before, *A. mellea* shows great variability in morphology and hosts. These species were first separated using interfertility tests using cultures of *Armillaria* haploid tester strains and morphology. Now, *A. mellea* is considered as an independent species, with two North American biological species (Bérubé and Dessureault 1989; Volk et al. 1996) (Fig. 1).

Molecular-based identification and diversity

Problems surrounding the identification of *Armillaria* have led to important advances in developing robust but rapid DNA techniques. Such techniques have initially included DNA-base composition (Jahnke et al. 1987) DNA-DNA hybridization (Miller et al. 1994), sequence analyses of

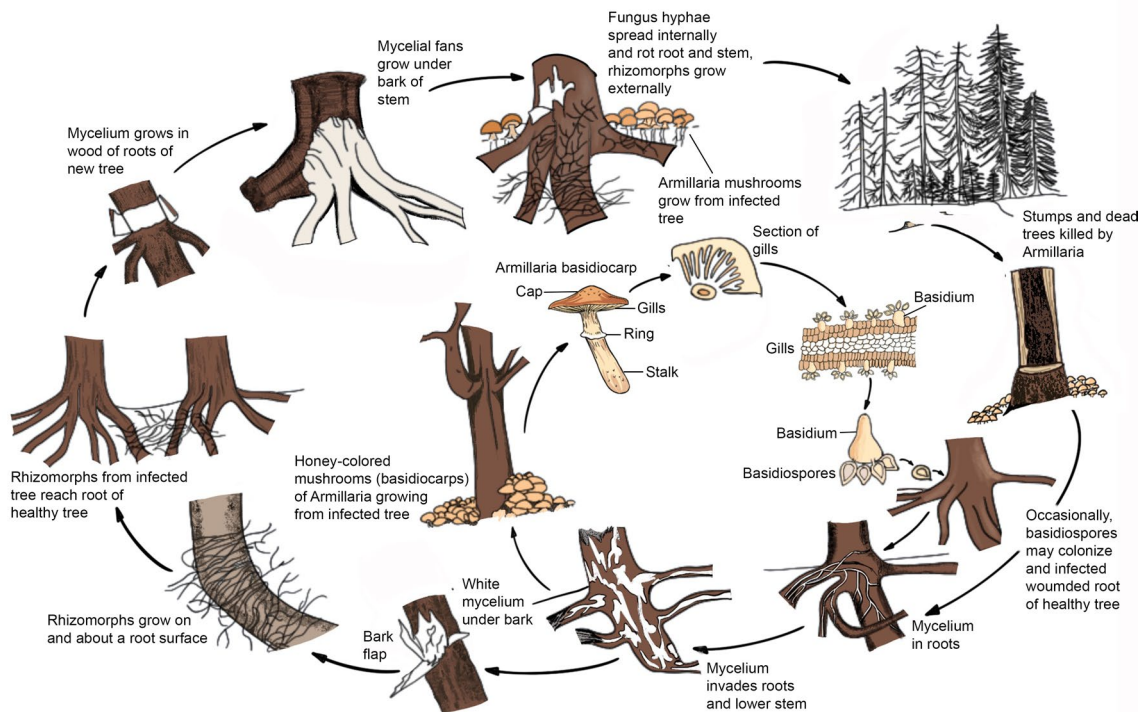


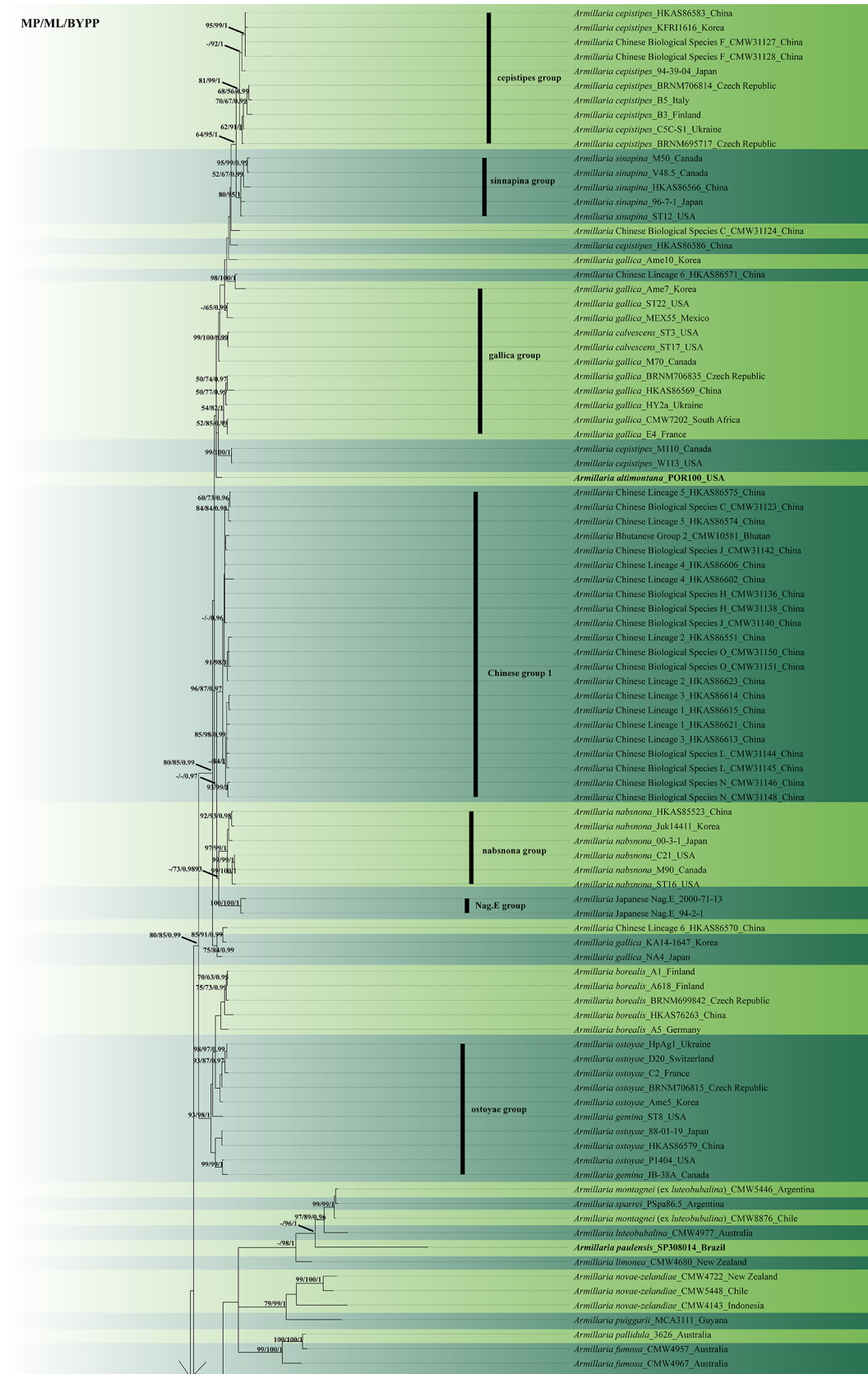
Fig. 1 Disease cycle of *Armillaria mellea* (redrawn from Agrios 2005)

the IGS-1 (Anderson and Stasovski 1992) and ITS (Coetzee et al. 2001a, b), RFLPs without PCR (Smith and Anderson 1989) and RFLPs of IGS-1 amplicons (Harrington and Wingfield 1995). Although several of these techniques might pose some problems (Pérez-Sierra et al. 2000), by their relative simplicity they have gradually replaced traditional, morphological methods.

The amount of DNA sequence data on *Armillaria* species has increased substantially since the first publication on the phylogeny of the genus in the northern hemisphere (Anderson and Stasovski 1992). As with many other fungal genera, the focus of such studies initially was set on species of Europe and North America (Chillali et al. 1998; Coetzee et al. 2000b). Later, substantial datasets for species in Africa, Australasia and southeast Asia have become available (Terashima et al. 1998; Coetzee et al. 2000a, 2001a). At present, ITS, IGS-1 and *tefl* sequences are available in GenBank for the best-known species of *Armillaria*. However, there are disjunctions in data sets and relatively little is known about species from Indo-Malaysia and South America. *Armillaria* fruiting bodies are produced seasonally and not every year; they are, therefore, often not available during fieldwork (Kile et al. 1991).

Identification using the biological species concept with species identification based on sexual compatibility tests (Korhonen 1978a) has been examined for its utility by some mycologists, but its application was soon abandoned. This

was because of complications due to the absence of known tester strains, lack of haploid strains, ambiguous mating interactions and degeneracy of cultures. For these reasons, DNA-based molecular techniques have finally been preferred in *Armillaria* taxonomy, either complementing other methods or on their own. The techniques utilized for the taxonomy of *Armillaria* species include comparisons of RFLPs (Harrington and Wingfield 1995), AFLPs (Pérez-Sierra et al. 2004), and the use of sequences from the ITS, IGS-1 and *tefl* gene in phylogenetic studies (Coetzee et al. 2000b, 2001a; Maphosa et al. 2006; Kim et al. 2006). Phylogenetic methods have made it possible to differentiate the lineages of the genus in southern Argentina (Pildain et al. 2009). Lineages I and II grouped with *A. novae-zelandiae* and *A. luteobubalina*, respectively, while Lineages III and IV represented unique taxa that were closely related to *A. hinnulea*, *Armillaria* 4th species from New Zealand (established by Coetzee et al. 2001a, b) and *Armillaria* Group III from Kenya (Mwenje et al. 2006). Modern approaches to identification of *Armillaria* species are mostly based on the analyses of DNA sequences. The present study reconstructs the phylogeny of *Armillaria* based on a combined ITS, IGS and *tefl* sequence data (Fig. 2, Table 2). However, insufficient data are available for the LSU gene region in GenBank. Then, it is difficult to have comparative phylogenetic analyses but the single gene analysis of each gene was carried out to compare the topology of the tree and clade stability.



◀ **Fig. 2** Phylogenetic tree generated by maximum likelihood analysis of combined ITS-IGS-*tef1* sequence data of *Armillaria* species. Related sequences were obtained from GenBank. One hundred and thirty-nine strains are included in the analyses, which comprise 4557 characters including gaps. The tree was rooted with *Guyanagaster lucianii* (G31.4) and *Guyanagaster necrorhizus* (MCA 3950). Single gene analyses were carried out to compare the topology of the tree and clade stability. Tree topology of the ML analysis was similar to the MP and BYPP. ML phylogenetic tree inference was performed using RAxML version 8.2.12 on the CIPRES web server, using a mixed-model analysis and the GTRCAT model of substitution. The four partitions were defined as ITS, IGS, *tef1* exons and *tef1* introns. The best scoring RAxML tree with a final likelihood value of -25308.198187 is presented. The matrix had 1957 distinct alignment patterns, with 65.74% of undetermined characters or gaps. Estimated base frequencies of ITS were as follows: A=0.227071, C=0.203923, G=0.235701, T=0.333305; substitution rates AC=0.628852, AG=3.751709, AT=1.365607, CG=1.467905, CT=2.788595, GT=1.000000. Estimated base frequencies of IGS were as follows: A=0.244624, C=0.196588, G=0.242370, T=0.316418; substitution rates AC=0.954911, AG=3.055115, AT=1.041498, CG=1.278095, CT= 3.421100, GT=1.000000. Estimated base frequencies of *tef1*

exons were as follows: A=0.228587, C=0.301128, G=0.255865, T=0.214420; substitution rates AC=0.905728, AG=3.660986, AT=1.564184, CG=0.648739, CT= 28.048363, GT=1.000000. Estimated base frequencies of *tef1* introns were as follows: A=0.215042, C=0.222693, G=0.185633, T=0.376631; substitution rates AC=1.170263, AG=5.878084, AT=0.847943, CG=1.087990, CT= 5.095797, GT=1.000000; gamma distribution shape parameter α =0.1000000000. The maximum parsimonious dataset consisted of 2908 constant, 1172 parsimony-informative and 477 parsimony-uninformative characters. The parsimony analysis: CI = 0.610, RI = 0.861, RC = 0.525, HI = 0.390 in the first tree. Bayesian posterior probability was performed using the Markov chain Monte Carlo (MCMC) method implemented in MrBayes 3.2.6 with a mixed-model partition identical to the ones defined in the ML analysis. The best-fit nucleotide substitution model was separately determined for each partition with jModeltest version 2.1.10 on CIPRES, using the Akaike Information Criterion. K80+I, K80+I, SYM+G and HKY+G were selected as best-fit models for ITS, IGS, *tef1* exons and *tef1* introns, respectively. At the end of the runs, the average deviation of split frequencies was 0.016675. MP and RAxML bootstrap support value \geq 50% and BYPP \geq 0.95 are shown, respectively, near the nodes. Holotype or ex-type strains are in bold

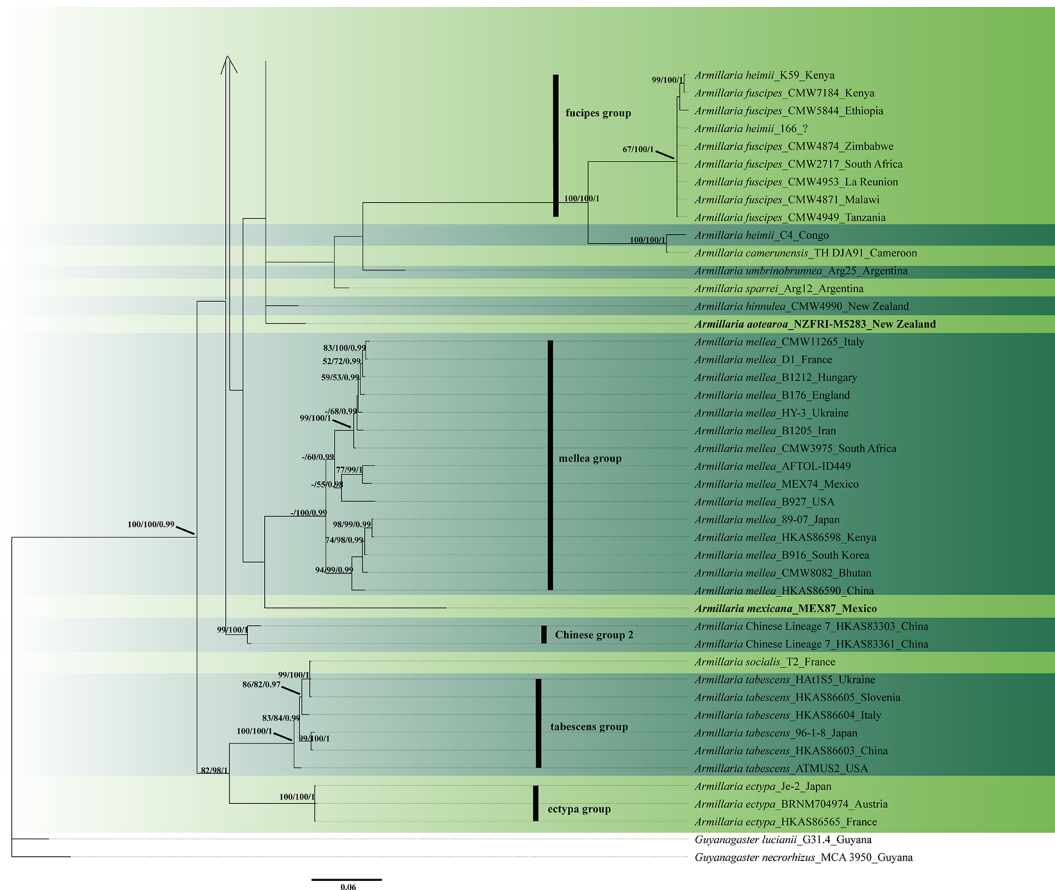


Fig. 2 (continued)

Table 2 DNA barcodes available for *Armillaria*

Species	Sources	Country	ITS	LSU	<i>tefl</i>	IGS1
<i>Armillaria affinis</i>	JMCR.126	Central America?	–	AF261356	–	–
<i>A. altimontana</i>	POR100*	USA	AY213579, AY213580	–	JN944606, JF313117	AY509181
<i>A. aotearoa</i>	NZFRI-M 5283*	New Zealand	NR_151846	–	KU295542	–
<i>A. borealis</i>	CMW31075	Belarus	–	–	KM205252	KM205305
	CMW31072	China	–	–	KM205251	KM205304
	HKAS 76263, Gt571	China	KT822294	–	KT822426	–
	BRNM 699842, MUAF 501	Czech Republic	EU257713	–	EU251402	EU257708
	CMW3172	Finland	–	DQ338540	DQ435623	–
	A1	Finland	JN657467	–	JN657494	JN657440
	A5	Germany	JN657468	–	JN657495	JN657441
	A618	Switzerland	JN657469	–	JN657496	JN657442
<i>A. calvescens</i>	ST3	USA	AY213559	JF895899	JF313138, JF895835	AY509163
	ST17	USA	AY213560, AY213561	JF895900	JF313130, JF895836	AY509164
	TH DJA 91/PUL F2895	Cameroon	KU170952	KU170942	KU289112	–
<i>A. cepistipes</i>	BRNM 706814, MUAF 516	Czech Republic	EU257715	–	EU251395	EU257709
	M110	Canada	AY213581	–	JF313121	AY509182
	HKAS 86583, 01108/1	China	KT822290	–	KT822417	–
	B3	Finland	JN657445	–	JN657472	JN657418
	B5	Italy	JN657446	–	JN657473 KJ414321	JN657419, KJ414318
	94-39-04	Japan	AB510853	–	AB510786	AB510809
	SY1Ra	UK?	–	–	JF746917	JF288720
	C5C-S1	Ukraine	JN657450	–	JN657477	JN657423
	W113	USA	AY213583	–	JF313115	AY509184
	BRNM 695717	Czech Republic	EU257716	–	EU251396	EU257710
	HKAS 86586, 97033/1	China	KT822263	–	KT822416	–
	KFRI1616	Korea	MG543860	–	MG544785	–
<i>A. ectypa</i>	BRNM 704974	Austria	EU257720	–	EU251403	EU257712
	CMW15693	France	–	DQ338547	FJ875698	–
	HKAS 86565, 70011/13	France	KT822340	–	KT822438	–
	TFM27105, Je-2	Japan	AB559000	–	AB558992	–
<i>A. fumosa</i>	CMW4957, 123	Australia	AF329917	DQ338552	DQ435646	–
<i>A. fuscipes</i>	CBS 118122, CMW5844, WGII	Ethiopia	AY882969	–	–	AY172032
	CMW7184	Kenya	AY882973	–	–	AY882965
	CMW4953	La Reunion	AY882974	DQ338556	DQ435622	AY882963
	CMW4871	Malawi	AY882976	–	–	AY882959
	CMW2717	South Africa	AY882971	–	–	AF204821
	CMW4949	Tanzania	AY882978	–	–	AY882961
	CMW4874	Zimbabwe	AY882967	–	–	AF489481
<i>A. gallica</i>	M70	Canada	AY213568	–	JF313123	AY509171
	CMW31087	China	–	–	KM205260	KM205313

Table 2 (continued)

Species	Sources	Country	ITS	LSU	<i>tefl</i>	IGS1
	HKAS 86569, 93421/1	China	KT822277	–	KT822414	–
	BRNM 706835, MUAF 575	Czech Republic	EU257718	–	EU251390	EU636240
	E4	France	JN657452	–	JN657479	JN657425
	86-016/3	Germany	–	–	KJ200952	KJ200946
	86-008/2	Iran	–	–	KJ200954	KJ200948
	NA4	Japan	AB510881	–	AB510761	AB510834
	MEX55	Mexico	JX281809	–	KC111014	JX281799
	CMW7202	South Africa	AY190247	–	–	AY190245
	HY2a	Ukraine	JN657455	–	JN657482	JN657428
	Aga235	USA	–	JF895911	JF895847	–
	ST22, EL-1	USA	AY213569, AY213570	JF895912	JF313126, JF895848	AY509172
	Ame10	Korea	MG543850	–	MG544774	–
	KA14-1647	Korea	MG543859	–	MG544784	–
	Ame7	Korea	MG543852	–	MG544777	–
<i>A. gemina</i>	JB-38A	Canada	FJ664586	FJ618757	FJ618670	–
	ST8	USA	AY213555	–	JF313136	AY509158, AY509159
<i>A. heimii</i>	C4	Congo	AY333917	–	–	AY330630
	166	–	AY333913	–	–	AY330634
	K59	Kenya	AY333916	–	–	AY330627
<i>A. hinmulea</i>	CMW4980	Australia	–	DQ338555	DQ435648	AF445077
	CMW4990	New Zealand	AF329905	DQ338555	DQ435648	–
<i>A. jezoensis</i>	HUA9116	Japan	–	–	–	D89921
<i>A. limonea</i>	CMW4680	New Zealand	AF329930	DQ338560	DQ435655	AF445073
<i>A. lutea</i>	90-4 (Alut)	USA	–	–	–	AF243066
<i>A. luteobubalina</i>	CMW4977	Australia	AF329912	DQ338559	DQ435657	AF445069
<i>A. mellea</i>	AFTOL-ID449	USA	AY789081	AY700194	AY881023	–
	B176	England	AF163578	–	–	AF163602
	HKAS 86590, 00020/6	China	KT822251	–	KT822354	–
	D1	France	JN657464	–	JN657491	JN657437
	B1212, CMW4615, 94056/1	Hungary	AF163581	–	–	AF163605
	B1205, CMW4613, 86009/1	Iran	AF163583	–	DQ435637	AF163606
	CBS122232, CMW11265, 426	Italy	FJ875692	FJ875694	DQ435636	–
	FFPRI420861, WD2588, 89-07	Japan	AB510852	–	AB510796	AB510808
	HKAS 86598, PFD84-103	Kenya	KT822248	–	KT822348	–
	MEX74	Mexico	JX281807	–	KC111011	JX281797
	CMW3975	South Africa	AF310329	–	–	AF310327
	B916, CMW4610, A-5	South Korea	AF163592	–	DQ435639	AF163612
	HY-3	Ukraine	JN657466	–	JN657493	JN657439
	Am115	USA	–	JF895920	JF895856	–
	B927	USA	AF163595	FJ875695	DQ435634	AF163608
	CMW31161	China	–	–	KM205267	KM205320

Table 2 (continued)

Species	Sources	Country	ITS	LSU	<i>tefl</i>	IGS1
	CMW8082	Bhutan	AY554333	–	–	AY554335
	HUA93110	Japan	–	–	–	D89922
<i>A. mexicana</i>	MEX87*	Mexico	KR061310	–	KR061314	KR061306
<i>A. montagnei</i> (ex <i>luteobubulina</i>)	CMW5446	Argentina	AF448422	DQ338562	DQ435650	AF445068
<i>A. montagnei</i> (ex <i>luteobubulina</i>)	CMW8876	Chile	AF448423	–	DQ435658	AF445065
<i>A. montagnei</i> (Lineage II)	Arg309	Argentina	FJ660939	FJ711625	–	–
<i>A. montagnei</i> (Lineage II)	Arg270*	Argentina	FJ711609	–	–	–
<i>A. nabsnona</i>	ST16	USA	AY213574	–	JF313124	AY509178
	HKAS 85523, Gt798	China	KT822333	–	KT822411	–
	M90	Canada	AY213573	–	JF313122	AY509176, AY509177
	00-3-1	Japan	AB510899	–	AB510766	AB510850
	C21	USA	AY213572	–	JF313119	AY509174, AY509175
	CMW6905	USA	–	DQ338542	DQ435631	–
	Juk14411	Korea	MG543857	–	MG544782	–
<i>A. novae-zelandiae</i>	CMW4967	Australia	AF329921	–	DQ435651	–
	CMW5448	Chile	AF448417	DQ338554	DQ435653	–
	CMW4143	Indonesia	AF448421	DQ338564	DQ435654	–
	CMW3951	Malaysia	AF448419	DQ338553	–	–
	CMW4722	New Zealand	AF329926	DQ338551	DQ435652	–
<i>A. novae-zelandiae</i> (Lineage I)	Arg49	Argentina	FJ660935	FJ711629	–	–
<i>A. ostoyae</i>	SP308014*	Brazil	EF639348	–	–	–
	BRNM706815	Czech Republic	EU257717	–	EU251400	EU257711
	CMW31102	China	–	–	KM205272	KM205325
	HKAS 86579, 96043/11	China	KT822310	–	KT822428	–
	C2	France	JN657459	–	JN657486	JN657432
	88-01-19	Japan	AB510859	–	AB510784	AB510815
	D20	Switzerland	JN657463	–	JN657490	JN657436
	HpAg1	Ukraine	JN657462	–	JN657489	JN657435
	P1404	USA	AY213554	–	JF313140	AY509157
	Ame5	Korea	MG543851	–	MG544776	–
	3626	Australia	FJ664607	FJ618752	FJ618665	–
<i>A. puiggarii</i>	MCA 3111/PUL F2896/BRG 41295	Guyana	KU170954	KU254228	KU289104	–
<i>A. sinapina</i>	V48.5	Canada	FJ664609	FJ618763	FJ618676	–
	M50	Canada	AY213563, AY213564	–	JF313114	AY509167
	CMW31112	China	–	–	KM205277	KM205330
	HKAS 86566, 96015/39	China	KT822323	–	KT822422	–
	96-7-1	Japan	AB510873	–	AB510774	AB510827
	P2-7	USA	–	JF895916	JF895850	–
	ST12	USA	AY213565	–	JF313132	AY509168
<i>A. singula</i>	HUA9101*	Japan	–	–	–	D89926

Table 2 (continued)

Species	Sources	Country	ITS	LSU	<i>tefl</i>	IGS1
<i>A. socialis</i>	T2	France	DQ784801	–	–	–
<i>A. solidipes</i>	MS2-11	USA	–	JF895918	JF895852	–
	CMW31107	Finland	–	–	KM205275	KM205328
<i>A. sparrei</i>	PSpa86.5	Argentina	FJ664612	FJ618750	–	–
	Arg12	Argentina	FJ660948	FJ711618	–	–
<i>A. umbrinobrunnea</i>	Arg25	Argentina	FJ660946	FJ711621	–	–
<i>A. tabescens</i>	CMW31118	China	–	–	KM205280	KM205333
	99122/13	China	KT822339	–	KT822441	–
	CMW3165	France	–	DQ338546	DQ435642	–
	CMW31119	Italy	–	–	KM205281	KM205334
	HKAS 86604, CT1097.3	Italy	KT822338	–	KT822440	–
	96-1-8	Japan	AB510867	–	AB510804	AB510823
	HKAS 86605, 901582	Slovenia	KT822337	–	KT822439	–
	HAt1S5	Ukraine	HQ232292	–	HQ285906	HQ232284
	ATMUS2	USA	AY213588	–	JF313113	AY509189, AY509190
	Bhutanese Group 2	CMW10581	Bhutan	AY554329	–	FJ875699
Chinese Biological species C	CMW31123	China	–	–	KM205284	KM205337
	CMW31124	China	–	–	KM205285	KM205337
Chinese Biological species F	CMW31127	China	–	–	KM205286	KM205339
	CMW31128	China	–	–	KM205287	KM205340
Chinese Biological species H	CMW31136	China	–	–	KM205293	KM205346
Chinese Biological species J	CMW31138	China	–	–	KM205294	KM205347
	CMW31140	China	–	–	KM205296	KM205349
Chinese Biological species L	CMW31142	China	–	–	KM205297	KM205350
	CMW31144	China	–	–	KM205298	KM205351
Chinese Biological species N	CMW31145	China	–	–	KM205299	KM205352
	CMW31146	China	–	–	KM205300	KM205353
Chinese Biological species O	CMW31148	China	–	–	KM205301	KM205354
	CMW31150	China	–	–	KM205302	KM205355
Chinese Lineage 1	CMW31151	China	–	–	KM205303	KM205356
	HKAS 86615	China	KT822315	–	KT822384	–
Chinese Lineage 2	HKAS 86621	China	KT822306	–	KT822386	–
	HKAS 86623	China	KT822318	–	KT822363	–
Chinese Lineage 3	HKAS 86551	China	KT822279	–	KT822367	–
	HKAS 86613	China	KT822319	–	KT822388	–
Chinese Lineage 4	HKAS 86614	China	KT822305	–	KT822391	–
	HKAS 86602	China	KT822308	–	KT822378	–
Chinese Lineage 5	HKAS 86606	China	KT822281	–	KT822359	–
	HKAS 86574	China	KT822324	–	KT822361	–
Chinese Lineage 6	HKAS 86574	China	KT822327	–	KT822364	–
	HKAS 86570	China	KT822320	–	KT822402	–
	HKAS 86571	China	KT822288	–	KT822404	–

Table 2 (continued)

Species	Sources	Country	ITS	LSU	<i>tefl</i>	IGS1
Chinese Lineage 7	HKAS 83303	China	KU378047	–	KT822437	–
	HKAS 83361	China	KU378048	–	KT822436	–
Japanese Nag. E	94-2-1	Japan	AB510888	–	AB510768	AB510840
	2000-71-13	Japan	AB510879	–	AB510773	AB510832

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold

This phylogenetic tree is largely in accordance with earlier studies from Coetzee et al. (2018) and provides the most conclusive phylogeny of the genera to date. Genealogical concordance phylogenetic species recognition (GCPSR) using the concordance among several gene trees (Taylor et al. 2000; Dettman et al. 2003) to delineate species has become standard in fungal taxonomy. However, except for a few studies (Guo et al. 2016; Tsykun et al. 2013), this taxonomic method has not been widely implemented in *Armillaria* taxonomy. Sequences of the genomes of key species are already providing prospects to study the evolution and systematics of *Armillaria*. They are certain to lead to important breakthroughs regarding not only the taxonomy but the biology and ecology of these fungi in the future (Sipos et al. 2017).

Recommended genetic marker (genus level)—ITS

Recommended genetic markers (species level)—ITS, IGS1, *tefl*

Additional genetic markers (species level)—LSU, *tub2*

Accepted number of species—There are 278 epithets in Index Fungorum (2020) listed for this genus. However, sequence data are only available for 31 species including 16 groups of unnamed species (Table 2).

References—Watling et al. (1991), Pegler (2000), Harrington and Wingfield (1995) (morphology); Coetzee et al. (2000a, b, 2001a, b), Maphosa et al. (2006), Mwenje et al. (2006), Kim et al. (2006), Coetzee et al. (2018) (molecular phylogeny).

77. *Barriopsis* A.J.L. Phillips, A. Alves & Crous, in Phillips et al., *Persoonia* 21: 39 (2008)

Background

Stevens (1926) originally described the type species of *Barriopsis* in *Physlospora* as *Physlospora fusca* and Petrak and Deighton (1952) transferred it to *Phaeobotryosphaeria*. The fungus that was considered by Stevens (1926), and Petrak and Deighton (1952) did not have apiculi on its ascospores and was not similar to *Phaeobotryosphaeria* which had small, hyaline apiculi on the ascospores. von Arx and Müller (1954) considered *Phaeobotryosphaeria* as

a synonym of *Botryosphaeria*. Based on morphological difference and molecular sequence data, Phillips et al. (2008) introduced *Barriopsis*. Species of *Barriopsis* are mostly saprobic and weak pathogens (Phillips et al. 2013).

Classification—Ascomycota, Dothideomycetes, Incertae sedis, Botryosphaeriales, Botryosphaeriaceae

Type species—*Barriopsis stevensiana* A.J.L. Phillips & Pennycook

Distribution—Species appear to be confined to regions with tropical or subtropical climates including Australia, Cuba, Iran and Thailand (Phillips et al. 2008; Abdollahzadeh et al. 2009; Liu et al. 2012; Phillips et al. 2013; Doilom et al. 2014; Konta et al. 2016; Dissanayake et al. 2016; Hyde et al. 2018b; Burgess et al. 2019).

Disease symptoms—*Barriopsis* species can be weak pathogens and their pathogenicities are uncertain (Phillips et al. 2008; Dissanayake et al. 2016). *Barriopsis stevensiana* and *B. iraniana* were isolated from infected branches, fruits and leaves with various disease symptoms, including dieback, canker, rot and necrosis, from *Cupressus sempervirens*, *Mangifera indica*, *Citrus* sp. and *Olea* sp. in northern and southern provinces of Iran (Abdollahzadeh et al. 2009). Species of this genus may be future emerging pathogens.

Hosts—*Archontophoenix alexandrae*, *Cassia* sp., *Citrus* sp., *Mangifera indica*, *Olea* sp. *Tectona grandis* (Phillips et al. 2008, 2013; Abdollahzadeh et al. 2009; Liu et al. 2012; Doilom et al. 2014; Konta et al. 2016; Dissanayake et al. 2016; Hyde et al. 2018b, 2020b).

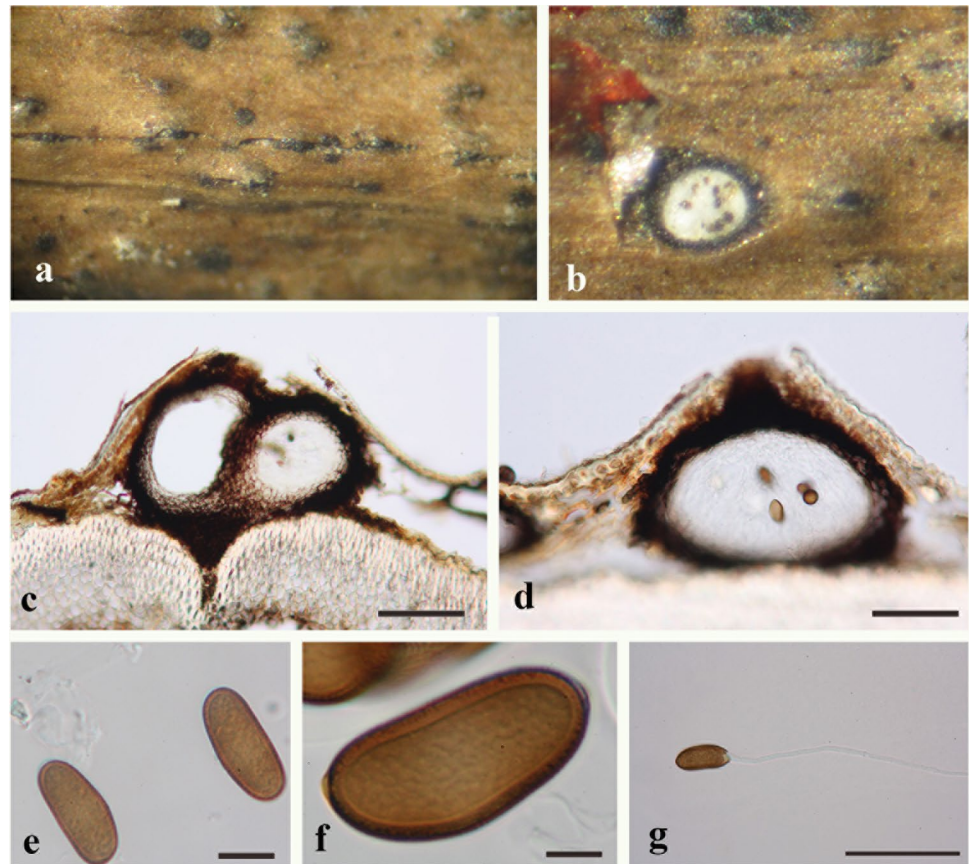
Pathogen biology, disease cycle and epidemiology

Barriopsis in this article is considered as an emerging pathogen. Further studies to identify the biology, disease cycle and epidemiology are needed.

Morphological based identification and diversity

The sexual morph is characterized by brown aseptate ascospores that are widest in the center and lack terminal apiculi (Phillips et al. 2008, 2013; Doilom et al. 2014; Dissanayake et al. 2016; (Fig. 3)). *Barriopsis archontophoenicis* forms the sexual morph in culture medium after long

Fig. 3 *Barriopsis stevensiana* MFLU 19–1560. **a** Ascomata on dead twigs of *Cassia* sp. **b** Ascomata cut through horizontally showing the white contents with dark spots. **c, d** Sections through ascomata. **e, f** Ascospores. **g** Germinated ascospore. Scale bars: **c, d** = 200 μm , **e, f** = 20 μm , **g** = 100 μm



periods of incubation (up to 6 months, Konta et al. 2016). The asexual morph is lasiodiplodia-like with hyaline conidia that become dark-brown and septate with irregular longitudinal striations (Stevens 1926). Abdollahzadeh et al. (2009) observed the asexual morphs of *B. fusca* and *B. iraniana* and confirmed that the morphology is similar to the description given by Stevens (1926). In their study, they revealed that this genus can be distinguished from other genera of Botryosphaeriaceae by the presence of visible striations on conidia at an early stage of development.

However, using morphology alone in identifying these species is not wise due to the overlapping of morphological characters within the genus. Therefore, the use of multi loci phylogeny along with morphology is recommended for this genus. Very little is known about the diversity and pathogenicity of this botryosphaeriaceous genus and future studies are needed to confirm its pathogenic nature.

Molecular based identification and diversity

Phillips et al. (2008) using SSU, ITS, LSU, *tef1* and *tub2* sequence data established *Barriopsis* which is sister to *Phaeobotryon*. Based on ITS and *tef1* sequence data, Abdollahzadeh et al. (2009) introduced *B. iraniana*. Doilom et al. (2014) introduced *B. tectonae* based on ITS, *tub2* and *tef1* sequence data. In this study, it was mentioned that ITS and *tub2* sequence data

have lesser variation, while *tef1* sequence data have considerable variation. Konta et al. (2016) added a new species, *B. archontophoenicis* with the use of ITS, LSU, SSU and *tef1* sequence data. In this study, we construct the phylogenetic tree for the accepted species based on ITS and *tef1* sequence data (Fig. 4).

Recommended genetic marker (genus level)—ITS

Recommended genetic marker (species level)—*tef1*

Accepted number of species—There are six species epithets in Index Fungorum (2020), however only five species have DNA sequence data (Table 3).

References—Phillips et al. (2008), Abdollahzadeh et al. (2009) (morphology and phylogeny); Dissanayake et al. (2016) (accepted number of species, phylogeny); Doilom et al. (2014), Konta et al. (2016) (new species).

78. *Cercospora* Fresen. ex Fuckel, Hedwigia 2(15): 133 (1863)

Background

Cercospora includes pathogens, saprobes and endophytes. Species are widely distributed, occurring on numerous flowering and ornamental plants, ferns, other fungi (as parasites), gymnosperms, grasses and other monocotyledons such as lilies, magnoliids and palms, mostly causing leaf spots. The well-known asexual morph, which is phycomycetous, are

Fig. 4 Phylogram generated from maximum likelihood analysis based on combined ITS, and *tef1* sequence data of *Barriopsis* species and closely related taxa. Fifteen strains are in the combined sequence analyses, which comprise 865 characters including gaps. *Diplodia mutila* (CBS 112553 and CBS 230.30) was used as the outgroup taxa. Tree topology of the ML analysis was similar to the one generated from BI. The best scoring RAxML tree with a final likelihood value of -2372.487246 is presented. The matrix had 201 distinct alignment patterns, with 12.30% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.207721, C = 0.288041, G = 0.271092, T = 0.233145; substitution rates AC = 1.068561, AG = 2.489613, AT = 0.682766, CG = 1.417925, CT = 4.236517, GT = 1.000000; gamma distribution shape parameter $\alpha = 1.343820$. RAxML bootstrap support value $\geq 50\%$ and BYPP ≥ 0.95 are shown respectively, near the nodes. Ex-type strains are in bold

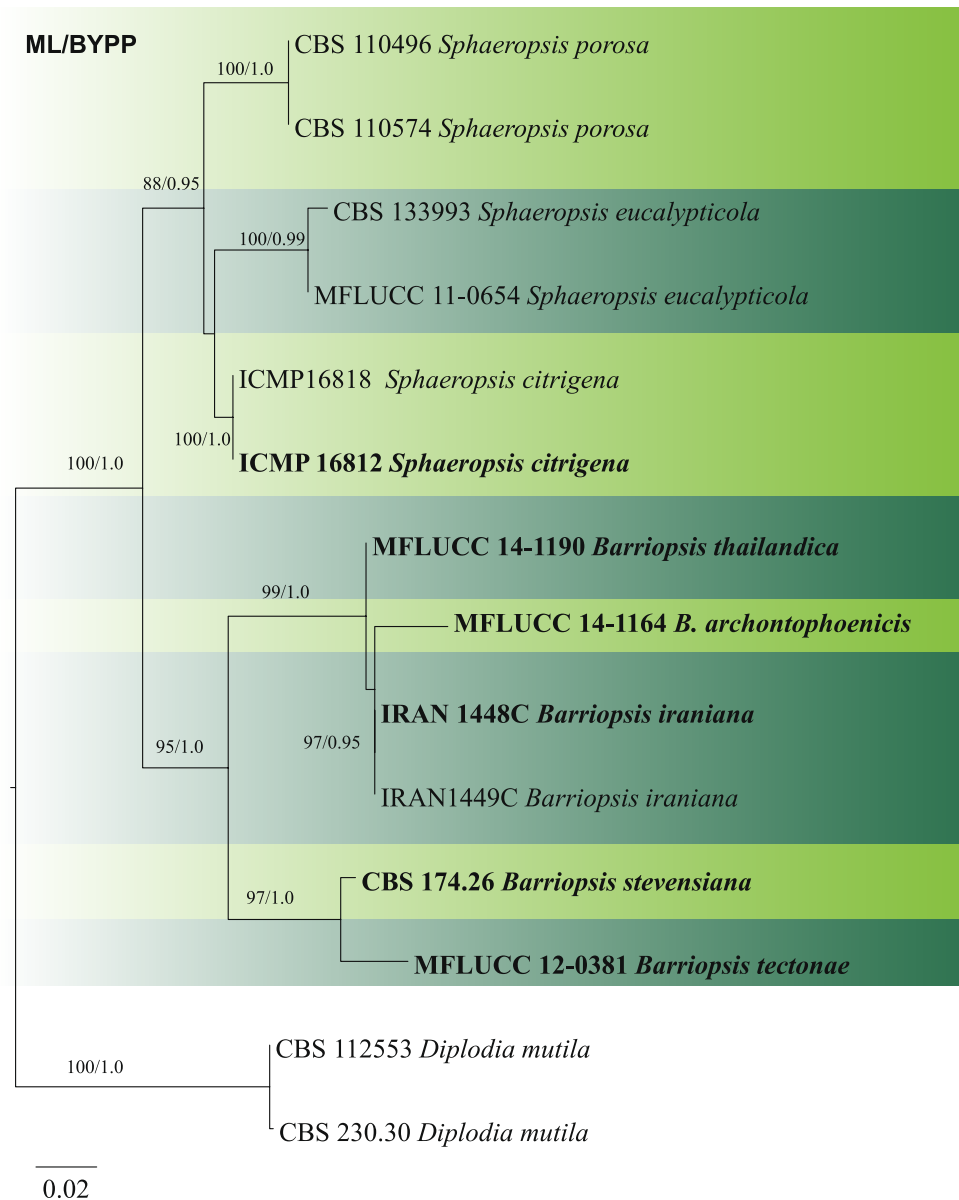


Table 3 DNA barcodes available for *Barriopsis*

Species	Isolate	ITS	<i>tef1</i>
<i>Barriopsis archontophoenicis</i>	MFLUCC 14-1164*	KX235306	KX235305
<i>B.iraniana</i>	IRAN 1448C*	FJ919663	FJ919652
	IRAN1449C	FJ919665	FJ919654
<i>B.tectonae</i>	MFLUCC 12-0381*	KJ556515	KJ556516
<i>B.thailandica</i>	MFLUCC 14-1190*	KY115675	KY115676
<i>B.stevensiana</i>	CBS 174.26*	NR119698	–

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold

among the largest groups of plant pathogenic fungi causing leaf spots, leading to diseases on many economically important crops (Agrios 2005; To-Anun et al. 2011; Groenewald et al. 2013; Guatimosim et al. 2016; Park et al. 2017). Comparatively only a few sexual morphs have been studied (Hyde et al. 2013). A photosensitizing toxic compound named ‘cercosporin’ is responsible for *Cercospora* species inhabiting such a wide host range (Daub et al. 2005; Thomas et al. 2020).

Classification—Ascomycota, Dothideomycetes, Dothideomycetidae, Capnodiales, Mycosphaerellaceae

Type species—*Cercospora apii* Fresen., Beitr. Mykol. 3: 91 (1863)

Distribution—Worldwide

Disease symptoms—Leaf blights and spots

This disease affects the leaves, petioles, stems and peduncles of the tree. Infection and lesion formation initially occur on older leaves before progressing to newer ones. Small, brown flecks develop with a reddish border, expanding to circular spots with an ashy-grey centre. Concentric rings may be observed as individual lesions expand. This tissue becomes thin and brittle, and often drops out, leaving a ragged hole. These lesions often resemble frogeyes, giving this disease its common name. Severely affected leaves wither and die from coalescing lesions (Shane and Teng 1992; Steddom et al. 2005).

Species of *Cercospora* cause blights and spots on the leaves, petioles, stems and peduncles of trees. Often infection and lesion formation occurs on older leaves before progressing to newer ones. Common symptoms include small, brown lesions that develop with a reddish border, eventually expanding to larger circular or angular spots. Concentric rings may be observed as individual lesions expand. The tissue becomes thin and brittle, and often drops out, leaving a ragged hole. Severely affected leaves wither and die from coalescing lesions (Shane and Teng 1992; Steddom et al. 2005).

Hosts—Wide host range including plant genera in Amaranthaceae, Apiaceae, Asteraceae, Arecaceae, Chenopodiaceae, Convolvulaceae, Cryptogamaceae, Cucurbitaceae, Cyatheaceae, Dennstaedtiaceae, Dioscoreaceae, Euphorbiaceae, Fabaceae, Gunneraceae, Hydrangeaceae, Lamiaceae, Lygodiaceae, Musaceae, Myrtaceae, Onagraceae, Plumbaginaceae, Poaceae, Pteridaceae, Scrophulariaceae, Solanaceae, Thelypteridaceae and Urticaceae (Farr and Rossman 2020).

Cercospora apii causes leaf spot disease on celery and *C. beticola* on sugar beet (Braun et al. 2013; Guatimosim et al. 2016). The pathogen *Cercospora* cf. *sigesbeckiae* infects various plant families, including economically valuable crops such as soybean, causing ‘Cercospora leaf blight’, a disease characterized by leaf bronzing (Albu et al. 2016, 2017). Some other species identified as causative organisms of the leaf blight are *C. kikuchii* and *C. cf. flagellaris* (Soares et al. 2015; Rezende et al. 2020). The yield losses related to *Cercospora* disease have been reported from Canada, China, India and other regions in the USA and South America (Almeida et al. 2005; Cai et al. 2009; Hershman 2009; Wrather et al. 2010; Geisler 2013; Albu et al. 2017; Bandara et al. 2020). *Cercospora* is among the leading fungal pathogens that cause a severe threat to soybean, which is an important grain legume crop, by reducing seed production and quality (Arantes et al. 2020). Two notable pathogens on soybean are *C. kikuchii* (leaf blight and purple seed stain) and *C. sojina* (frog-eye leaf spot) (Soares et al. 2015).

Other notable reports include *Cercospora* leaf spots, which are the most common and destructive of the *Hibiscus* diseases, often resulting in complete crop loss (Park et al. 2017) and more than 200 fungal species in association with

various diseases of ‘kenaf’ (*Hibiscus cannabinus*) worldwide (Park et al. 2017). Key proteins and expression of genes that could inhibit the pathogen *C. kikuchii* in soybean (Arantes et al. 2020) have been investigated. However, based on previous reports, morphological characters, phylogeny and pathogenicity of *Cercospora* cf. *nicotianae* was identified as one of several cryptic species causing *Cercospora* leaf blight (Sautua et al. 2019, 2020). Thomas et al. (2020) proposed the expression of fungal cercosporin auto resistance genes and silencing of the cercosporin pathway as effective strategies to combat *Cercospora* diseases.

Pathogen biology, disease cycle and epidemiology

The taxa survive on undecomposed residues in soil, on weed hosts and seeds. Leaf spot disease is favoured by warm, wet weather. Severe outbreaks generally require a period of showery weather. Infection from germinating fungal spores occurs via penetration of leaf stomata by fungal hyphae. Spores spread in wind, rain, irrigation or via mechanical tools (Vereijssen 2004; Lin and Kelly 2018).

Morphological based identification and diversity

Cercospora has been widely applied to all kinds of dematiaceous hyphomycetous asexual morphs characterized by holoblastic conidiogenesis and some associated with “Mycosphaerella”-like sexual morphs (Hyde et al. 2013; Groenewald et al. 2013). Species resembling the genus type, *C. penicillata*, characterized by pigmented conidiophores, thickened and darkened conidiogenous loci and singly formed colourless conidia are identified as *Cercospora sensu stricto* (Ellis 1971, 1976). Chupp (1954) published a worldwide monograph of this group which listed 1,419 species. A vast number of studies related to *Cercospora* are based on morphology or confined to specific regions or hosts (Phengsintham et al. 2013a, b). Hence, more than 3000 species of *Cercospora* have been described (Pollack 1987), often as a result of taxa being considered as host-specific at a genus or family level (Crous and Braun 2003; Groenewald et al. 2005). However, based on morphological features of the structure of conidiogenous loci and hila, absence or presence of pigmentation in conidiophores and conidia, Crous and Braun (2003) revised the generic circumscription of *Cercospora*, resulting in the reduction of the number of species to 659. A series of publications related to *Cercospora* and its allied genera in Mycosphaerellaceae, along with illustrations and descriptions of sexual morphs was published by Braun et al. (2013, 2014, 2015a, b, 2016).

Molecular based identification and diversity

Cercospora is monophyletic (Stewart et al. 1999; Hyde et al. 2013). Groenewald et al. (2013) provided a comprehensive phylogenetic analysis of 360 isolates which included ITS,

and protein-coding genes; translation elongation factor 1-alpha (*tef1*), actin (*act*), calmodulin (*cal*) and histone 3 (*his*). This provided a basis for the identification of *Cercospora* species, indicating most to be host-specific (Park et al. 2017). Bakhshi et al. (2018) subjected 170 *Cercospora* isolates to an eight-gene analysis (*tef1*, *act*, *cal*, *his*, *tub2*, *rpb2*, *gapdh*) which resulted in several new clades within the *C. apii*, *C. armoraciae*, *C. beticola*, *C. cf. flagellaris* and *Cercospora* sp. G. complexes. The combination of *tef1*, *cal*, *tub2*, *rpb2* and *gapdh* provided high phylogenetic resolution for distinguishing *Cercospora* species with *gapdh* being the gene effective in distinguishing the species complexes (Bakhshi et al. 2018). The genomes for several species—*Cercospora arachidicola*, *C. aff. canescens*, *C. cf. sigesbeckiae*, *C. kikuchii*, *C. sojina* and *C. zea-maydis* have been published, of which *C. cf. sigesbeckiae* and *C. sojina* are important soybean pathogens (Albu et al. 2017; Sautua et al. 2019). The mating-type genes of some asexual *Cercospora* species have been characterised (Groenewald et al. 2013), of which *C. beticola*, *C. zea-maydis* and *C. zeina* are heterothallic, while only one mating type was discovered in populations of *C. apii* and *C. apiicola* (Groenewald et al. 2006, 2010).

In soybean cultivation regions such as China, Latin America or the USA, *C. sojina* occurs as several pathotypes named as races, and their existence differs from soybean cultivar-to-cultivar (Athow et al. 1962; Yorinori and Henechin 1978; Mian et al. 2008; Gu et al. 2020). Apart from being differentiated physiologically, several molecular genetic tools such as AFLPs (Amplified Fragment Length Polymorphisms), SSR markers and SNP markers have been utilized to characterize their population diversity (Gu et al. 2020). The combination of DNA sequence data with ecology, morphological and cultural characteristics named as the Consolidated Species Concept (Quaedvlieg et al. 2014) is an effective method for delimiting *Cercospora* species (Groenewald et al. 2013; Bakhshi et al. 2015, 2018). Here we provide an updated phylogenetic tree of combined ITS, *tef1*, *act*, *cal*, *his*, *tub2*, *rpb2* and *gapdh* (Fig. 5).

Recommended genetic markers (genus level)—LSU, ITS
Recommended genetic markers (species level)—ITS, *tef1*, *act*, *cal*, *his*, *tub2*, *rpb2*, *gapdh*

Accepted number of species—There are over 3100 epithets listed in Index Fungorum (2020), however, only 93 have DNA sequence data (Table 4).

References—Braun et al. (2013, 2014, 2015a, b, 2016) (morphology), Groenewald et al. (2013) (morphology, phylogeny), Albu et al. (2017) (morphology, phylogeny), Guatimosim et al. (2016) (morphology, phylogeny), Bakhshi et al. (2015, 2018) (morphology, phylogeny).

Fig. 5 The most parsimonious tree generated by MP analysis of combined ITS, *tef1*, *act*, *cal*, *his*, *tub2*, *rpb2* and *gapdh* sequence data of *Cercospora* species is presented. Related sequences were obtained from previous publications and GenBank. One hundred and fourteen strains are included in the analysis comprising 4222 characters including gaps, of which 2942 characters are constant, 514 characters are parsimony-uninformative and 766 are parsimony-informative. The parsimony analysis of the data matrix resulted in the maximum of 84 equally most parsimonious trees with a length of 3092 steps (CI = 0.557, RI=0.678, RC = 0.382, HI = 0.443) in the first tree. The tree was rooted with *Septoria provencialis* (CBS 118910). Tree topology of the MP analysis was similar to the ML and BYPP analyses. ML and MP bootstrap support values $\geq 70\%$ and BYPP ≥ 0.95 (ML/ MP/ BYPP) are shown respectively near the nodes. Ex-type strains are in bold.

79. *Clinoconidium* Pat., Bulletin de la Société Mycologique de France 14: 156 (1898)

Background

Clinoconidium is an important genus that causes smut disease on plants in the family Lauraceae. This genus was established by Patouillard (1898) and typified with *Clinoconidium farinosum*. Taxonomically, *Clinoconidium* is placed in Cryptobasidiaceae (Exobasidiales, Exobasidiomycetes, Basidiomycota) and characterized by aseptate, colourless, and globose to ovoid basidiospores which are dispersed individually. The name *Clinoconidium* was considered illegitimate because of the designation of an illegitimate type species name; however, it was later validated by Saccardo (1902).

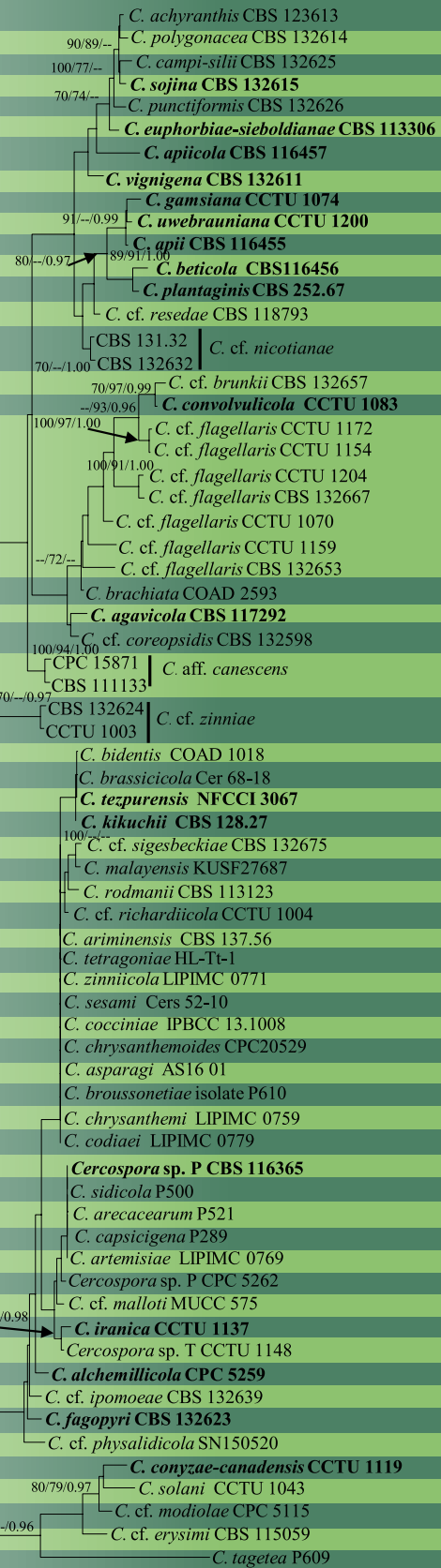
Clinoconidium is a gall producing genus which was once named as *Ustilago* by Ito (1935, 1936) due to the presence of a powdery spore mass on the surface of the galls. This genus was also transferred to another gall producing genus *Melanopsichium* by Kakishima (1982). However, it was renamed as *Clinoconidium* as its sorus structure and spore features are quite different from those of *Ustilago* (Saccardo 1902). The spores of *Ustilago* species are formed from sporogenous hyphae, whereas this fungus produces spores from hymenial layers in the galls. Spore walls are comparatively thinner than those of *Ustilago*. The differentiation from *Melanopsichium*, a gall producing taxon on plants in Polygonaceae (Vánky 2013) includes variation in gall structures and sporulation. *Melanopsichium* produces spores in chambers formed inside of gall tissues, while this genus produces spores in peripheral lacunae on the surface of gall tissues. The morphological characters of these taxa showed its close similarity to *Clinoconidium*.

Classification—Basidiomycota, Ustilaginomycotina, Exobasidiomycetes, Exobasidiomycetidae, Exobasidiales, Cryptobasidiaceae

Type species—*Clinoconidium farinosum* Pat. ex Sacc. & P. Syd

Distribution—Brazil, China, Costa Rica, India, Japan, Panama, Spain, Taiwan and Venezuela

MP/ML/BYPP



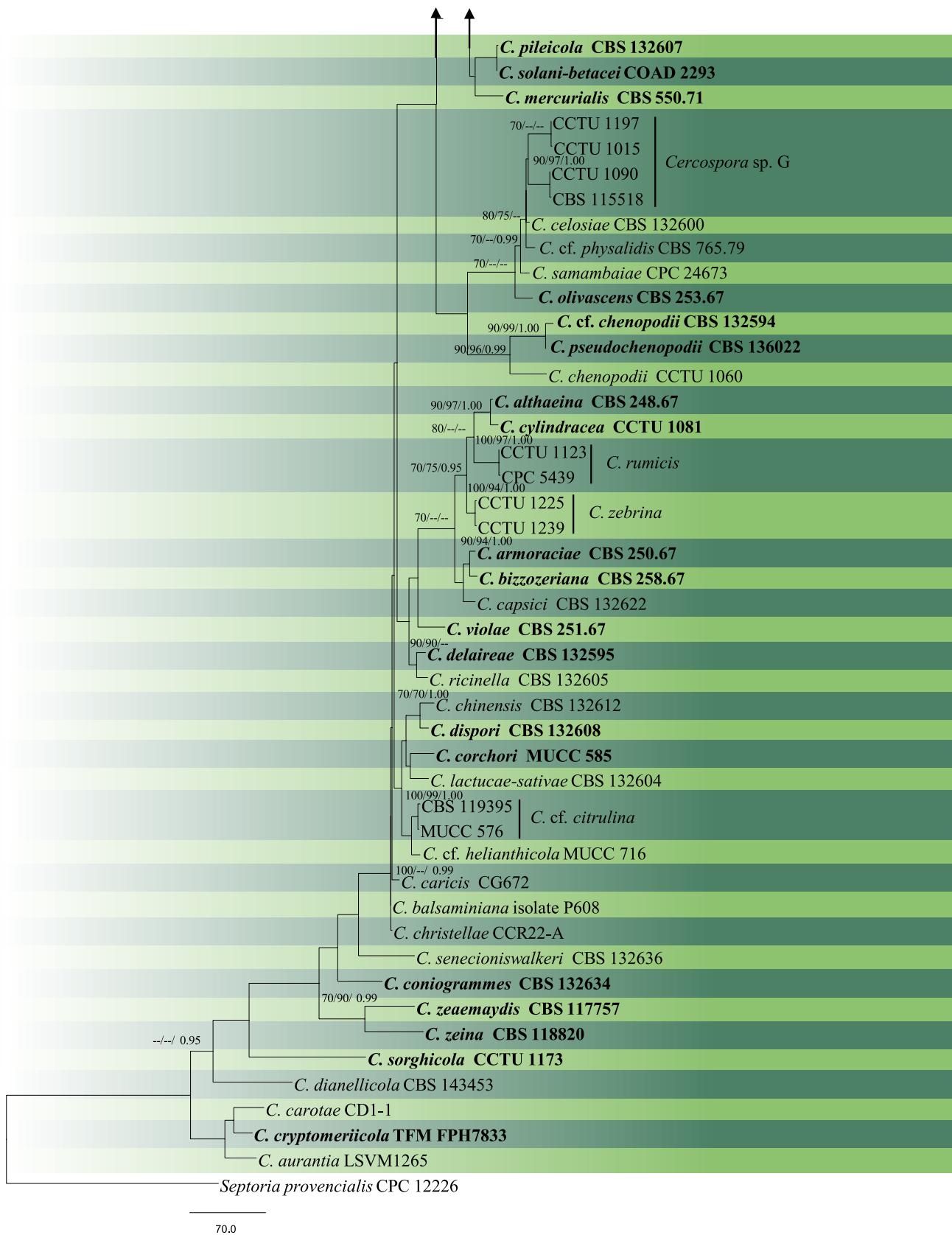


Fig. 5 (continued)

Disease symptoms—mainly observed as powdery pappus gall in fruits. Infection initiates on very young fruits, converted into round, wrinkled galls. The fruit galls are then covered with a powdery mass of spores during early days of infection, withering in the rainy season, leaving behind hard, earthy, brown galls. On **Cinnamon**, entire young fruits are molded with buff and spongy smut like taxa in the full bloom of disease. Interestingly this infection is restricted to fruits only (Fig. 6).

Hosts—different plants of Lauraceae including, *Apollonias barbujana*, *Cinnamomum burmannii*, *C. camphora*, *C. daphnoides*, *C. tamala*, *C. tenuifolium*, *Nectandra* sp., *Ocotea* sp., *Oreodaphne* sp. and *Phoebe neurophylla* (Farr and Rossman 2020).

Morphological based identification and diversity

This is an important pathogenic genus; producing galls on shoot buds of host plants belonging to the family Lauraceae. Fruits of the host are completely or partially transformed into reddish-brown to dark brown, irregularly malformed, enlarged, globose to subglobose galls; larger than normal fruits. Hymenia formed in peripheral lacunae of the galls are pale yellow to whitish and covered by the host epidermis. Inner tissues of galls consist of hyphae and deformed plant cells. Hyphae are intercellular, hyaline, compact, septate, smooth-walled and lack clamp connections, while haustoria are intercellular, slightly lobed to irregular and observed in deformed host cells. Upon maturation, galls rupture, exposing orange to dark brown or creamish white spore masses which cover the entire infected young fruits. Sterile hyphae can be found intermingled between the basidia in some species and are indistinguishable from young basidia or absent in some species of *Clinoconidium*. Basidia are clavate, hyaline, depressed, difficult to observe and gastroid, densely aggregated in masses, formed in irregular fascicles from basally agglutinated hyphae and the wall is densely foveolate when mature. Basidiospores are ellipsoid, clavate, pyriform, fusoid, globose, subglobose to oval, aggregated in a creamish white to brown coloured masses on the surface of the galls, hyaline or wall pale brown to brown, rugose when mature; producing long branched hyphae with septa when germinated on culture media and proliferating sympodially.

Molecular based identification and diversity

There are seven epithets of *Clinoconidium* recorded on various plant hosts. Sequence data for *Clinoconidium bullatum*, *C. cinnamomi*, *C. onumae* and *C. sawadae* are available in GenBank, including sequence data for LSU and ITS. *Clinoconidium farinosum* and *C. globosum* lack sequence

data in GenBank. ITS and LSU are the most suitable loci for f (Fig. 7).

Recommended genetic markers (genus level)—ITS, LSU

Recommended genetic markers (species level)—ITS, LSU
Accepted number of species—There are seven species epithets in Index Fungorum (2020), however, only **four** species have DNA molecular data (Table 5).

References—Hendrichs et al. (2003), Jiang and Kirschner (2016), Kakishima et al. (2017a, b) (morphology, phylogeny)

80. *Cylindrocladiella* Boesew., Canadian Journal of Botany 60 (11): 2289 (1982)

= *Nectricladiella* Crous & C.L. Schoch, Studies in Mycology 45: 54 (2000)

Background

Boeswinkel (1982) established *Cylindrocladiella* to accommodate five *Cylindrocladium*-like species producing small, cylindrical conidia. Even though the generic status of *Cylindrocladiella* was initially opposed by Crous and Wingfield (1993), later studies on morphological comparisons by Crous et al. (1994) and molecular data (Victor et al. 1998; Schoch et al. 2000) supported the establishment of *Cylindrocladiella* as a genus. This genus is commonly confused with the asexual morph of *Calonectria* but can be distinguished by clear morphological differences, such as aseptate stipe extensions, different branching patterns of the conidiophores and comparatively small, aseptate conidia. Although species are generally not regarded as important plant pathogens, correct identification is essential for disease control and biosecurity implications.

Classification—Ascomycota, Sordariomycetes, Hypocreomycetidae, Hypocreales, Nectriaceae

Type species—*Cylindrocladiella parva* (P.J. Anderson) Boesew.

Distribution—as a soil-borne fungus, the species in *Cylindrocladiella* have a cosmopolitan distribution in various geographically and climatically distinct regions around the world (Farr and Rossman 2020).

Disease symptoms—black-foot disease, damping-off, leaf spot, root rot and shoot die-back

Many species belonging to *Cylindrocladiella* are opportunistic plant pathogens but they are not considered as primary pathogens. They can be isolated associated with disease symptoms such as leaf spot, damping off and shoot die-back (Scattolin and Montecchio 2007; Pham 2018). Chocolate brown lesions around the shoots spread primarily to be followed by wilting of the shoot tip, reddish

discolouration, dropping of leaves, and finally plant death (Briellmaier-Liebetanz et al. 2013). Characteristic symptoms of the black-foot disease include a reduction in root biomass and root hairs with sunken and necrotic root lesions (Agustí-Brisach and Armengol 2013). Symptoms of *Cylindrocladiella* root rot are black lesions on the tap and lateral roots, wilting and foliar necrosis, and the outer bark of the seedlings will crack and become loose (Sinclair and Lyon 2005).

Hosts—Species are soil-borne, weak pathogens of forestry, agricultural and horticultural crops. There are 270 records of *Cylindrocladiella* associated with different plant species (Farr and Rossman 2020). Among them, different *Vitis* species and *Eucalyptus* species are common hosts associated with different species of *Cylindrocladiella*.

Morphological based identification and diversity

Cylindrocladiella can be distinguished from related species by penicillate and/or subverticillate symmetrically branched conidiophores which produce small, cylindrical, 1-septate conidia and aseptate stipe extensions (Lombard et al. 2012). The generic status of *Cylindrocladiella* was earlier strongly contested (Sharma and Mohanan 1991), however, based on morphological evaluation and comparisons by Crous and Wingfield (1993) and Crous et al. (2017) confirmed its generic status. Victor et al. (1998) and Schoch et al. (2000) provided molecular data to support generic status. Lombard et al. (2012) in his revision of *Cylindrocladiella* mentioned that only two species have been recognized with their respective *Nectriadiella* sexual morph. Rossman et al. (2013) proposed that the generic name *Cylindrocladiella* be used rather than *Nectriadiella*. Lombard et al. (2015) showed that *Cylindrocladiella* formed a monophyletic group in *Nectriaceae* (Wijayawardene et al. 2020).

Molecular based identification and diversity

Using RFLPs and AT-DNA data, Victor et al. (1998) recognised seven species in the genus. Schoch et al. (2000) added another species based on ITS and partial *tub2*. Van Collier et al. (2005) introduced the use of *his3* sequence data for this group. A combined multilocus phylogeny of *his*, *tef1*, *tub2* and ITS was used by Lombard et al. (2012) which resulted in 18 new *Cylindrocladiella* species and several unresolved species complexes. Lombard et al. (2017) introduced six new species based on a combined ITS, *tef1* and *tub2* dataset. Pham (2018) introduced five new species based on *his*, *tef1*, *tub2* and ITS sequence data and Marin-Felix et al. (2019) introduced two new species based on ITS, *tef1* and *tub2* sequence data. Here we reconstruct the phylogenetic analyses of these species based on ITS, *tef1* and *tub2* sequence data (Fig. 8).

Recommended genetic markers (genus level)—ITS, LSU
Recommended genetic markers (species level)—*his*, *tef1*, *tub2*

Accepted number of species—There are 47 species epithets in Index Fungorum (2020). However, only 46 species have DNA sequence data (Table 6).

References—Crous and Wingfield (1993), Lombard et al. (2012) (morphology); Victor et al. (1998), Schoch et al. (2000), Lombard et al. (2015) (morphology, phylogeny).

81. *Dothidotthia* Höhn., *Berichte der Deutschen Botanischen Gesellschaft* 36: 312 (1918)

Background

Dothidotthia was assigned to Botryosphaeriaceae, because of its coelomycetous asexual morph, and characteristic peridium, pseudoparaphyses and asci (Barr 1989). Ramaley (2005) reported that *Thyrostroma* is the asexual morph of *Dothidotthia* based on the production of hyphomycetes in culture. Phillips et al. (2008), introduced a new family Dothidotthiaceae to accommodate *Dothidotthia* and considered *Thyrostroma* as the asexual morph of *Dothidotthia*. However, the links between the sexual and asexual morphs are not supported by molecular evidence. Recent molecular and morphology studies (Marin-Felix et al. 2017; Crous et al. 2019; Senwanna et al. 2019), based on a taxon sampling of current species indicates that *Dothidotthia* does not cluster near *Thyrostroma*. Thus, *Dothidotthia* is a distinct genus.

Classification—Ascomycota, Pezizomycotina, Dothideomycetes, Pleosporomycetidae, Pleosporales, Dothidotthiaceae

Type species—*Dothidotthia symphoricarpi* (Rehm) Höhn.

Distribution—in both temperate and tropical countries (Italy, Russia, Thailand, Ukraine and the USA)

Disease symptoms—species cause canker, dieback and leaf spot diseases on twig, branch, bark and leaf

Hosts—Pathogens of *Acer negundo*, *Diapensia lapponica*, *Fendlera rupicola*, *Euonymus alatus*, *Robinia pseudoacacia*, *Verbena asparagoides* (Barr 1989; Farr and Rossman 2020; Index Fungorum 2020).

Morphological based identification and diversity

In previous studies, the asexual morphs of *Dothidotthia* have been reported as *Thyrostroma* (Ramaley 2005), however, phylogenetic analyses indicated that *Dothidotthia* can be separated from *Thyrostroma* (Marin-Felix et al. 2017; Crous et al. 2016; Senwanna et al. 2019). *Dothidotthia* is characterized by fusiform to obclavate or obpyriform, 0–3-transversely septate conidia and a sexual morph with clavate, short pedicellate asci, ellipsoid, 1-septate ascospores (Fig. 9). The sexual morphs of *Dothidotthia* and *Thyrostroma* have similar morphological characteristics in shape and overlapping

Table 4 DNA barcodes available for *Cercospora*

Species	Isolate no	ITS	<i>tefl</i>	<i>act</i>	<i>cal</i>	<i>his</i>	<i>tub2</i>	<i>rpb2</i>	<i>gapdh</i>
<i>Cercospora achyranthis</i>	CBS 132613	JX143523	JX143277	JX143031	JX142785	JX142539	–	–	–
	CPC 10091	JX143524	JX143278	JX143032	JX142786	JX142540	–	–	–
<i>C. agavicola</i> [#]	CBS 117292*	AY647237	AY966897	AY966898	AY966899	AY966900	–	–	–
<i>C. alchemillicola</i> [#]	CPC 5259*	JX143525	JX143279	JX143033	JX142787	JX142541	–	–	–
<i>C. althaeina</i>	CBS 248.67*	JX143530	JX143284	JX143038	JX142792	JX142546	MH496340	–	MH496170
<i>C. apii</i> [#]	CBS 116455*	AY840519	AY840486	AY840450	AY840417	AY840384	MH496343	–	MH496173
<i>C. apiicola</i> [#]	CBS 116457*	AY840536	AY840503	AY840467	AY840434	AY840401	–	–	–
<i>C. areacearum</i>	P 521	KC677879	–	–	–	–	–	–	–
<i>C. ariminensis</i>	CBS 137.56	KF251297	KF253245	KF253606	KF253960	–	KF252779	KF252303	–
<i>C. armoraciae</i> [#]	CBS 250.67*	JX143545	JX143299	JX143053	JX142807	JX142561	MH496351	–	MH496181
<i>C. artemisiae</i>	LIPIMC 0769	KC776169	–	–	–	–	–	–	–
<i>C. asparagi</i> [#]	ICMP 21630	KY549097	KY549101	KY549091	KY549093	–	–	–	–
<i>C. aurantia</i>	LSVM12 65	MG956773	–	–	–	–	–	–	–
<i>C. balsaminiana</i>	P608	KC677880	–	–	–	–	–	–	–
<i>C. beticola</i> [#]	CBS 116456*	AY840527	AY840494	AY840458	AY840425	AY840392	MH496355	KT216555	MH496185
<i>C. bidentis</i>	COAD 1018	JX117826	–	–	–	–	–	–	–
<i>C. bizzozzeriana</i> [#]	CBS 258.67*	JX143546	JX143300	JX143054	JX142808	JX142562	MH496368	–	MH496198
<i>C. brachiata</i>	COAD 2593	–	MK118086	MK118087	–	–	–	–	–
<i>C. brassicicola</i>	Cer 68-18	MN209932	–	–	–	–	–	–	–
<i>C. broussonetiae</i>	P610	KC677882	–	–	–	–	–	–	–
<i>C. cf. brunckii</i>	CBS 132657	JX143559	JX143313	JX143067	JX142821	JX142575	–	–	–
<i>C. campi-silii</i>	CBS 132625	JX143561	JX143315	JX143069	JX142823	JX142577	–	–	–
<i>C. canescens</i> [#]	CPC 15871	JX143567	JX143321	JX143075	JX142829	JX142583	–	–	–
	CBS 111133	AY260065	DQ835084	DQ835103	DQ835130	DQ835157	–	–	–
<i>C. capsici</i> [#]	CBS 132622	JX143568	JX143323	JX143077	JX142831	JX142585	–	–	–
<i>C. capsicigena</i>	P289	KC677884	–	–	–	–	–	–	–
<i>C. caricis</i>	CG672	AF284390	–	–	–	–	–	–	–
<i>C. carotae</i>	CD1-1	KF941306	–	–	–	KF941303	–	–	–
<i>C. celosiae</i>	CBS 132600	JX143570	JX143326	JX143080	JX142834	–	–	–	–
<i>C. chenopodii</i> [#]	CBS 132594*	JX143572	JX143328	JX143082	JX142836	JX142590	–	–	–
	CCU 1060	KJ886438	KJ886277	KJ885955	KJ885794	KJ886116	MH496371	MH511862	MH496201
<i>C. chinensis</i>	CBS 132612	JX143578	JX143334	JX143088	JX142842	JX142596	–	–	–
<i>C. christellae</i>	CCR22 isolate A	FJ460222	–	–	–	–	–	–	–
<i>C. chrysanthemi</i>	LIPIMC 0759	KC776154	–	–	–	–	–	–	–
<i>C. chrysanthemoides</i>	CPC 20529	KC005779	KC005813	KC005764	KC005767	–	–	–	–
<i>C. citrullina</i> [#]	CBS 119395	EU514222	JX143335	JX143089	JX142843	–	–	–	–
	MUCC 576	JX143579	JX143337	JX143091	JX142845	–	–	–	–
<i>C. coccinia</i>	IPBCC 13.1008	KC776158	–	–	–	–	–	–	–
<i>C. codiae</i>	LIPIMC 0779	KC776170	–	–	–	–	–	–	–
<i>C. coniogrammes</i>	CBS 132634*	JX143583	JX143341	JX143095	JX142849	JX142603	–	–	–
<i>C. convolvulicola</i>	CCU 1083*	KJ886441	KJ886280	KJ885958	KJ885797	KJ886119	MH496374	MH511865	MH496204
<i>C. conyzae-canadensis</i>	CCU 1119*	KJ886445	KJ886284	KJ885962	KJ885801	KJ886123	MH496377	MH511868	MH496207
<i>C. corchori</i>	MUCC 585*	JX143584	JX143342	JX143096	JX142850	JX142604	–	–	–
<i>C. cf. coreopsidis</i>	CBS 132598	JX143585	JX143343	JX143097	JX142851	JX142605	–	–	–
<i>C. cryptomeriicola</i>	TFM:FPH7833	AB277789	–	–	–	–	–	–	–
<i>C. cylindracea</i>	CCU 1081*	KJ886449	KJ886288	KJ885966	KJ885805	KJ886127	MH496381	MH511872	MH496211
<i>C. delaireae</i>	CBS 13259*	JX143587	JX143345	JX143099	JX142853	JX142607	–	–	–
<i>C. dianellicola</i>	CBS 143453*	MG386075	–	MG674152	MG674153	–	–	–	–
<i>C. dispori</i>	CBS 13260*	JX143591	JX143349	JX143103	JX142857	JX142611	–	–	–
<i>C. cf. erysimi</i>	CBS 115059	JX143592	JX143350	JX143350	JX142858	JX142612	–	–	–
<i>C. euphorbiaesieboldianae</i>	CBS 113306*	JX143593	JX143351	JX143105	JX142859	JX142613	–	–	–
<i>C. fagopyri</i>	CBS 132623*	JX143594	JX143352	JX143106	JX142860	JX142614	–	–	–

Table 4 (continued)

Species	Isolate no	ITS	<i>tefl</i>	<i>act</i>	<i>cal</i>	<i>his</i>	<i>tub2</i>	<i>rpb2</i>	<i>gapdh</i>
<i>C. cf. flagellaris</i> [#]	CCTU 1159	KJ886493	KJ886332	KJ886010	KJ885849	KJ886171	MH496388	MH511879	MH496218
	CBS 132653	JX143603	JX143361	JX143115	JX142869	JX142623	MH496390	MH511881	MH496220
	CCTU 1204	KJ886505	KJ886344	KJ886022	KJ885861	KJ886183	MH496399	MH511890	MH496229
	CBS 132667	JX143604	JX143362	JX143116	JX142870	JX142624	MH496401	MH511892	MH496231
	CCTU 1172	KJ886501	KJ886340	KJ886018	KJ885857	KJ886179	MH496409	MH511900	MH496239
	CCTU 1154	KJ886489	KJ886328	KJ886006	KJ885845	KJ886167	MH496410	MH511901	MH496240
<i>C. gamsiana</i>	CCTU 1074*	KJ886426	KJ886265	KJ885943	KJ885782	KJ886104	MH496446	MH511937	MH496276
<i>C. cf. gossypii</i>	CCTU 1070	KJ886467	KJ886306	KJ885984	KJ885823	KJ886145	MH496452	MH511943	MH496282
<i>C. helianthicola</i> [#]	MUCC 716	JX143615	JX143374	JX143128	JX142882	JX142636	–	–	–
<i>C. ipomoeae</i> [#]	CBS 132639	JX143616	JX143375	JX143129	JX142883	JX142637	–	–	–
<i>C. iranica</i>	CCTU 1137*	KJ886513	KJ886352	KJ886030	KJ885869	KJ886191	MH496455	MH511946	MH496285
<i>C. kikuchii</i>	CBS 128.27*	DQ835070	DQ835088	DQ835107	DQ835134	DQ835161	–	–	–
<i>C. lactuca-sativae</i>	CBS 132604	JX143621	JX143380	JX143134	JX142888	JX142642	–	–	–
<i>C. malayensis</i>	KUS-F27687	KR400012	KY082663	KY082664	KY082665	KY082666	–	–	–
<i>C. cf. malloti</i>	MUCC 575	JX143625	JX143384	JX143138	JX142892	JX142646	–	–	–
<i>C. mercurialis</i>	CBS 550.71*	JX143628	JX143628	JX143141	JX142895	JX142649	–	–	–
<i>C. cf. modiolae</i>	CPC 5115	JX143630	JX143389	JX143143	JX142897	JX142651	–	–	–
<i>C. cf. nicotianae</i>	CBS 131.32	DQ835073	DQ835099	DQ835119	DQ835146	DQ835173	–	–	–
	CBS 132632	JX143631	JX143390	JX143144	JX142898	JX142652	–	–	–
<i>C. olivascens</i>	CBS 253.67*	JX143632	JX143391	JX143145	JX142899	JX142653	–	–	–
<i>C. cf. physalidicola</i>	SN150520	–	KT275242	KT223391	KT275241	KT275240	–	–	–
<i>C. cf. physalidis</i> [#]	CBS 765.79	JX143633	JX143392	JX143146	JX142900	–	–	–	–
<i>C. pileicola</i>	CBS 132607*	JX143634	JX143393	JX143147	JX142901	JX142655	–	–	–
<i>C. plantaginis</i>	CBS 252.67*	DQ233318	DQ233342	DQ233368	DQ233394	DQ233420	MH496461	–	MH496291
<i>C. polygonacea</i>	CBS 132614	JX143637	JX143396	JX143150	JX142904	JX142658	–	–	–
<i>C. pseudochenopodii</i>	CBS 136022*	KJ886516	KJ886355	KJ886033	KJ885872	KJ886194	MH496464	MH511954	MH496294
<i>C. punctiformis</i>	CBS 132626	JX143638	JX143397	JX143151	JX142905	JX142659	–	–	–
<i>C. cf. resedae</i>	CBS 118793	JX143639	JX143398	JX143152	JX142906	JX142660	–	–	–
<i>C. cf. richardiicola</i> [#]	CBS 132627	JX143640	JX143399	JX143153	JX142907	JX142661	MH496465	MH511955	MH496295
<i>C. ricinella</i> [#]	CBS 132605	JX143646	JX143405	JX143159	JX142913	JX142667	–	–	–
<i>C. rodmanii</i>	CBS 113123	DQ835076	AF146136	DQ835122	DQ835149	DQ835176	–	–	–
<i>C. rumicis</i>	CCTU 1123	KJ886521	KJ886360	KJ886038	KJ885877	KJ886199	MH496466	MH511956	MH496296
<i>C. rumicis</i>	CPC 5439	JX143648	JX143407	JX143161	JX142915	JX142669	–	–	–
<i>C. samambaiae</i>	CPC 24673	KT037514	KT037474	KT037596	KT037463	KT037555	–	–	–
<i>C. senecioniswalkeri</i>	CBS 132636	JX143649	JX143408	JX143162	JX142916	JX142670	–	–	–
<i>C. sesami</i>	Cers52-10	MK027103	–	–	–	–	–	–	–
<i>C. sidicola</i>	P500	KC677888	–	–	–	–	–	–	–
<i>C. cf. sigesbeckiae</i> [#]	CBS 132675	JX143655	JX143414	JX143168	JX142922	JX142676	–	–	–
<i>C. sojina</i>	CBS 132615	JX143659	JX143419	JX143173	JX142927	JX142681	–	–	–
<i>C. solani</i> [#]	CCTU 1043	KJ886523	KJ886362	KJ886040	KJ885879	KJ886201	MH496469	MH511959	MH496299
<i>C. sorghicola</i>	CCTU 1173*	KJ886525	KJ886364	KJ886042	KJ885881	KJ886203	MH496471	MH511961	MH496301
<i>Cercospora</i> sp. P	CBS 116365*	AY752141	AY752176	AY752204	AY752235	AY752266	–	–	–
<i>Cercospora</i> sp. P	JZG-2013	JX143714	JX143473	JX143227	JX142981	JX142735	–	–	–
<i>Cercospora</i> sp. G	CCTU 1197	KJ886540	KJ886379	KJ886057	KJ885896	KJ886218	MH496472	MH511962	MH496302
<i>Cercospora</i> sp. G	CCTU 1015	KJ886528	KJ886367	KJ886045	KJ885884	KJ886206	MH496473	MH511963	MH496303
<i>Cercospora</i> sp. G	CCTU 1090	KJ886536	KJ886375	KJ886053	KJ885892	KJ886214	MH496476	MH511965	MH496306
<i>Cercospora</i> sp. G	CBS 115518	JX143681	JX143441	JX143195	JX142949	JX142703	MH496480	–	MH496310
<i>Cercospora</i> sp. T	CCTU 1148	KJ886541	KJ886380	KJ886058	KJ885897	KJ886219	MH496488	MH511976	MH496318
<i>C. tagetea</i>	P609	KC677890	–	–	–	–	–	–	–
<i>C. tetragoniae</i>	HL_Tt-1	MT095118	–	–	–	–	–	–	–
	NFCCI3067*	KC351743	KC513746	KC355808	KC513745	KC355807	–	–	–
<i>C. uwebaruniana</i>	CCTU 1200*	KJ886408	KJ886247	KJ885925	KJ885764	KJ886086	MH496489	MH511977	MH496319
<i>C. vignigena</i>	CBS 132611*	JX143734	JX143493	JX143247	JX143001	JX142755	–	–	–

Table 4 (continued)

Species	Isolate no	ITS	<i>tef1</i>	<i>act</i>	<i>cal</i>	<i>his</i>	<i>tub2</i>	<i>rpb2</i>	<i>gapdh</i>
<i>C. violae</i> [#]	CBS 251.67*	JX143737	JX143496	JX143250	JX143004	JX142758	MH496492	–	MH496322
<i>C. zeaе-maydis</i> [#]	CBS 117757*	DQ185074	DQ185086	DQ185098	DQ185110	DQ185122	–	–	–
<i>C. zebrina</i> [#]	CCTU 1225	KJ886550	KJ886389	KJ886067	KJ885906	KJ886228	MH496495	MH511981	MH496325
	CCTU 1239	KJ886551	KJ886390	KJ886068	KJ885907	KJ886229	MH496504	MH511987	MH496334
<i>C. zeina</i> [#]	CBS 118820*	DQ185081	DQ185093	DQ185105	DQ185117	DQ185129	–	–	–
<i>C. cf. zinniae</i>	CBS 132624	JX143756	JX143518	JX143272	JX143026	–	–	–	–
	CCTU 1003	KJ886552	KJ886391	KJ886069	KJ885908	KJ886230	MH496505	MH511988	MH496335
<i>C. zinnicola</i>	LIPIMC 0771	KC776162	–	–	–	–	–	–	–

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold. Species confirmed with pathogenicity studies are marked with[#]

Fig. 6 *Clinoconidium* sp. on *Cinnamomum* sp. **a** host plant with infected and healthy fruits, **b** healthy fruits, **c, d** infected fruits at various stages of infection



dimensions of asci and ascospores (Barr 1989; Ramaley 2005; Phillips et al. 2008; Hyde et al. 2013; Senwanna et al. 2019). However, *Dothidotthia* can be differentiated from *Thyrostroma* by peridium structure and conidial morphology and molecular phylogeny (Senwanna et al. 2019). Crous et al. (2019) introduced *Neodothidotthia* to accommodate *N. negundinicola* and *Dothidotthia aspera* was synonymized under *N. negundinis* based on analysis of LSU sequence data. However, Senwanna et al. (2019) showed that *Neodothidotthia negundinicola* and *N. negundinis* group with *D. robiniae* and *D. symphoricarpi* (type species). Furthermore, the conidial morphology of *Neodothidotthia* is similar to *Dothidotthia symphoricarpi* (*Pseudothia symphoricarpi*) and *D. robiniae* (Phillips et al. 2008; Zhang et al. 2012; Crous et al. 2019; Senwanna et al. 2019). Therefore, *Neodothidotthia* had been treated as a synonym of *Dothidotthia*.

Molecular based identification and diversity

Dothidotthia species can be separated from *Thyrostroma* based on LSU sequence data (Marin-Felix et al. 2017; Crous et al. 2019). Multigene phylogenetic analyses of a combined LSU, SSU, ITS and *tef1* dataset for *Dothidotthia* is presented in this study, which is similar to Senwanna et al. (2019) (Fig. 10).

Recommended genetic markers (genus level)—LSU, SSU
Recommended genetic markers (species level)—ITS, *tef1*, *rpb2* and *tub2*

Accepted number of species—There are 14 epithets listed in Index Fungorum (2020), however only **four** species have DNA molecular data (Table 7).

References—Barr (1989), Ramaley (2005) (morphology); Phillips et al. (2008), Zhang et al. (2012), Hyde et al. (2013),

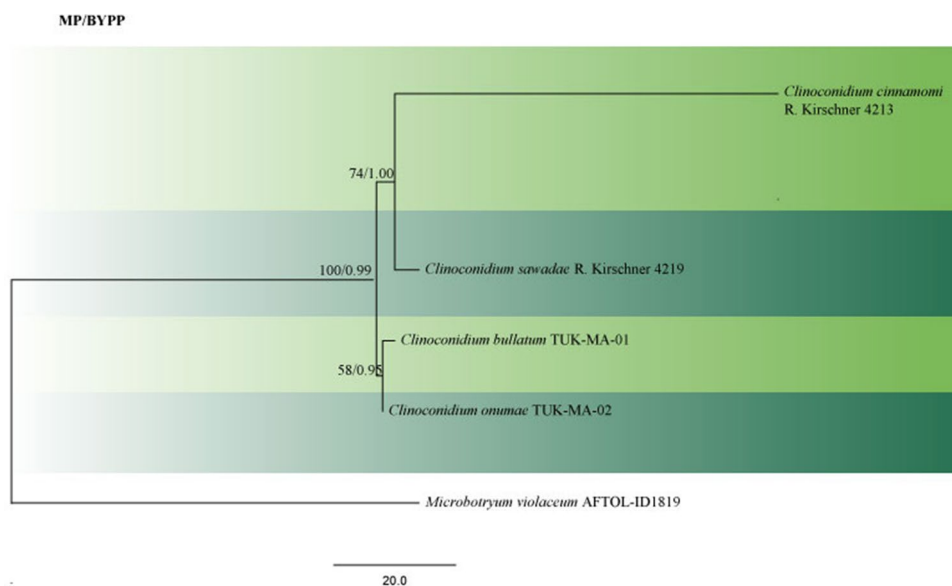


Fig. 7 Phylogram generated from MP analysis based on combined sequences of LSU and ITS sequences of all the species of *Clinocooidium* with molecular data. Related sequences were obtained from GenBank. Five taxa are included in the analyses, which comprise 1100 characters including gaps, of which 910 characters are constant, 182 characters are parsimony-uninformative, eight characters parsimony-informative. The parsimony analysis of the data matrix

resulted in the maximum of two equally most parsimonious trees with a length of 202 steps (CI = 0.980, RI 0.500, RC = 0.490, HI = 0.020) in the first tree. Single gene analyses were carried out and compared with each species, to compare the topology of the tree and clade stability. The tree was rooted with *Microbotryum violaceum* (AFTOL-ID1819). Maximum parsimony bootstrap support value $\geq 50\%$ and BYPP ≥ 0.9 are shown respectively near the nodes

Table 5 DNA barcodes available for *Clinocooidium*

Species name	Strain Name	ITS	LSU
<i>Clinocooidium bullatum</i>	TUK-MA-01	–	AB178259
<i>C. cinnamomi</i>	R. Kirschner 4213	KX196602	KX196604
<i>C. onumae</i>	TUK-MA-02	–	AB178260
<i>C. sawadae</i>	R. Kirschner 4219	KX196600	KX196603

Marin-Felix et al. (2017), Crous et al. (2019), Senwanna et al. (2019) (morphology and phylogeny)

82. Erysiphaceae Tul. & C. Tul. [as ‘Erysiphei’], Select. fung. carpol. (Paris) 1: [191] (1861)

Background

Powdery mildews belong to *Erysiphales* of *Ascomycota* (Mori et al. 2000). Powdery mildews are one of the most prevalent and easily recognizable of plant diseases (Glawe 2008). *Mucor erysiphe*, published by Linnaeus (1753), was the first binomial referring to powdery mildew (now known as *Phyllactinia guttata*) (Braun and Cook 2012). Infections are often conspicuous owing to the profuse production of conidia that give them their common name. Powdery mildews are also models for basic research on host-parasite interactions, developmental morphology, cytology, and molecular biology (Glawe 2008). *Erysiphaceae* is obligately parasitic and as such, their life cycle depends completely on living hosts, from which they

obtain nutrients without killing host cells and without which they are unable to survive. As they are obligate plant pathogens, researchers have not had the advantage of routinely cultivating these taxa on artificial media. However, many powdery mildews have been grown on detached leaves of their hosts (Hirose et al. 2005). Powdery mildews seldom kill their host, but are responsible for water and nutrient loss and impaired growth and development. They can increase respiration and transpiration and interfere with photosynthesis and reduce yields.

Changes in host range directly cause the niche separation of powdery mildews and thus may become a trigger of speciation in their evolution. It is possible that studying the evolutionary history of powdery mildews will not only reveal facts on fungal evolution but may also lead us to consider the evolutionary history of angiosperm plants (Takamatsu 2004; Matsuda and Takamatsu 2003; Hirata et al. 2000; Mori et al. 2000).

The first systematic trial to identify the conidial states of powdery mildews at the species level was made by Ferraris (1910), who grouped species of *Oidium* according to the size and shape of their conidia and provided a key to its species. Foex (1913), Jaczewski (1927), and Brundza (1934) contributed to the classification of the conidiophore types. Jaczewski (1927) introduced the terms ‘Euoidium and Pseudoidium’ for *Oidium* states with catenate and solitary conidia, respectively. Yarwood (1957) provided a survey on the Erysiphaceae, including the asexual morphs.

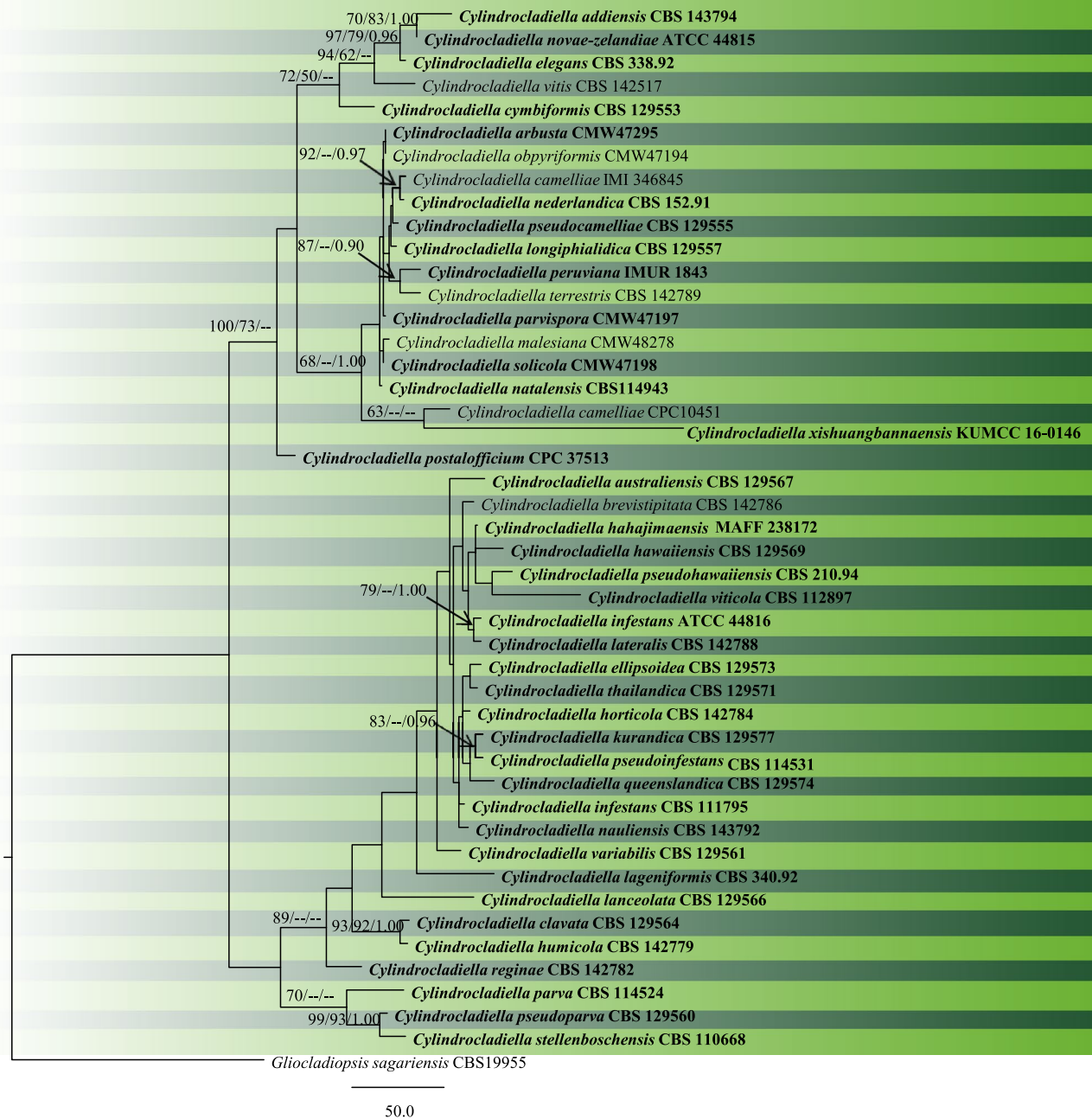


Fig. 8 Phylogram generated from MP analysis based on combined sequences of ITS, *tef1* and *tub2* sequences of all the accepted species of *Cylindrocladiella*. Related sequences were obtained from GenBank. Forty-six taxa are included in the analyses, which comprise 2460 characters including gaps. Single gene analyses were carried out and compared with each species, to compare the topology of the tree and clade stability. The tree was rooted with *Gliocladiopsis sagariensis* (CBS 19955). The best scoring RAXML tree with a final

likelihood value of -6772.195394 is presented. The matrix had 261 distinct alignment patterns, with 0.96% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.230657, C = 0.279364, G = 0.252128, T = 0.237852; substitution rates AC = 1.388608, AG = 2.845402, AT = 2.389715, CG = 0.838197, CT = 7.220493, GT = 1.000000; gamma distribution shape parameter = 0.650385. Maximum likelihood and MP bootstrap support value > 50% are shown respectively near the nodes. Ex-type strains are in bold

Boesewinkel (1980) provided the first comprehensive key based on a combination of more than 12 morphological characteristics observed on conidia, conidiophores, appressoria, haustoria, fibrosin bodies, and mycelium. Braun

(1987) issued a second comprehensive monograph of the *Erysiphales* encompassing all powdery mildew taxa known at that time. Shin and La (1993) and Shin and Zheng (1998) introduced some new morphological features of taxonomic

Table 6 DNA barcodes available for *Cylindrocladiella*

Species	Isolate No	ITS	<i>tefl</i>	<i>tub2</i>
<i>Cylindrocladiella addiensis</i>	CBS 143794*	MH111383	MH111393	MH111388
<i>C. arbusta</i> [#]	CMW 47295*	MH017015	MH016977	MH016958
<i>C. australiensis</i>	CBS 129567*	JN100624	JN099060	JN098747
<i>C. brevistipitata</i>	CBS 142786*	–	MF444940	MF444926
<i>C. camelliae</i>	IMI 346845	AF220952	JN099087	AY793471
<i>C. clavata</i>	CBS 129564*	JN099095	JN098974	JN098752
<i>C. cymbiformis</i>	CBS 129553*	JN099103	JN098988	JN098753
<i>C. elegans</i>	CBS 338.92*	AY793444	JN099039	AY793474
<i>C. ellipsoidea</i>	CBS 129573*	JN099094	JN098973	JN098757
<i>C. hahajimaensis</i>	MAFF 238172*	JN687561	JN687562	–
<i>C. hawaiiensis</i>	CBS 129569*	JN100621	JN099057	JN098761
<i>C. horticola</i>	CBS 142784*	MF444911	MF444938	MF444924
<i>C. humicola</i>	CBS 142779*	MF444906	MF444933	MF444919
<i>C. infestans</i>	CBS 111795*	AF220955	JN099037	AF320190
<i>C. kurandica</i>	CBS 129577*	JN100646	JN099083	JN098765
<i>C. lageniformis</i>	CBS 340.92*	AF220959	JN099003	AY793481
<i>C. lanceolata</i>	CBS 129566*	JN099099	JN098978	JN098789
<i>C. lateralis</i>	CBS 142788*	MF444914	MF444942	MF444928
<i>C. longiphialidica</i>	CBS 129557*	JN100585	JN098966	JN098790
<i>C. longistipitata</i>	CBS 116075*	AF220958	JN098993	AY793506
<i>C. malesiana</i> [#]	CMW 48278*	MH017019	MH016981	MH016962
<i>C. microcylindrica</i>	CBS 111794*	AY793452	JN099041	AY793483
<i>C. natalensis</i>	CBS 114943*	JN100588	JN099016	JN098794
<i>C. nederlandica</i>	CBS 152.91*	JN100603	JN099033	JN098800
<i>C. novazelandica</i>	CBS 486.77*	AF220963	JN099050	AY793485
<i>C. nauliensis</i>	CBS 143792*	MH111387	MH111397	MH111392
<i>C. obpyriformis</i> [#]	CMW 47194*	MH017022	–	MH016966
<i>C. parva</i>	CBS 114524	AF220964	JN099009	AY793486
<i>C. parvispora</i> [#]	CMW 47197*	MH017025	MH016987	MH016968
<i>C. peruvianum</i>	IMUR 1843*	AF220966	JN098968	AY793500
<i>C. postalofficium</i>	CPC 37513*	MN562148	–	MN556845
<i>C. pseudocamelliae</i>	CBS 129555*	JN100577	JN098958	JN098814
<i>C. pseudohawaiiensis</i>	CBS 210.94*	JN099128	JN099012	JN098819
<i>C. pseudoinfestans</i>	CBS 114531*	AF220957	JN099004	AY793508
<i>C. pseudoparva</i>	CBS129560*	JN100620	JN099056	JN098824
<i>C. queenslandica</i>	CBS 129574*	JN099098	JN098977	JN098826
<i>C. reginae</i>	CBS 142782*	MF444909	MF444936	MF444922
<i>C. solicola</i> [#]	CMW47198*	MH017021	MH016983	MH016964
<i>C. stellenboschensis</i>	CBS 110668*	JN100615	JN099051	JN098829
<i>C. terrestris</i>	CBS 142789*	MF444915	MF444943	MF444929
<i>C. thailandica</i>	CBS 129571*	JN100582	JN098963	JN098834
<i>C. variabilis</i>	CBS 129561*	JN100643	JN099080	JN098719
<i>C. viticola</i> [#]	CBS 112897*	AY793468	JN099064	AY793504
<i>C. vitis</i> [#]	CBS 142517*	KY979751	KY979891	KY979918
<i>C. xishuangbannaensis</i>	KUMCC 16-0146*	MH388337	MH388372	–

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold. Species confirmed with pathogenicity studies are marked with [#]

relevance. A progressive report was provided by the work of Cook et al. (1997), who examined the surface of conidia by scanning electron microscopy and separated *Oidium*

into eight subgenera. Braun (1999) discussed the classification of Erysiphaceae as proposed by Cook et al. (1997) and introduced some corrections and alterations. Fundamental

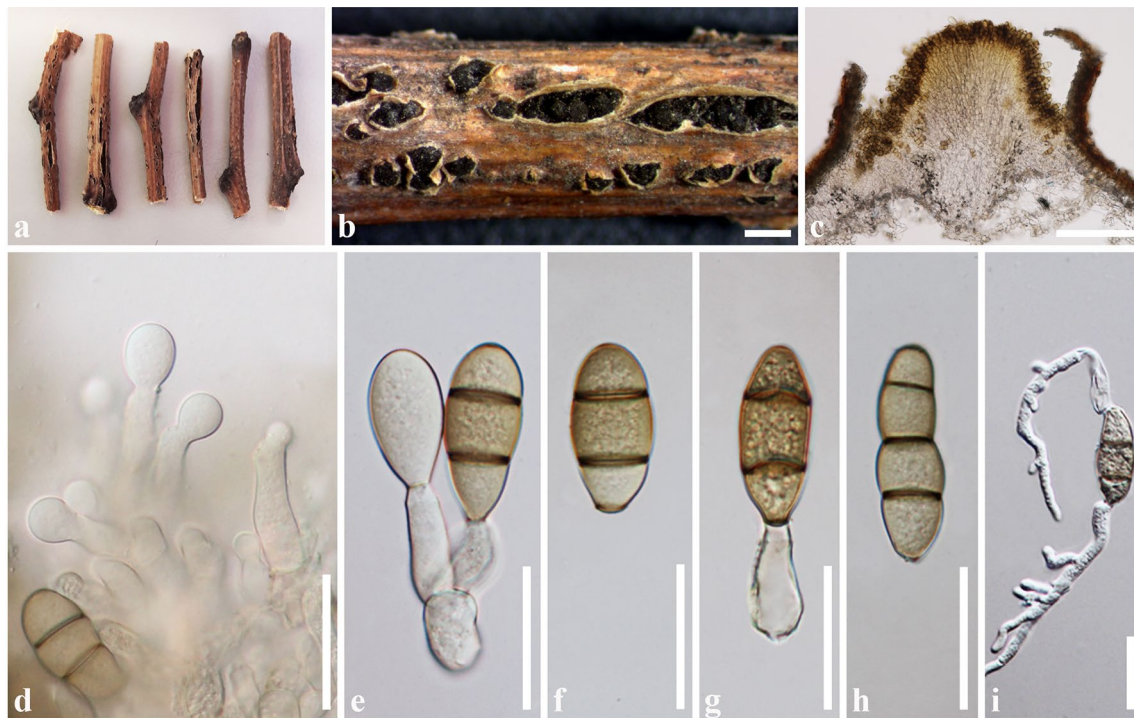


Fig. 9 *Dothidotthia robiniae* (MFLU 16-1704). **a, b** Sporodochia on the host surface. **c** Vertical section of sporodochium. **d** Conidiogenesis. **e, g** Conidia attached with the conidiogenous cells. **f, h** Conidia. **i** Germinated conidium. Scale bars: **b** = 1000 μ m, **c** = 200 μ m, **d–i** = 30 μ m

innovations in the generic taxonomy of the group based on molecular and SEM examination and a better insight into the phylogeny are results of comprehensive investigations over the last decade (Takamatsu et al. 1998, 1999, 2000, 2005a, b, 2008; Matsuda and Takamatsu 2003; Hirose et al. 2005; Liberato et al. 2006; Braun and Cook 2012).

Classification—Ascomycota, Pezizomycotina, Leotiomyces, Leotiomycetidae, Erysiphales

Type genus—*Erysiphe* R. Hedw. ex DC.

Distribution—worldwide

Disease symptoms—powdery mildew

The initial signs of infection appear on young leaves in the form of small, raised blisters, which cause the leaves to curl and expose the under surfaces. As the disease progresses, round, pinpoint powdery white spots dusting the upper surfaces of leaves, as well as stems and occasionally fruiting occurs. As the disease becomes severe, the spots will become larger, and more interconnected and irregular in shape. Over time they progress from younger to older leaves and the undersides of leaves. However, mature leaves are usually much less severely infected than new or young leaves. If the white patches (which have a granular, powdery texture) are wiped away, the growths will return in a matter of days. Severely infected leaves will turn yellow, dry out and drop from the plant. Buds and growing tips of shoots can also become infected, eventually becoming distorted and

stunted (Bushnell and Allen 1962; Davis et al. 2001; Romero et al. 2003; Oberti et al. 2014; Saharan et al. 2019).

Hosts—The host range of this fungal group is strictly confined to angiosperms and powdery mildews have never been reported to infect ferns or gymnosperms (Amano 1986; Hirata et al. 2000; Takamatsu et al. 2010). They affect a wide range of angiosperms such as cereals and grasses, vegetables, ornamentals, weeds, shrubs, fruit trees, and broad-leaved shade and forest trees. Powdery mildews are considered as host-specific.

Pathogen biology, disease cycle and epidemiology

Powdery mildews tend to grow superficially, or epiphytically, on plant surfaces. During the growing season, hyphae are produced on both the upper and lower leaf surfaces, although some species are restricted to one leaf surface. Infections can also occur on stems, flowers or fruit. Specialized absorption cells, termed haustoria, extend into the plant epidermal cells to obtain nutrition. While most powdery mildews produce epiphytic mycelium, a few genera produce hyphae that are within the leaf tissue; this is known as endophytic growth. Conidia are produced on plant surfaces during the growing season. They develop either singly or in chains on conidiophores. Conidiophores arise from the epiphytic hyphae, or in the case of endophytic hyphae, the conidiophores emerge through leaf stomata. At the end of the growing season, powdery mildews produce ascospores,

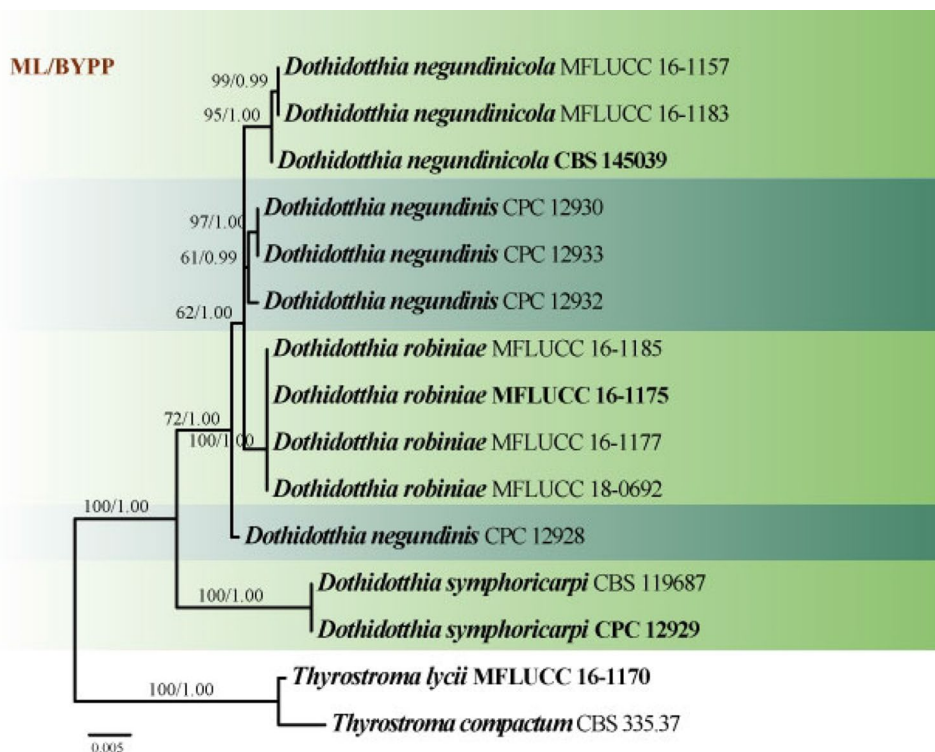


Fig. 10 Phylogenetic tree generated by ML analysis of LSU, SSU, ITS and *tef1* sequence data of *Dothidotthia* species. Related sequences were obtained from GenBank. The tree was rooted with *Thyrostroma compactum* (CBS 335.37) and *T. lycii* (MFLUCC 16-1170). Tree topology of the ML analysis was similar to the Bayesian analysis. The best scoring RAxML tree with a final likelihood value of -5116.933762 is presented. The matrix had 115 distinct alignment patterns, with 25.41% of

undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.245094, C = 0.237101, G = 0.269739, T = 0.248067; substitution rates AC = 3.925871, AG = 7.445430, AT = 2.745308, CG = 2.728664, CT = 20.049514, GT = 1.000000; gamma distribution shape parameter $\alpha = 0.790240$. Maximum likelihood bootstrap support values greater than 60% and BYPP probabilities ≥ 0.95 are indicated above the nodes. Ex-type (ex-epitype) and voucher strains are in bold

Table 7 DNA barcodes available for *Dothidotthia*

Species	Isolate no	LSU	SSU	ITS	<i>tef1</i>
<i>Dothidotthia negundinicola</i>	CBS 145039*	MK442537	–	MK442597	–
	MFLUCC 16-1157	MK751815	MK751760	MK751725	MK908015
	MFLUCC 16-1183	MK751816	MK751761	MK751726	MK908016
<i>D. negundinis</i>	CPC 12930	EU673274	EU673226	MK442599	–
	CPC 12932	EU673275	EU673227	MK442600	–
	CPC 12933	EU673276	EU673228	MK442601	–
<i>D. robiniae</i>	MFLUCC 16-1175*	MK751817	MK751762	MK751727	MK908017
	MFLUCC 16-1177	MK751818	MK751763	MK751728	MK908018
	MFLUCC 16-1185	MK751819	MK751764	MK751729	MK908019
	MFLUCC 18-0692	MK751821	MK751766	MK751731	MK908021
<i>D. symphoricarpi</i>	CPC 12929*	EU673273	EU673224	–	–
	CBS 119687	MH874618	–	MH863064	–

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold

in a sac-like ascus enclosed in a fruiting body called a chasmothecium. The chasmothecium is generally spherical with no natural opening; asci with ascospores are released when a crack develops in the wall of the fruiting body. A variety of appendages may occur on the surface of the chasmothecia.

These appendages are thought to act as the hooks of a velcro fastener, attaching the fruiting bodies to the host, particularly to the bark of woody plants, where they overwinter. They can survive winter conditions as dormant mycelia within the buds and other plant tissue of the host. These infected parts

of the host can be the source of primary inoculum that can initiate further infection when conditions are right (Misra 2001; Amsalem et al. 2006; Heffer et al. 2006; Te Beest et al. 2008; Saharan et al. 2019; Fig. 11).

Morphological based identification and diversity

Members of Erysiphaceae cause powdery mildew disease on about 10,000 angiosperm species (Takamatsu et al. 2010). The Erysiphaceae are divided into five tribes and two basal genera (Cook et al. 1997). Both tree-parasitic and herb-parasitic species are included in three of the five tribes: Cystothecae, Erysipheae and Phyllactinieae. Tree-parasitic species usually take basal positions in these tribes and herb-parasitic species have derived positions. The tribe, Golovinomycetea is a group derived from a single ancestor (Mori et al. 2000). The monophyly of the tribe is also supported by the common characteristics, i.e., ectophytic parasitism, polyascal ascospores, and *Euoidium* asexual morphs, with the latter producing conidia in chains without distinct fibrosin bodies. Of these five lineages, four consists of taxa infectious to dicotyledons. *Blumeria graminis*, which is infectious to monocotyledon plants, formed an independent lineage. Therefore, *Blumeria graminis* was accommodated in a monotypic tribe Blumerieae in the new system (Inuma et al. 2007).

The powdery mildew belonging to the tribe Cystothecae have both herbaceous and woody plants as hosts and consist of three genera, *Cystotheca*, *Podosphaera* and *Sawadaea*, of which *Cystotheca* and *Sawadaea* are restricted to a narrow range of host families (Meeboon et al. 2013). *Podosphaera* consists of two sections, *Podosphaera* and *Sphaerotheca*. Section *Podosphaera* parasitizes woody plants (Takamatsu et al. 2000). The tribe Golovinomyceteae consists of three genera, *Golovinomyces*, *Neoerysiphe*, and *Arthrocladiella*. *Arthrocladiella* is a monotypic genus consisting of a single species *A. mougeottii* and has only the host genus *Lycium*. *Neoerysiphe* is also a small genus composed of four species and has about 300 herbaceous host species ranging across five plant families including *Lamiaceae*. *Golovinomyces* is a large genus comprising 27 species (Braun 1987), and it is widely distributed in the world. The tribe Phyllactinieae comprises the genera *Phyllactinia*, *Leveillula*, *Pleochaeta* and *Queirozia* which typically have hemi-endophytic (partly external and partly internal mycelia in common (Braun 1987; Liberato 2007; Liberato et al. 2006; Khodaparast et al. 2001; Ramos et al. 2013).

The tribe Erysipheae forms a separate, monophyletic clade, which is characterized by asexual morphs belonging to *Oidium* subgen. *Pseudoidium* Jacz (Takamatsu et al. 1999; Mori et al. 2000). This clade comprises *Erysiphe* and its sections *Erysiphe*, *Microsphaera* and *Uncinula*. *Uncinula forestalis* differs from the species of *Erysiphe* sect. *Uncinula* in having terminal, fasciculate, septate, ascospore appendages and *Euoidium*-like asexual morph (conidia catenate) and therefore it was placed in *Caespiototheca* (Takamatsu et al. 2005b).

Because of the lack of asexual morphs in *Uncinula septata* and *U. curvispora* and multiseptate chasmothecial appendages arising from the upper half the fruiting body, the two species were assigned to *Parauncinula* (Braun and Takamatsu 2000; Takamatsu et al. 2005a). A unique taxon, *Oidium phyllanthi*, on *Phyllanthus acidus*, *P. amarus* and *P. reticulatus* produces a germination type designated as *Microidium*-type and was placed in a new genus *Microidium* (To-anun et al. 2005). With these new classifications, Erysiphales contains 17 accepted genera, 16 based on the holomorph and one on the asexual morph (Braun and Cook 2012). With the descriptions of several new species, the number of recognized powdery mildew species has increased from 515 (including 435 sexual morphs/holomorphs) in Braun (1987), to about 820 species (including about 685 sexual morphs/holomorphs) (Braun and Takamatsu 2000; Braun et al. 2002; Takamatsu et al. 2005a, b; Liberato et al. 2006; Braun and Cook 2012).

Molecular based identification and diversity

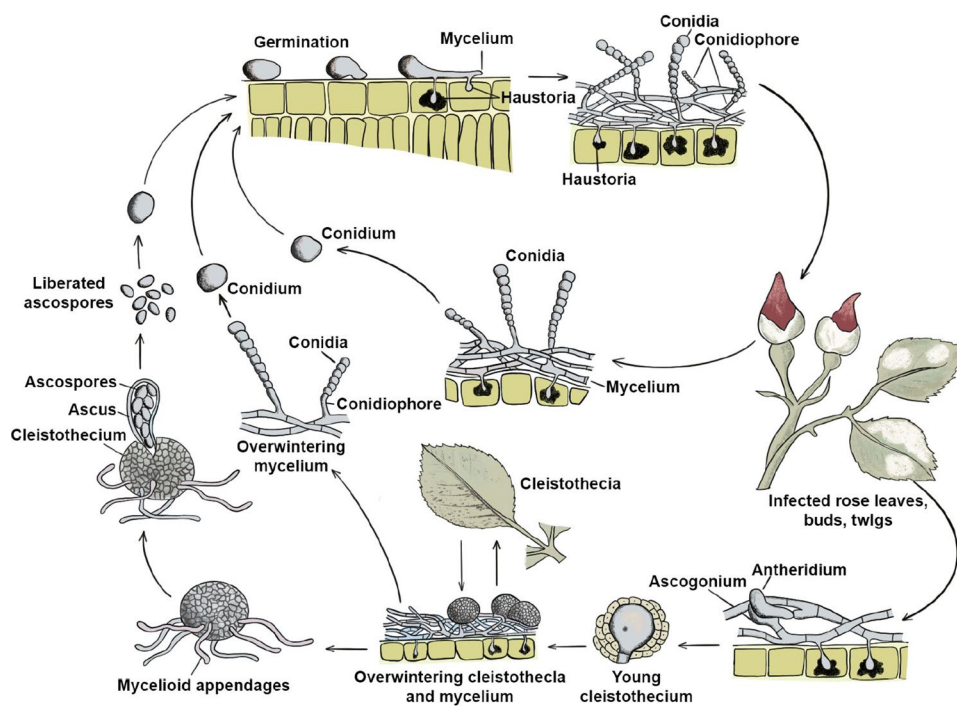
Molecular data have proven useful in reassessing species and clarifying the taxonomic significance of morphology and host data. Only a few of the described species have been reassessed using molecular data (Braun and Cook 2012). Reports began appearing in the 1990s, that used ITS and 18S rDNA sequences to infer phylogenetic relationships of Erysiphales and other major ascomycete groups (Saenz and Taylor 1999; Saenz et al. 1994). Analyses of 18S rDNA, ITS1–5.8S-ITS2, and 28S rDNA sequences led to the opinion that Erysiphales can be placed in Leotiomycetes along with Cyttariales, Helotiales, and Rhytismatales (Wang et al. 2006). Phylogenetic analyses demonstrated that Erysiphaceae formed a distinct monophyletic group (Hirata et al. 2000). Thus, Erysiphaceae is derived from a single ancestral taxon that may have acquired parasitism just once (Mori et al. 2000a; Takamatsu 2004; Wang et al. 2006). Shirouzu et al. (2020) using nrDNA and *mcm7* sequence data showed that Phyllactinieae is not monophyletic. However, there is a need to re-assess the tribes in this family to establish them as subfamilies or genera. In this paper, we present a phylogenetic tree with combined ITS and LSU sequences obtained from available type material and voucher specimens (Table 8, Fig. 12). This can be used as a backbone in the identification of powdery mildew species.

Recommended genetic markers (genus level)—ITS, LSU and SSU

Recommended genetic markers (species level)—*tub2*, *chs*, *tef1*

The ITS region of the precursor molecules of rRNA was revealed to form a secondary structure including several stem-loop structures, and some conserved sequences are found in the stem regions (Takamatsu et al. 1998). This makes it possible to design PCR primers that work for a wide range of the powdery mildews. Takamatsu and Kano (2001) designed

Fig. 11 The life cycle of a powdery mildew fungus on roses. Redrawn from Agrios (2005) and Mulbrhan et al. (2016)



four new PCR primers that are useful to determine the nucleotide sequences of the rDNA of the powdery mildews. These primers provide stability to work on a wide range of powdery mildews and specificity to eliminate contaminating DNA by PCR. Primer sets PM3/P3, ITS1/PM4, PM5/P3, and ITS1/PM6 were tested with universal primer set ITS1/ITS4 (White et al. 1990) covering all major clades of Erysiphales. Meeboon and Takamatsu (2013a) used LSU, ITS and IGS (Inter generic spacer) sequences to identify two different genetic groups of *Erysiphe japonica* (= *Typhulochaeta japonica*), powdery mildew on *Quercus* species based on the differences in host range. Cho et al. (2014) used ITS and 28S rDNA for the introduction of the powdery mildew species *Erysiphe magnoliicola* in *Erysiphe* sect. *Microsphaera*. Wang et al. (2014) also used ITS differences for phylogenetic analysis of powdery mildew disease on mulberry in Yunnan Province. Meeboon and Takamatsu (2013b) also used the 28S rDNA sequences and a combined alignment of the 28S, ITS, and IGS (Intergeneric spacer) rDNA sequences to construct a phylogeny of *Erysiphe* sect. *Uncinula* on *Carpinus* species and showed the cryptic species *Erysiphe paracarpinicola*. de Oliveira et al. (2015) used ITS sequences of *Erysiphe platani* on *Platanus × acerifolia* in Brazil as new records of taxa. Liyanage et al. (2017) used ITS, SSU and LSU sequences to identify *E. quercicola* infected rubber trees. Phylogenetic analyses of *B. graminis* based on the DNA sequences of four DNA regions, *i.e.* ITS, 28S rDNA, chitin synthase 1, and β -tubulin were conducted by Inuma et al. (2007) to revealed distinct groups in the *B. graminis* isolates from a single host genus belonged to a single group.

83. *Fomitopsis* P. Karst., Meddn Soc. Fauna Flora fenn. 6: 9 (1881)

Background

Fomitopsis was established by Karsten (1881) based on four species, with *F. pinicola* as the generic type (Murrill 1903; Donk 1960). The genus has a cosmopolitan distribution and comprises species causing brown rot on both living and dead trees (Han et al. 2016). *Fomitopsis* species also contribute to the decomposition of coarse woody debris in forest communities (Gilbertson 1980; Haight et al. 2019). There are certain instances of their pathogenic role in orchards of cultivated species where they cause heart rot on *Citrus* (Rocchetti et al. 2014) and *Prunus* species (Adaskaveg 1993). A *Fomitopsis* sp. was also recorded in oil palm (*Elaeis guineensis*) as an endophyte (Rungjindamai et al. 2008; Pinruan et al. 2010).

Classification—Basidiomycota, Agaricomycetes, Incertae sedis, Polyporales, Fomitopsidaceae

Type species—*Fomitopsis pinicola* (Sw.) P. Karst.

Distribution—Worldwide

Disease symptoms—*Fomitopsis* causes brown cubical rot on both living and dead trees (Mounce 1929). The basidiospores can be dispersed by wind, or by vectors such as bark beetles (Castello et al. 1976; Pettey and Shaw 1986; Lim et al. 2005; Persson et al. 2011; Jacobsen et al. 2017; Vogel et al. 2017). Upon infecting standing trees, stumps, or logs through wounds, or through the tunnels of penetrating vectors, the fungus establishes itself in the xylem (Mounce 1929). The growth rate of *Fomitopsis* species in the substrata

can differ depending on their ecological requirements (Markovic et al. 2011; Haight et al. 2019). When the decay starts, the wood turns yellowish-brown, which later splits into cubical fragments. The colour is generally lighter in case of *F. pinicola* than other agents of brown rot decay (Markovic et al. 2011). White mycelial felts can also develop in shrinkage cracks of the decayed wood (Ryvarden and Gilbertson 1993). After establishment, the perennial basidiome appears relatively rapidly (Mounce 1929, Fig. 13). The infection results in the breakage of treetops, or further infection of the base of the trees and weakening of larger roots, which may lead to eventual windthrow of standing trees.

Hosts—The type species, *F. pinicola* mostly appears on gymnosperms, such as *Abies*, *Larix*, *Picea* and *Pinus*, but can also be found on angiosperms such as *Acer*, *Alnus*, *Betula*, *Carpinus*, *Corylus*, *Elaeagnus*, *Fagus*, *Fraxinus*, *Malus*, *Populus*, *Prunus*, *Pyrus*, *Quercus*, *Salix*, *Sorbus*, *Tilia*, *Ulmus* (Ryvarden and Gilbertson 1993; Dai 2012). The North American species in the *Fomitopsis pinicola* species complex have also been reported from *Pseudotsuga*, *Sequoiia* and *Tsuga* (Haight et al. 2019). Other *Fomitopsis* species can be found on *Ginkgo*, *Pinus* and various angiosperm genera, such as *Betula*, *Castanopsis*, *Cinamomum*, *Citrus*, *Delonix*, *Fagus*, *Eucalyptus*, *Ligustrum*, *Prunus*, *Quercus* and *Tilia* (Ryvarden and Gilbertson 1993; Dai 2012; Li et al. 2013; Han et al. 2016; Liu et al. 2019).

Morphological based identification and diversity

Based on morphological evidence, over 40 species were accepted in *Fomitopsis* (e.g. Ryvarden and Johansen 1980; Gilbertson and Ryvarden 1986; Ryvarden and Gilbertson 1993; Núñez and Ryvarden 2001; Hattori 2001). However, phylogenetic studies showed that the morphologically defined *Fomitopsis* was polyphyletic and taxa clustered with other brown-rot genera in the antrodia clade (Ortiz-Santana et al. 2013; Han et al. 2016). Han et al. (2016) showed that *Pilatoporus* and *Piptoporus* are synonyms of *Fomitopsis sensu stricto*, while the segregation of *Rhodofomes* was confirmed and five new genera were proposed. *Fomitopsis sensu stricto* is characterized by annual to perennial, mostly sessile, occasionally effused-reflexed or substipitate, soft, corky, tough to woody basidiocarps, a dimitic hyphal system with clamped generative hyphae and cylindrical to ellipsoid, hyaline, thin-walled, smooth basidiospores which are negative in Melzer's reagent, and cause brown rot (Fig. 13).

Molecular based identification and diversity

Comprehensive multigene analyses by Han et al. (2016) accepted ten species in *Fomitopsis sensu stricto*. Two new *Fomitopsis* species were described from Brazil, *F. flabellata* and *F. rosealba* (Tibpromma et al. 2017). *Fomitopsis flabellata* was transferred to *Rhodofomitopsis* and the new combination *Fomitopsis bondartsevae* was proposed (Soares et al.

2017). Mating studies and molecular phylogenetic analyses resolved four cryptic lineages in the *F. pinicola* species complex (Haight et al. 2016), that represents three North American species (*F. mounceae*, *F. ochracea* and *F. schrenkii*), and *F. pinicola sensu stricto*, which is restricted to Eurasia (Ryvarden and Stokland 2008; Haight et al. 2019). Three new species were proposed by Liu et al. (2019) from Australia (*F. eucalypticola*), Puerto Rico (*F. caribensis*), and China (*F. ginkgonis*).

The phylogenetic tree of *Fomitopsis* presented here is based on analyses of a combined ITS, LSU, *tefl* and *rpb2* sequence data (Fig. 14). In our analyses, it appears that the type of *F. bondartsevae* is identical to *F. iberica* and *F. hemitephra sensu stricto* (Han et al. 2016), which are grouped close to *F. palustris* and other species formerly discussed in *Pilatoporus*. Therefore, a thorough revision of the pilatoporus clade is recommended to clarify the status of these species.

Recommended genetic marker (genus level)—LSU

Recommended genetic markers (species level)—ITS, *tefl*, *rpb2*

Accepted number of species—There are 104 epithets listed in Index Fungorum (2020). However, only 17 species have DNA sequence data (Table 9).

References—Li et al. (2013) (phylogeny, new species), Han et al. (2016) (phylogeny), Haight et al. 2019 (phylogeny, new species), Floudas et al. (2012) (genome, *F. pinicola*), Hong et al. (2017) (genome, *F. palustris*), Liu et al. (2019) (phylogeny, new species).

84. *Ganoderma* P. Karst., Revue mycol., Toulouse 3(no. 9): 17 (1881)

Background

Ganoderma was established by Karsten (1881) based on *G. lucidum* and characterized by double-walled basidiospores with truncate apices and ornamented endospores, and a crusty or shiny pileus surface (Moncalvo and Ryvarden 1997). This genus was divided into two subgenera, *Ganoderma* and *Elfvingia* by Karsten (1889). Various authors used different taxonomic characters for the identification of species (e.g., Murrill 1902, 1903; Atkinson 1908; Coleman 1927; Corner 1947), which resulted in an intricate taxonomy, with 344 species names in speciesfungorum.org, but an estimated 180 species (He et al. 2019) and Steyaert (1972, 1980) worked extensively on the genus and introduced many new species, transferred many to the genus and removed several synonyms. Ryvarden (1985) and Gottlieb and Wright (1999a,b) studied the macro- and micromorphology. *Ganoderma* presently comprises sections *Amauroderma* and *Ganoderma*, subgenera: *Ganoderma* and *Trachyderma* (Index Fungorum 2020, Wijayawardene et al. 2020).

Relevant characteristics for *Ganoderma* species delimitation are based on the macro and micromorphological characteristics (see in Fig. 15). The basidiomes are annual or

Table 8 Genera in *Erysiphaceae*

Genera	Species name	Strain no	Host	ITS	LSU
<i>Arthrocladiella</i>	<i>Arthrocladiella mougeotii</i>	SqGq-1	<i>Lycium chinense</i>	JX546296	AB022379
<i>Blumeria</i>	<i>Blumeria graminis</i>	MUMH1723	<i>Festuca arundinacea</i>	AB273556	AB103065
<i>Brasiliomyces</i>	<i>Brasiliomyces malvastri</i>	NA	<i>Malvastrum coromandelianum</i>	NA	NA
<i>Caespitotheca</i>	<i>Caespitotheca forestalis</i>	MUMH1461	<i>Schinopsis balansae</i>	AB193466	AB193467
<i>Cystotheca</i>	<i>Cystotheca wrightii</i>	KUS-F27309	<i>Quercus glauca</i>	KF735066	AB022355
	<i>Cystotheca lanestris</i>	NA	<i>Quercus agrifolia</i>	AB000933	AB022353
<i>Erysiphe</i>	<i>Erysiphe polygoni</i>	UTC206	<i>Polygonum arenastrum</i>	AF011307	NA
	<i>Erysiphe heraclei</i>	NA	<i>Daucus carota</i>	AB000942	AB103371
	<i>Erysiphe monascogera</i>	MUMH4190	<i>Styrax japonica</i>	AB331647	NA
	<i>Erysiphe blasti</i>	MUMH2	<i>Lindera umbellata</i>	AB015918	NA
	<i>Erysiphe juglandis</i>	MUMH48s	<i>Microsphaera juglandis</i>	AB015928	NA
	<i>Erysiphe hedwigii</i>	VPRI 22225	NA	AF298539	NA
	<i>Erysiphe pulchra</i> var.	MUMH90	<i>Cornus controversa</i>	AB000941	AB022389
	<i>japonica</i>	MUMH1428	<i>Symphoricarpos albus</i>	AB078970	NA
	<i>Erysiphe symphoricarpi</i>	MUMH 4992	<i>Castanopsis diversifolia</i>	AB622218	JQ220158
	<i>Erysiphe asiatica</i>	MUMH 4987	<i>Castanopsis argyrophylla</i>	AB622213	JQ220154
	<i>Erysiphe monoperidiata</i>	NA	<i>Quercus cuspidata</i>	AB022416	AB022415
	<i>Erysiphe japonica</i> var.	MUMH40	NA	D84383	AB022374
	<i>crispulae</i>	MUMH 4648	<i>Aphananthe aspera</i>	AB69396	NA
	<i>Erysiphe adunca</i>	MUMH1429	<i>Aesculus hippocastanum</i>	AB091774	NA
	<i>Erysiphe aphananthes</i>	NA	<i>Morus bombycis</i>	AB000946	AB022418
	<i>Erysiphe flexuosa</i>	KW:34760F	<i>Ulmus minor</i>	AB475118	AB475109
	<i>Erysiphe mori</i>	MUMH776	<i>Prunus domestica</i>	AB046984	AB709961
	<i>Erysiphe kenjiana</i>	MUMH1534	<i>Fagus crenata</i>	AB091776	NA
	<i>Erysiphe prunastri</i> var.				
<i>prunastri</i>					
<i>Erysiphe wadae</i>					
<i>Golovinomyces</i>	<i>Golovinomyces</i>	MUMH623	<i>Mycelis muralis</i>	AB077661	NA
	<i>cichoracearum</i>	MUMH144	<i>Adenophora triphylla</i> var.	AB077633	AB077632
	<i>Golovinomyces adenophorae</i>	MUMH3196	<i>japonica</i>	AB769454	AB077683
	<i>Golovinomyces cynoglossi</i>	MUMH1343	<i>Cynoglossum asperrimum</i>	AB769450	AB769452
	<i>Golovinomyces fischeri</i>	MUMH1406	<i>Senecio doronicum</i>	AB246765	NA
<i>Golovinomyces leuceriae</i>	MUMH683	<i>Leuceria thermarum</i>			
<i>Golovinomyces</i>	<i>Golovinomyces orontii</i>	MUMH2433	<i>Cirsium japonicum</i>	AB769413	AB077678
	<i>Golovinomyces sonchicola</i>	BCRU934	<i>Sonchus arvensis</i>	AB077673	AB077672
	<i>Golovinomyces sordidus</i>	MUMH938	<i>Plantago sp.</i>	AB769467	AB077657
	<i>Golovinomyces sparsus</i>	HMNWAFU-CF2011034	<i>Euphorbia collina</i>	AB769461	NA
	<i>Golovinomyces valerianae</i>		<i>Valeriana officinalis</i>	AB769471	NA
<i>Leveillula</i>	<i>Leveillula taurica</i>	WSP71133	<i>Triglochin maritime</i>	AY912077	NA
	<i>Leveillula elaeagni</i>	IRAN11138	<i>Elaeagnus angustifolia</i>	AB048350	NA
	<i>Leveillula lactucae-serriolae</i>	NA	<i>Hexinia polydichotoma</i>	HQ821500	HQ821501
<i>Microidium</i>	<i>Microidium phyllanthi</i>	MUMH(JPN)3361	<i>Phyllanthus acidus</i>	AB719943	AB120758
<i>Neoerysiphe</i>	<i>Neoerysiphe cumminsiana</i>	MUMH 522	<i>Cacalia delphiniifolia</i>	AB329669	NA
	<i>Neoerysiphe galeopsidis</i>	MUMH4680	<i>Chelonopsis moschata</i>	AB498949	AB022369
	<i>Neoerysiphe galii</i>	MUMH 4682	<i>Galium aparine</i>	AB498951	AB103365
	<i>Neoerysiphe geranii</i>	MUMH4665 MUMH 4668	<i>Geranium sp.</i>	AB498956 AB498976	AB498952
	<i>Neoerysiphe joerstadii</i>	DAR 33493	<i>Phagnalon rupestre</i>	GU356546	NA
	<i>Neoerysiphe kerribeeensis</i>	MUMH 4671	<i>Senecio glossanthus</i>	AB498975	NA
	<i>Neoerysiphe nevoi</i>		<i>Scolymus hispanicus</i>		NA
<i>Parauncinula</i>	<i>Parauncinula septata</i>	MUMH585	<i>Quercus cuspidata</i> var. <i>horikawae</i>	AB183533	AB022420

Table 8 (continued)

Genera	Species name	Strain no	Host	ITS	LSU
<i>Phyllactinia</i>	<i>Phyllactinia guttata</i>	MUMH927	<i>Corylus</i> sp.	AB080565	AB080456
	<i>Phyllactinia actinidiae</i>	MUMH497	<i>Actinidia arguta</i>	AB080508	HQ821501
	<i>Phyllactinia alni</i>	MUMH449	<i>Alnus japonica</i>	AB080502	AB080393
	<i>Phyllactinia betulae</i>	MUMH506	<i>Betula platyphylla</i> var.	AB080507	AB080398
	<i>Phyllactinia- broussonetiae-kaempferi</i>	MUMH531	<i>japonica</i>	AB080510	AB080445
	<i>Phyllactinia kaempferi</i>	MUMH527	<i>Broussonetia kazinoki</i>	AB080504	AB080408
	<i>Phyllactinia enkianthi</i>	MUMH165	<i>Lyonia ovalifolia</i> var.	AB080498	AB080402
	<i>Phyllactinia eupteleae</i>	MUMH907	<i>elliptica</i>	AB080543	AB080453
	<i>Phyllactinia fraxini</i>	MUMH927	<i>Euptelea polyandra</i>	AB080565	AB080394
	<i>Phyllactinia guttata</i>	TUAMH2072	<i>Syringa vulgaris</i>	AB080531	AB080422
	<i>Phyllactinia juglandis</i>	MUMH531	<i>Corylus</i> sp.	AB080526	AB080416
	<i>Phyllactinia magnoliiae</i>	MUMH619	<i>Juglans mandshurica</i> var.	AB080523	AB080414
	<i>Phyllactinia mali</i>	MUMHn36	<i>sachalinensis</i>	AB080518	AB080373
	<i>Phyllactinia moricola</i>		<i>Magnolia quinquepeta</i>		
<i>Pleochaeta</i>	<i>Pleochaeta indica</i>	MUMH3208	<i>Celtis australis</i>	AB243757	NA
	<i>Pleochaeta shiraiana</i>	MUMH20	NA	D84380	AB022403
<i>Podosphaera</i>	<i>Podosphaera myrtilina</i>	NA	<i>Vaccinium myrillus</i>	NA	NA
	<i>Podosphaera leucotricha</i>	HMLAC120001	<i>Photinia serrulata</i>	JQ999954	NA
	<i>Podosphaera spiraeae</i>	MUMH 2490	<i>Spiraea cantoniensis</i>	AB525940	AB022384
	<i>Podosphaera cercidiphylli</i>	MUMHS67	<i>Cercidiphyllum japonicum</i>	AB026140	NA
	<i>Podosphaera clandestine</i>	MUMH 2535	<i>Spiraea japonica</i>	AB525941	AB103367
	<i>Podosphaera astericola</i>	MUMH333	<i>Aster ageratoides</i> subsp.	AB040335	AB462779
	<i>Podosphaera balsaminae</i>	NA	<i>ovatus</i>	FJ625796	AB462788
	<i>Podosphaera carpesiicola</i>	MUMH344	<i>Impatiens balsamina</i>	AB040350	NA
	<i>Podosphaera elsholtziae</i>	MUMHS131	<i>Carpesium abrotanoides</i>	AB026142	AB462794
	<i>Podosphaera euphorbiae-hirtae</i>	MUMH319	<i>Ajuga reptans</i>	AB040306	AB462770
	<i>Podosphaera hirtae</i>	NA	<i>Acalypha australis</i>	AF154324	AB103369
	<i>Podosphaera fusca</i>	MUMH809	NA	AB046986	AB462761
	<i>Podosphaera fuliginea</i>	MUMH605	<i>Verbena spicata</i>	AB040308	NA
	<i>Podosphaera hibiscicola</i>	MUMH331	<i>Hibiscus mutabilis</i>	AB026145	AB462777
	<i>Podosphaera intermedia</i>	MUMH774	<i>Clerodendrum trichotomum</i>	AB040332	NA
	<i>Podosphaera phtheiros-permi</i>	MUMH346	<i>Melampyrum nemorosum</i>	AB040320	NA
	<i>Podosphaera permii</i>	MUMH74	<i>Fatoua villosa</i>	AB040351	JX512556
	<i>Podosphaera pseudofusca</i>		<i>Youngia denticulata</i>	NA	NA
<i>Podosphaera xanthii</i>				NA	
<i>Queirozia</i>	<i>Queirozia turbinata</i>	VIC 26558	<i>Platycyamus regnellii</i>	AB218773	NA
<i>Sawadaea</i>	<i>Sawadaea bicornis</i>	MUMH904	<i>Acer pseudoplatanus</i>	AB193380	AB103370
	<i>Sawadaea nankinensis</i>	MUMH4232	<i>Acer buergerianum</i>	AB353762	NA
	<i>Sawadaea polyfida</i>	MUMH486	<i>Acer amoenum</i> var. <i>matsumurae</i>	AB193358	AB193393
	<i>Sawadaea tulasnei</i>	MUMHS112	<i>Acer mono</i> var. <i>marmoratum</i>	AB193388	AB193400
<i>Takamatsuella</i>	<i>Takamatsuella circinata</i>	NA	<i>Stachys distans</i>	NA	NA

Type strains are in bold

perennial, dimidiate, sessile or substipitate to stipitate, with distinctive non-laccate (dull) or weakly to strongly laccate, glossy, shiny, smooth, spatulate, furrows, which are sulcate on the pileus surface. Some strains have several layers of thick, dull cuticles or shiny, with thin cuticle or cuticle of clavate end cells. The context is cream to dark purplish brown, brown to dark brown, sometimes spongy to firm-fibrous. Pores are 4–7 per mm, angular, entire, subcircular to circular, regular, mostly cream or white when young, light yellow to brown when mature, which are usually white to

cream when fresh, turning pale yellow on drying, with bruising brown of pore surface. The tube layer is single or stratified, with pale to purplish brown, hard, and becomes woody when dry. The stipe is central or lateral when present.

The *Ganoderma* hyphal system is di-trimitic and generative hyphae are thin-walled or occasionally thick-walled, with clamp connections. Skeletal hyphae are hyaline to brown, thick-walled, often long, unbranched. Binding hyphae are almost colourless, thin to thick-walled, branched and with clamp connections. Basidiospores are 7–30 µm

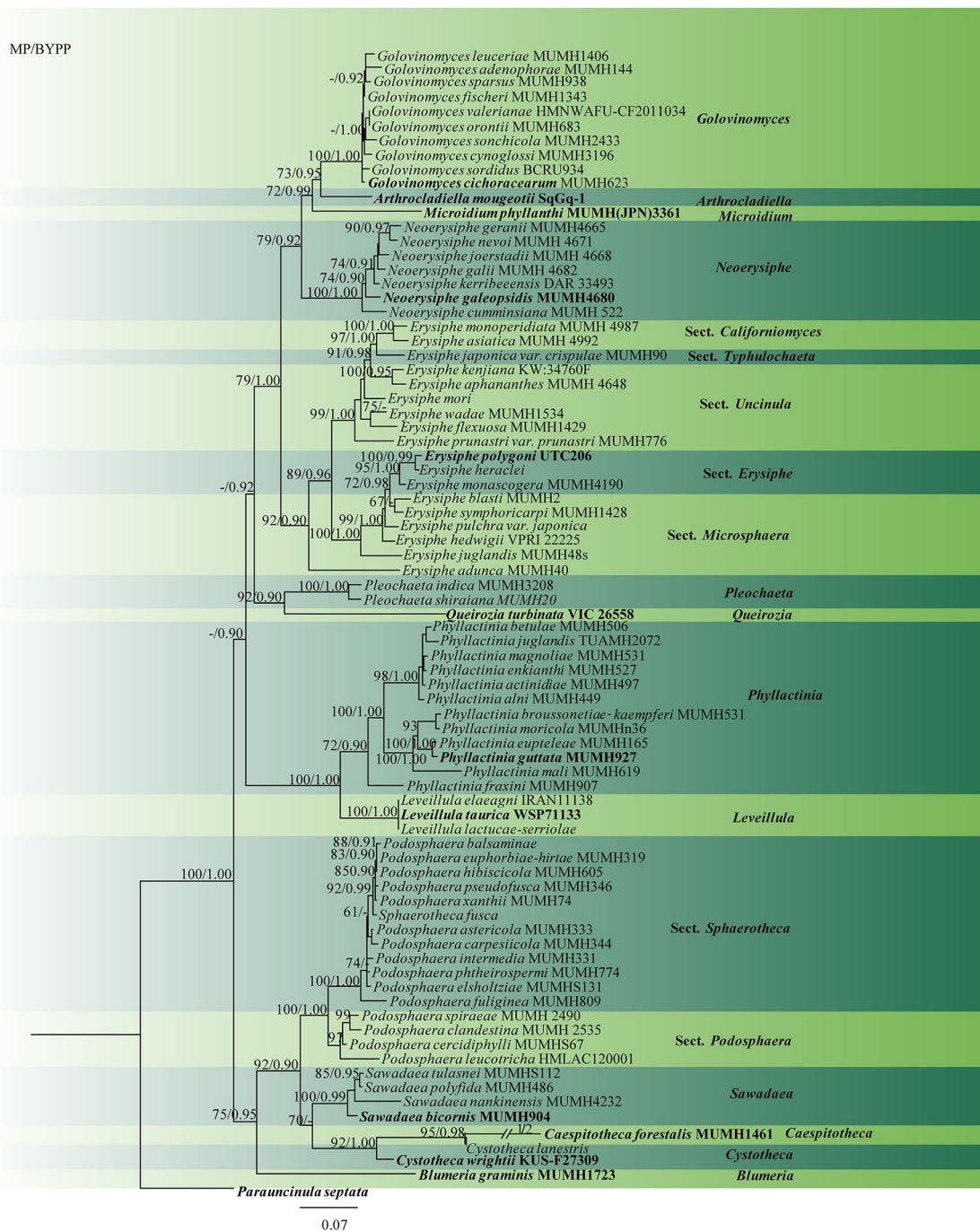


Fig. 12 Phylogram generated from parsimony analysis based on combined ITS and LSU sequenced data *Erysiphaceae*. Maximum parsimony bootstrap support values greater than 60% and BYPP greater

than 0.90 are indicated above the nodes. The type specimens (ex-epitypes) are in bold. The tree is rooted with *Parauncinula septata*

long, usually broadly to narrowly ellipsoid, truncate, double-walled, and with an apical germ pore. The endosporium is brown and separated from the hyaline exosporium by inter-wall pillars, negative in Melzer's reagent (Núñez and Ryvarden 2000; Ryvarden 2004). Basidia are broadly ellipsoid, tapering abruptly at the base, and cystidia are lacking.

Ganoderma species are widely distributed in temperate, subtropical and tropical regions, and appear to thrive in hot and humid conditions (Pilotti et al. 2004; Hapuarachchi et al. 2019a, b; Luangharn et al. 2019). Basidiomes are commonly in the form of a bracket (Pilotti et al. 2004). *Ganoderma* is cosmopolitan and an important wood-decaying genus. Some

Fig. 13 *Fomitopsis pinicola* **a** basidiomes on living European spruce, **b** causing brown-rot decay on narrow-leaved ash, **c**, **d** basidiomes on dead standing conifer tree, **e** young basidiome on hardwood log, **f** hyphal structure in the trama, **g**, **h** basidiospores. Scale bars: **f** = 20 μ m, **g**, **h** = 5 μ m



species of *Ganoderma* are pathogenic, causing root and stem rot on a variety of monocotyledons, dicotyledons and gymnosperms, including a wide range of economically important trees and perennial crops which results in the death of affected trees (Hapuarachchi et al. 2018b). *Ganoderma* grows as facultative parasites of trees but can also live as saprobes on rotting stumps and roots (Turner 1981; Pilotti et al. 2004). Hence, they have ecological importance in the breakdown of woody plants for nutrient mobilization. Taxa also possess effective machinery of lignocellulose-decomposing enzymes which may be useful for bioenergy production and bioremediation (Hepting 1971; Kües et al. 2015; Hyde et al. 2019).

Several *Ganoderma* species are prolific sources of highly active bioactive compounds such as polysaccharides, proteins, steroids and triterpenoids. These bioactive compounds show a huge structural and chemical diversity (Shim et al. 2004; Qiao et al. 2005; Wang and Liu 2008; Teng et al. 2011; De Silva et al. 2012a, b; 2013; Hapuarachchi et al. 2017; Li et al. 2018; Hyde et al. 2019). The bioactive constituents have anti-cancer, anti-inflammatory, anti-tumour, anti-oxidant, immunomodulatory, immunodeficiency, anti-diabetic, anti-viral, anti-bacterial, anti-fungal, anti-hypertensive, anti-atherosclerotic, anti-ageing, anti-androgenic, hepatoprotective and radical scavenging properties. They are also promising in neuroprotection, sleep promotion, cholesterol synthesis inhibition, preventing hypoglycemia, inhibition of lipid peroxidation/oxidative DNA damage, maintenance of gut health, prevention of obesity, and stimulation of probiotics (De Silva et al. 2012a; Hapuarachchi et al. 2016a, b; Hapuarachchi et al. 2017).

Current studies are identifying secondary metabolites, developing models for prediction or early detection of diseases, finding biological control methods as well as understanding genomes. Using artificial neural network spectral analyses and foliage of four disease levels, Ahmadi et al. (2017) provided an early detection method for *Ganoderma* basal stem rot of oil

palm. Sitompul and Nasution (2020) suggested that to control *Ganoderma* diseases non or weakly pathogenic fungi can be considered as biological control agents. These agents could break down woody debris faster than the pathogen and occupy the same resource as the pathogen (compete for nutrients) as well as producing inhibitory secondary metabolites (Pateron 2007; Sitompul and Nasution 2020). Utomo et al. (2018) sequenced the nuclear genome of *G. boninense*, the main pathogen of basal stem rot, and the draft genome comprised of 79.24 megabases and 26,226 predicted coding sequences. Ramzi et al. (2019) conducted a study to understand the plant cell wall degradation and pathogenesis of *G. boninense* via comparative genome analysis. In their study, they found that similarly to *G. lucidum*, *G. boninense* was enriched with carbohydrate-active and cell wall degrading enzymes. Following plant-host interaction analysis, several candidate genes including polygalacturonase, endo β -1, 3-xylanase, β -glucanase and laccase were identified as potential cell wall degrading enzymes that contribute to the plant host interaction and pathogenesis. The study provided fundamental knowledge on the fungal genetic ability and capacity to secrete carbohydrate-active and cell wall degrading enzymes. Agudelo-Valencia et al. (2020) pointed out that information regarding the biotechnological importance of *Ganoderma* species (other than *G. lucidum*) is quite limited. Therefore, in their study they obtained and studied the genome of *G. australe*, resulting in gene prediction for the 84-megabase genome, prediction of 22,756 protein-coding genes, prediction of five putative genes and two enzyme complexes from a ganoderic acid pathway.

Most *Ganoderma* species are pathogenic or facultatively pathogenic, causing root and stem rot on a variety of monocotyledons, dicotyledons, and gymnosperms, including a wide range of economically important trees and perennial crops, which may result in death (Hapuarachchi et al. 2018a). Some species are saprobic and cause white-rot

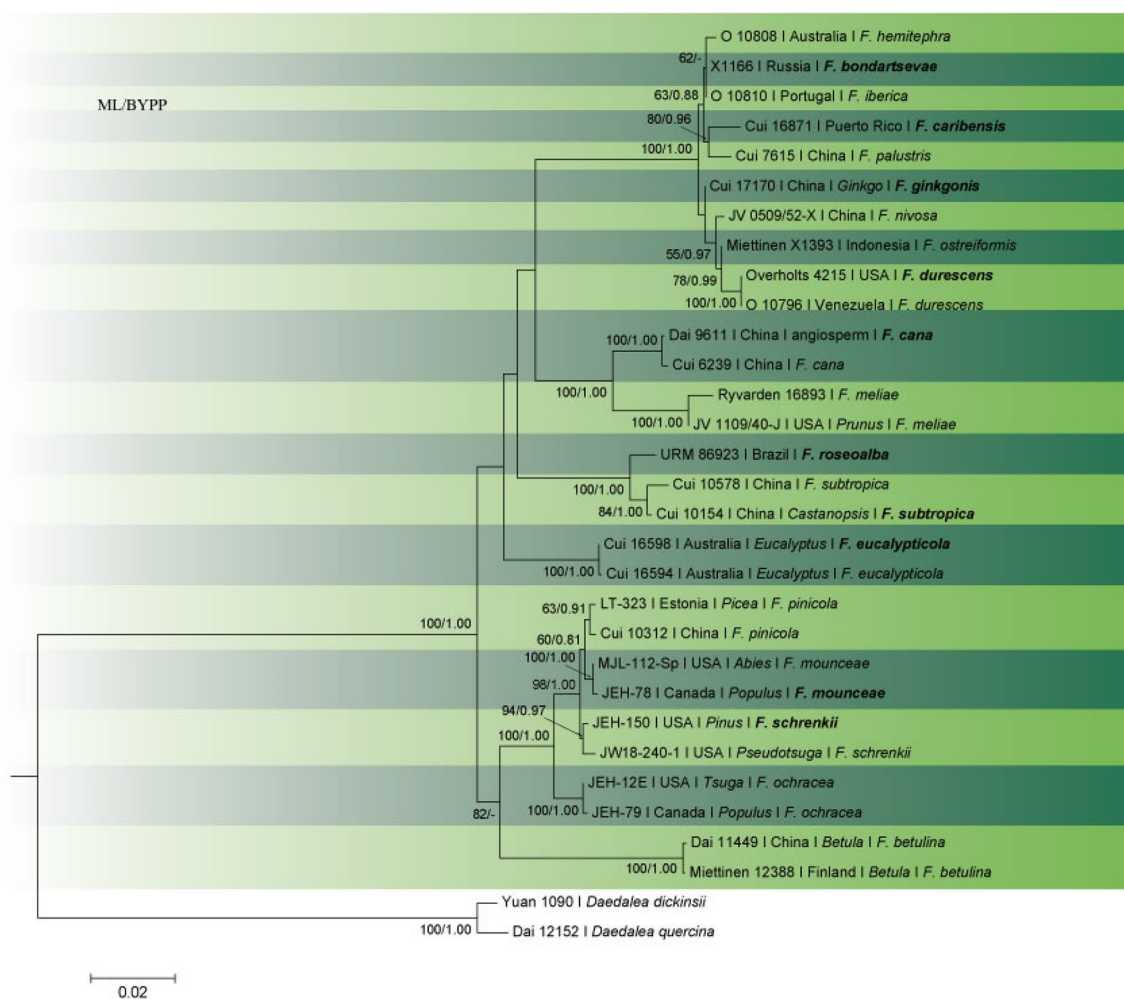


Fig. 14 Phylogram generated from RAxML analysis based on combined ITS, LSU, nSSU, *tef1* and *rbp2* sequence data of *Fomitopsis* species. Related sequences were obtained from GenBank. Thirty-one strains are included in the analyses, which comprised 4143 characters

including gaps. The tree was rooted with *Daedalea quercina* (Dai 12152) and *D. dickinsii* (Yuan 1090). Tree topology of the ML analysis was similar to the Bayesian analysis. ML bootstrap values $> 50\%$ and BYPP > 0.80 are shown respectively near the nodes

decay of wood (Muthelo 2009). Hence, they have ecological importance in the breakdown of woody plants for nutrient mobilization. They possess effective machinery of lignocellulose-decomposing enzymes useful for bioenergy production and bioremediation (Hepting 1971; Adaskaveg et al. 1991; Kües et al. 2015).

Classification—Basidiomycota, Agaricomycotina, Agaricomycetes, Incertae sedis, Polyporales, Ganodermataceae

Type species—*Ganoderma lucidum* (Curtis) P. Karst. 1881

Distribution—worldwide

Disease symptoms—basal stem, butt and root rot in economically important trees and perennial crops, especially in tropical regions. *Ganoderma* disease development is affected by environmental factors and tree death could be either slow or rapid depending on water availability and temperature (Coetzee et al. 2015).

Basal stem rot: Symptoms of basal stem rot disease can take several years to develop, and the presence of the pathogen is often only visible when the fungus is well-established and more than half of the tissue has been decayed. Soils with poor drainage and water stagnation during rainy seasons favour the disease (Kandan et al. 2010).

Butt rot and root rot: The primary symptoms include wilting, mild to severe, of either all leaves or just the lowest leaves in the canopy, premature death of the oldest leaves or a general decline of the tree. The advanced decay of the larger roots is evident after leaves are blown down. Decay may extend from several cms to over a metre into the lower (butt) portion of the tree, depending on the species of *Ganoderma*. It is quite common for basidiomes not to appear before the severe decline and death of a tree (Glen et al. 2009). Therefore, the only way to determine if *Ganoderma* butt rot is the cause is to cut cross-sections through the lower

Table 9 DNA barcodes for accepted species of *Fomitopsis*

Species	Strain	ITS	LSU	nSSU	<i>tef1</i>	<i>rpb2</i>
<i>Fomitopsis betulina</i>	Dai 11449	KR605798	KR605737	KR605895	KR610726	KR610816
<i>F. betulina</i>	Miettinen 12388	JX109856	JX109856	–	JX109913	JX109884
<i>F. bondartsevae</i>	X1166*	JQ700276	JQ700276	–	–	–
<i>F. cana</i>	Dai 9611*	JX435776	JX435774	KR605825	KR610660	KR610762
<i>F. cana</i>	Cui 6239	JX435777	JX435775	KR605826	KR610661	KR610761
<i>F. caribensis</i>	Cui 16871*	MK852559	MK860108	MK860124	MK900482	MK900474
<i>F. durescens</i>	Overholts 4215*	KF937293	KF937295	KR605835	–	–
<i>F. durescens</i>	O 10796	KF937292	KF937294	KR605834	KR610669	KR610766
<i>F. eucalypticola</i>	Cui 16598*	MK852562	MK860113	MK860129	MK900484	MK900479
<i>F. eucalypticola</i>	Cui 16594	MK852560	MK860110	MK860126	MK900483	MK900476
<i>F. ginkgonis</i>	Cui 17170*	MK852563	MK860114	MK860130	MK900485	MK900480
<i>F. ginkgonis</i>	Cui 17171	MK852564	MK860115	MK860131	MK900486	MK900481
<i>F. hemitephra</i>	O 10808	KR605770	KR605709	KR605841	KR610675	–
<i>F. iberica</i>	O 10810	KR605771	KR605710	KR605842	KR610676	KR610771
<i>F. meliae</i>	Ryvarden 16893	KR605776	KR605715	KR605849	KR610681	KR610775
<i>F. meliae</i>	JV 1109/40-J	KY264030	–	–	–	–
<i>F. mounceae</i>	JEH-78*	KF169629	–	–	KF178354	KF169698
<i>F. mounceae</i>	MJL-112-Sp	KF169636	–	–	KF178361	KF169705
<i>F. nivosa</i>	JV 0509/52-X	KR605779	KR605718	–	KR610686	KR610777
<i>F. ochracea</i>	JEH-12E	KF169597	–	–	KF178322	KF169666
<i>F. ochracea</i>	JEH-79	KF169604	–	–	KF178329	KF169673
<i>F. ostreiformis</i>	Miettinen X1393	KC595918	KC595918	–	–	–
<i>F. palustris</i>	Cui 7615	KR605780	KR605719	–	KR610688	KR610779
<i>F. pinicola</i>	Cui 10312	KR605781	KR605720	KR605856	KR610689	KR610780
<i>F. pinicola</i>	LT-323	KF169651	–	–	KF178376	KF169720
<i>F. roseoalba</i>	URM 86923*	KT189139	KT189141	–	–	–
<i>F. schrenkii</i>	JEH-150*	KU169365	–	–	MK236356	MK208858
<i>F. schrenkii</i>	JW18-240-1	KF169648	–	–	KF178373	KF169717
<i>F. subtropica</i>	Cui 10154*	JQ067652	JX435772	–	–	–
<i>F. subtropica</i>	Cui 10578	KR605787	KR605726	KR605867	KR610698	KR610791

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold

meter or so of the trunk after the tree is felled and examine the cross-sections for the typical pattern of rot: greatest near the soil line, decreasing in sections further from the soil line.

Ganoderma root rot may cause yellowing, wilting, or undersized leaves and dead branches. Tree vigour may decline as the decay of the sapwood advances. The first visible sign of infection is often the formation of basidiomes (solitary or in clusters) on the lower trunk and exposed root areas. There are two types: varnished and unvarnished. The upper surface of varnished fungus rot is typically red-brown with a white edge, shiny, and lacquered. Conks of the unvarnished fungus rot are brown with a white edge weathering to grey (Pilotti et al. 2004). When fresh, both have a white, porous surface on the underside. The rate of decay can lead to death in as little as 3 to 5 years from the time of infection and appears to be determined by tree vigour, which is often influenced by environmental stresses (Nirwan et al. 2016).

Hosts—*Ganoderma* has a wide host range, with more than 44 species from 34 potential host genera identified (Venkatarayan 1936). The root and stem rots caused by *Ganoderma* species, result in decreased forestry yields of e.g. *Areca catechu* (Palanna et al. 2020), *Camellia sinensis*, *Cocos nucifera*, (Kinge and Mih 2014), *Elaeis guineensis*, (Glen et al. 2009) and *Hevea brasiliensis* (Monkai et al. 2017) worldwide.

Pathogen biology, disease cycle and epidemiology

The fungus is spread by spores produced in the prominent basidiomes that form on the outside of the tree (conks). New spores released from the conks are dispersed throughout the summer during humid periods and infect open wounds on root flares and lower trunk areas of susceptible trees. The spores germinate, and the infection progresses to attack the sapwood of major roots and the lower tree trunk. Over the years, the number of decayed wood increases leading to



Fig. 15 Morphology of *Ganoderma* species. **a** An old basidiome of *Ganoderma australe*, **b** Mature basidiome of *G. casuarinicola*, **c**, **d** hyphae, **e** tube layer hyphae, **f–h** Basidiospores, **i** Pore characteristics. Scale bars: a, b = 2 cm; c, d = 3 μ m; e = 15 μ m; f, g, h. = 5 μ m; i = 500 μ m

dangerously soft, spongy wood in the part of the tree that functions as its anchor (Paterson 2007).

Morphology-based identification and diversity

Ganoderma species identification, limitations and their taxonomic segregation have been unclear and recently being debated (Moncalvo et al. 1995; Wang et al. 2009; Cao et al. 2012; Yao et al. 2013; Richter et al. 2015; Zhou et al. 2015a, b). Many *Ganoderma* collections and species have been misnamed because of the presence of heterogenic forms, taxonomic obstacles and inconsistencies in the way the genus has been subdivided (Mueller et al. 2007). *Ganoderma* species are genetically heterogeneous, hence a wide range of genetic variation has been reported and caused by outcrossing over generations and different geographical origins (Pilotti et al. 2004). This has led to variation in their listed morphological characteristics, even within the same species (Hong et al. 2001). Environmental factors, variability, inter hybridization and individual morphological bias, mean identification of *Ganoderma* species is difficult (Zheng et al. 2007a). Hence, naming a species is confused and traditional taxonomic methods based on morphology are inconclusive for establishing a stable classification system for *Ganoderma* species (Hseu et al. 1996; Hong et al. 2001) which in turn result in an uncertain nomenclature. This confusing situation is mainly the result of various criteria used in identification by different authors. Some authors strictly only focus on host-specificity, geographical distribution and macro morphology of basidiomes, while other authors only focus on spore characteristics as the primarily taxonomic characteristics (Sun et al. 2006; Ekandjo and Chimwamurombe 2012). Richter et al. (2015) suggested using a combination of morphological, chemotaxonomic and molecular methods to develop a more stable taxonomy for this genus.

Molecular identification and diversity

Isoenzyme analysis was the first molecular technique used to separate *Ganoderma* species (Park et al. 1994; Gottlieb et al. 1995, 1998; Gottlieb and Wright 1999a, b; Smith and Sivasithamparam 2000). Then, DNA sequences of the internal transcribed spacer (ITS), partial large subunit rDNA (Moncalvo et al. 1995, 2000; Cao et al. 2012; Yao et al. 2013; Richter et al. 2015) and nearly complete small subunit rDNA sequences (Hong and Jung 2004; Douanla-Meli and Langer 2009) were used. Later, multigene phylogenetic analyses with protein-coding genes such as β -tubulin (*tub2*), the largest subunit of RNA polymerase II gene (*rpb1*), the second-largest subunit of RNA polymerase II (*rpb2*), and translation elongation factor 1- α (*tef1*) were performed to resolve the taxonomic confusions within *Ganoderma* (Park et al. 2012; Zhou et al. 2015a, b; Hennicke et al. 2016; Jargalmaa et al. 2017). However, many problems remain in the resolution of

phylogenetic relationships within the genus. As a result of the intricate taxonomy of *Ganoderma*, 65% of the *Ganoderma* sequences available in GenBank were reported to be wrongly identified or ambiguously labelled, (Jargalmaa et al. 2017). In this study, we reconstruct the phylogenetic tree based on ITS, *tef1* and *rpb2* sequence data (Table 10, Fig. 16).

Recommended genetic marker (genus level)—ITS

Recommended genetic markers (species level)—*rpb2*, *tef1*
Accepted number of species—There are 456 species and infra-species epithets in Index Fungorum (2020), for 224 accepted species. However, only 64 species have DNA sequence data.

References—Coetzee et al. (2015); Xing et al. (2016, 2018); Tchoumi et al. (2019), Luangharn et al. (2019), Ye et al. (2019) (phylogeny, new species), Cabarroi-Hernández et al. (2019) (phylogeny).

85. *Golovinomyces* (U. Braun) V.P. Heluta, Biol. Zh. Armenii 41: 357 (1988)

Background

Braun (1978) introduced *Golovinomyces* as a section of *Erysiphe sensu lato* and Heluta (1988a) raised it to genus rank. Braun (1999) and Braun and Takamatsu (2000) accepted *Golovinomyces* as a distinct genus and established a new tribe, Golovinomyceteae. This is a strictly herb-parasitic genus in the Erysiphaceae. Host-parasite co-speciation was reported between *Golovinomyces* and Asteraceae hosts using molecular phylogenetic analyses (Matsuda and Takamatsu 2003). It was suggested that *Golovinomyces* first acquired parasitism on Asteraceae and then diverged to the host tribes Astereae, Cardueae, Heliantheae and Lactuceae. Bremer (1994) pointed out that *Golovinomyces* may have originated in South America and the geographic distribution expanded into the Northern Hemisphere. However, Takamatsu et al. (2006) suggest that *Golovinomyces* originated in the Northern Hemisphere, and not in South America. Fabro et al. (2008) profiled genome-wide expression on haustorium formation of *G. cichoracearum* in *Arabidopsis*. Research to understand pathogenesis towards plants has been undertaken. A draft whole genome of *G. magnicellulatus*, the causal agent of phlox powdery mildew was provided by Farinas et al. (2019). McKernan et al. (2020) identified 82 genes associated with resistance to *G. cichoracearum*, the causal agent of powdery mildew in cannabis.

Classification—Ascomycota, Pezizomycotina, Leotiomycetes, Leotiomycetidae, Erysiphales, Erysiphaceae

Type species—*Golovinomyces cichoracearum* (DC.) V.P. Heluta

Distribution—Worldwide (Mainly in northern hemisphere)

Disease symptoms—powdery mildew

Hosts—Has a wide range of hosts including Asteraceae, Boraginaceae, Cucurbitaceae, Malvaceae, Fabaceae, Lamiaceae, Polygonaceae, Scrophulariaceae, Solanaceae and Verbenaceae.

Pathogen biology, disease cycle and epidemiology

Discussed under Erysiphaceae.

Morphological based identification and diversity

Golovinomyces is characterized by chasmothecia with mycelioid appendages, several, mostly 2-spored asci, an asexual morph with catenulent conidia that lack fibrosin bodies, and mostly nipple-shaped appressoria (Braun 1978; Qiu et al. 2020a). Heluta (1988a) reallocated *Erysiphe cichoracearum* to *Golovinomyces* and now nearly all species of *E. cichoracearum* are assigned to *Golovinomyces*. Braun (1987) confined *E. cichoracearum* to powdery mildews on hosts of Asteraceae and assigned specimens on hosts belonging to other plant families to *Erysiphe orontii*. Braun and Cook (2012) split *G. cichoracearum* into several species based on molecular analyses of this complex which suggested a co-evolutionary relationship between *Golovinomyces* species and tribes of Asteraceae (Matsuda and Takamatsu 2003). *Golovinomyces cynoglossi sensu lato*, a complex of morphologically similar powdery mildews on the plant family Boraginaceae, was reassessed by Braun et al. (2018) and split into *G. asperifoliorum*, *G. asperifolii* and *G. cynoglossi* based on sequence analyses, biological aspects and morphological differences. Braun et al. (2019) revisited *G. orontii* and Qiu et al. (2020b) epitypified and confirmed *Erysiphe cucurbitacearum* was a synonym of *G. tabaci*.

Molecular based identification and diversity

A comprehensive phylogenetic analysis by Takamatsu et al. (2013) resulted in a polyphyletic complex that split into three genetically distinct clades. *Golovinomyces ambrosiae* and *G. spadiceus* were considered as separate species by Braun and Cook (2012). However, phylogenetic analyses of ITS and 28S rDNA sequences by Takamatsu et al. (2013), including *Golovinomyces* species on Asteraceae, found that these two species that occur on Asian species of *Eupatorium* and a multitude of other hosts, including those on other plant families, formed a single large, unresolved clade (lineage III in Takamatsu et al. (2013)). The taxonomic interpretation posed a serious problem as *G. ambrosiae* and *G. spadiceus* were treated as two morphologically differentiated species. Hence, the resolution based only on ITS sequence data was considered insufficient to distinguish closely allied species. Most subsequent authors followed the taxonomic treatments in Braun and Cook (2012) and recognized *G. ambrosiae* and *G. spadiceus* as separate species, within lineage III, based

on morphological differences (Qiu et al. 2020a). However, there is minimal multi loci data for the powdery mildews currently available. Most of the research involves the intra-specific genetic diversity in species such as *Blumeria graminis* (Walker et al. 2011), *Erysiphe necator* (de Oliveira et al. 2015), *Golovinomyces orontii* (Pirondi et al. 2015a) and *Podosphaera xanthii* (Pirondi et al. 2015b). Based on ITS and D1/D2 domain of 28S sequence data, Braun et al. (2019) introduced *G. bolayi* and *G. vincae*. Nayak and Bandamaravuri (2019) developed species-specific PCR primers CgF2 and CgR2 for *G. orontii* (the causal agent of powdery mildew in cucurbits), based on partial ITS and 5.8S rDNA, which resulted in a 233bp fragment of *G. orontii*.

Recommended genetic markers (genus level)—ITS, LSU

Recommended genetic markers (species level)—Comprehensive applications of multi loci approaches to solve complex taxonomic-phylogenetic problems connected with the species level classification of the powdery mildews are lacking. The phylogenetic analyses of multi loci sequence data, including ITS and LSU, IGS, *tub2*, *chs*, and consideration of morphological characters resolve species delimitation in a heterogeneous complex within *Golovinomyces*.

Accepted number of species—There are 81 epithets listed in Index Fungorum (2020), however, only 41 have molecular data (Table 11, Fig. 17).

References—Braun (1978, 1987), Heluta (1988a, b) (morphology); Braun and Cook (2012), Takamatsu et al. (2013), Braun et al. (2019), Qiu et al. (2020a, b) (morphology and phylogeny).

86. *Heterobasidion* Bref., Unters. Gesamtgeb. Mykol. (Liepzig) 8: 154 (1888)

Background

Heterobasidion was introduced by Brefeld (1888) and is typified by *H. annosum* (\equiv *Polyporus annosus*). Certain *Heterobasidion* species are important forest pathogens of the Northern Hemisphere, causing root and butt rot, mainly in conifers (Woodward et al. 1998). In coniferous plantations, *Heterobasidion* is one of the most widespread of wood decay agents, especially when the host is under intensive management. *Heterobasidion* greatly reduces site productivity and the amount of harvestable timber; estimated financial losses caused by *Heterobasidion* species in Europe were around 800 million euro per year (Korhonen et al. 1998; Garbelotto 2004; Asiegbu et al. 2005). On the other hand, these taxa have a relatively moderate pathogenic role in natural forest ecosystems. They affect stand species composition, density and structure, and they contribute to forest succession, nutrient recycling and even regeneration (Goheen and Otrosina 1998; Garbelotto 2004; Dai et al. 2006).

Table 10 DNA barcodes available for *Ganoderma*

Species	Voucher no	ITS	<i>rpb2</i>	<i>tefl</i>
<i>Ganoderma adspersum</i>	GACP15061220	MK345425	MK371437	MK371431
<i>G. angustisporum</i>	Cui 13817*	MG279170	MG367507	MG367563
<i>G. applanatum</i>	FIN131R610	EF060004	–	–
<i>G. aridicola</i>	Dai 12588*	KU572491	–	KU572502
<i>G. australe</i>	GACP14081671	MH106871	–	–
<i>G. australe</i>	MFLU 13-0534	KP142173	–	MN423152
<i>G. austroafricanum</i>	CBS138724	KM507324	–	–
<i>G. boninense</i>	WD 2028	KJ143905	KJ143964	KJ143924
<i>G. carocalcareus</i>	DMC 322*	EU089969	–	–
<i>G. casuarinicola</i>	Dai 16336*	MG279173	MG367508	MG367565
<i>G. casuarinicola</i>	HKAS104639	MK817650	MK840868	MK871328
<i>G. chocoense</i>	QCAM3123	MH890527	–	–
<i>G. curtisii</i>	CBS 100132	JQ781849	KJ143967	KJ143927
<i>G. destructans</i>	CMW43670*	KR183856	–	–
<i>G. ecuadoriense</i>	ASL799	KU128524	–	–
<i>G. eickeri</i>	CMW49692*	MH571690	–	MH567287
<i>G. ellipsoideum</i>	GACP14080966*	MH106867	–	–
<i>G. enigmaticum</i>	CBS 139792*	KR183855	–	–
<i>G. enigmaticum</i>	Dai 15970	KU572486	MG367513	KU572496
<i>G. flexipes</i>	Wei 5494	JN383979	–	–
<i>G. gibbosum</i>	SFC20150630-23	KY364264	–	–
<i>G. hoehnelianum</i>	Dai11995	KU219988	MG367497	MG367550
<i>G. knysnamense</i>	CMW47755*	MH571690	–	MH567287
<i>G. leucocontextum</i>	GDGM 40200*	KF011548	–	–
<i>G. lingzhi</i>	Wu 1006-38*	JQ781858	JX029980	JX029976
<i>G. lobatum</i>	JV1212/10J	KF605676	–	KU572501
<i>G. lucidum</i>	Rivoire 4195	KJ143909	KJ143969	–
<i>G. lucidum</i>	Cui 14404	MG279181	MG367519	MG367573
<i>G. martinicense</i>	LIP SWMart08-55*	KF963256	–	–
<i>G. mbrekobenum</i>	UMN7-3GHA*	KX000896	–	–
<i>G. mizoramense</i>	UMN-MZ4*	KY643750	–	–
<i>G. multiplicatum</i>	Dai 13122	KU572488	–	KU572498
<i>G. multipileum</i>	CWN 04670	KJ143913	KJ143972	KJ143931
<i>G. mutabile</i>	Yuan 2289*	JN383977	–	–
<i>G. nasalanense</i>	GACP17060211*	MK345441	–	–
<i>G. neojaponicum</i>	ASI 7032	JQ520193	–	–
<i>G. orbiforme</i>	Cui 13918	MG279186	MG367522	MG367576
<i>G. orbiforme</i>	GACP14061420	MK345447	–	–
<i>G. oregonense</i>	CBS 265.88	JQ781875	KJ143974	KJ143933
<i>G. philippii</i>	E7098	AJ536662	–	–
<i>G. podocarpense</i>	QCAM6422*	MF796661	–	–
<i>G. resinaceum</i>	CBS 194.76	KJ143916	–	KJ143934
<i>G. rywardenii</i>	HKAS 58053*	HM138671	–	–
<i>G. rywardenii</i>	HKAS 58054	HM138672	–	–
<i>G. sandunense</i>	GACP18012501*	MK345450	–	–
<i>G. sandunense</i>	GACP18012502	MK345451	–	–
<i>G. sessile</i>	JV 1209/9	KF605629	–	KJ143936
<i>G. shandongense</i>	Dai 15785	MG279190	MG367526	MG367580
<i>G. sichuanense</i>	HMAS 42798*	JQ781877	–	–
<i>G. sinense</i>	Wei 5327	KF494998	MG367529	KF494976
<i>G. steyaertanum</i>	MEL:2382783	KP012964	–	–

Table 10 (continued)

Species	Voucher no	ITS	<i>rpb2</i>	<i>tefl</i>
<i>G. steyaertanum</i>	6 WN 20B	KJ654462	–	–
<i>G. subresinosum</i>	7-SU-3-C-70(M)-B	KJ654472	–	–
<i>G. thailandicum</i>	HKAS104640*	MK848681	MK875831	MK875829
<i>G. tropicum</i>	Dai 16434	MG279194	MG367532	MG367585
<i>G. tropicum</i>	HKAS 97486	MH823539	MH883621	–
<i>G. tsugae</i>	Dai12751b	KJ143919	KJ143977	KJ143939
<i>G. valesiacum</i>	CBS428.84	JQ520218	–	–
<i>G. weberianum</i>	CBS219.36	JQ520219	–	–
<i>G. wiiroense</i>	UMN-20-GHA	KT952361	–	–
<i>G. williamsianum</i>	Dai 16809	MG279183	MG367535	MG367588
<i>G. wuzhishanensis</i>	GACP14081689	KU994772	–	–
<i>G. zonatum</i>	FL-02	KJ143921	KJ143979	KJ143941

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold

Classification—Basidiomycota, Agaricomycotina, Agaricomycetes, Incertaesedis, Russulales, Bondarzewiaceae

Type species—*Heterobasidion annosum* (Fr.) Bref., Unters. Gesamtgeb. Mykol. (Liepzig) 8: 154 (1888)

Distribution—North America, Europe, Asia, Australia and Oceania

Disease symptoms—There are two *Heterobasidion* species complexes –*H. insulare sensu lato* and *H. annosum sensu lato*—they cause the same symptoms. The *H. annosum* species complex is one of the major root-rot pathogenic genera of the northern temperate hemisphere (Garbelotto and Gonthier 2013; Kärhä et al. 2018). After the primary infection through stump tops, or stem and root wounds, the taxa can vegetatively infect uninjured trees (secondary infection) by the growth of the mycelium through root contacts (Rishbeth 1950, 1951a, b; Asiegbu et al. 2005; Garbelotto and Gonthier 2013). *Heterobasidion* could be considered both necrotrophs and saprotrophs; though some species in the *H. insulare* species complex (e.g. *H. austral*, *H. araucariae*) are mainly saprotrophs (Niemelä and Korhonen 1998; Dai and Korhonen 2009; Chen et al. 2014). In contrast to Europe, the pathogenicity of *H. annosum sensu lato* in China and Japan is uncertain; the complex seems to occur mostly on dead trees, and no symptoms of tree decline are usually visible near infected trees. These observations could be due to different, less intensive forest management strategies in the East-Asian regions, or lack of data on the butt rot symptoms (Dai et al. 2006; Tokuda et al. 2007).

The infection causes white pocket rot and heart rot in the roots and the butt of living trees (Korhonen and Stenlid 1998; Asiegbu et al. 2005). Resin, containing mycelium, may also exude from the infected roots, or the bark-scales (Rishbeth 1950). In invaded roots and the basal portions of the trunk, *H. annosum sensu lato* taxa colonize different plant tissues depending on the host. Heart rot is mainly

caused in trees more susceptible to the colonization of the heartwood, e.g. *Picea abies*. In the case of *Pinus*, cambium and sapwood are the most severely colonized, while the sapwood of *Calocedrus* or *Sequoiadendron* trees is the most colonized (Garbelotto 2004; Asiegbu et al. 2005; Garbelotto and Gonthier 2013).

After establishment, the basidiomata of *H. annosum sensu lato* appear. The localization of the sporocarps is governed by the species, environmental conditions and infection strategy. Some species prefer the root collar for fruiting (*H. annosum*, *H. irregular*). Some also produce sporocarps in decay pockets in stumps and fallen trees (*H. parviporum*, *H. abietinum* and *H. occidentale*), or under the intact surface of stumps (*H. irregulare*, *H. occidentale*). The sporocarps are sometimes located on the higher parts of the trunk. When moisture is limited, the fungi fruit inside stumps; if the climate is moist and humid, the basidiomata can be found near the ground in the duff at the base of diseased trees. If during primary infection the stump surface is infected, the basidiomata form under an intact top layer. During active pathogenesis, if the standing trees are infected the sporocarps could be found within decay columns in the sapwood (Rishbeth 1950; Otrosina and Garbelotto 2010).

The infection kills the functioning sapwood, cambium and heart wood in the roots and at the basal portions of the trunk, resulting in white rot, reduced growth rate, crown dieback (Omdal et al. 2004), and eventually mortality and windthrow of infected trees (Rishbeth 1950; Oliva et al. 2008; Garbelotto and Gonthier 2013).

Hosts—The host range of *Heterobasidion* is extremely wide. The genus has been reported from approximately 200 host species (Korhonen and Stenlid 1998). Taxa mostly occur on gymnosperms, such as *Abies*, *Agathis*, *Araucaria*, *Calocedrus*, *Juniperus*, *Keteleeria*, *Larix*, *Picea*, *Pinus*,

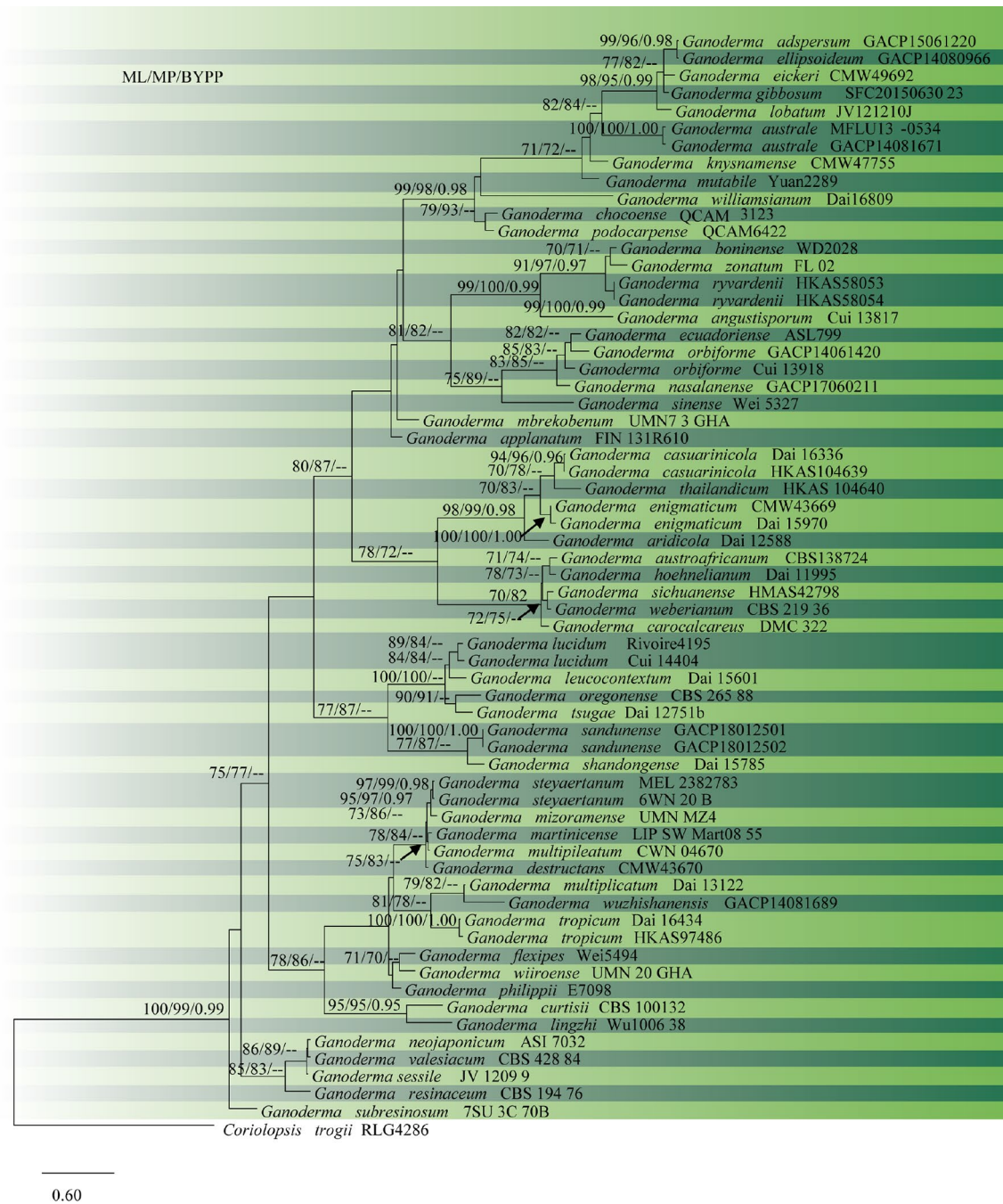


Fig. 16 Phylogram of 64 recognized *Ganoderma* species, obtained from ML of combined ITS, *rpb2*, and *tef1* datasets. Bootstrap values from ML (left) and MP (middle) greater than 70% and BYPP, greater

than 0.95, are indicated above the nodes. The tree is rooted with *Corioloopsis trogii*. Type specimens are indicated in bold

Podocarpus, *Pseudolarix*, *Pseudotsuga*, *Sequoia*, *Sequoiadendron*, *Thuja* and *Tsuga* (Buchanan 1988; Corner 1989; Dai and Korhonen 2009; Otrosina and Garbelotto 2010; Garbelotto and Gonthier 2013; Garbelotto et al. 2017). Occasionally, certain *Heterobasidion* species grow on broad-leaved trees of various angiosperm genera (Garbelotto and Gonthier 2013; Ryvardeen and Melo 2014).

Morphological based identification and diversity

There are 33 *Heterobasidion* epithets listed in Index Fungorum (2020). Of these, eight are related to other polypore genera, based on type studies and morphological observations (Ryvardeen 1972, 1985; Buchanan and Ryvardeen 1988; Dai and Niemelä 1995; Hattori 2003). Besides, the taxonomic status of three further species described from Asia is

unclear: viz. *H. arbitrarium*, *H. perplexum* and *H. insulare* (Corner 1989; Ryvarden 1989; Stalpers 1996; Hattori 2001; Dai et al. 2002; Tokuda et al. 2009). Given that no sequence data (*H. arbitrarium*, *H. perplexum*) or authentic sequences (*H. insulare sensu stricto*) are available for the molecular resolution, further studies are needed to clarify their status.

Formerly, *Heterobasidion* was considered as a group consisting of only the generic type, *H. annosum* and *H. araucariae* and *H. insulare* (Buchanan 1988; Chase 1989). However, mating studies on Eurasian and North American *Heterobasidion* collections revealed several intersterile groups, which later became the basis for designating separate taxonomic species within the *H. annosum* and *H. insulare* species complexes. Mating experiments revealed three intersterile groups of *H. annosum sensu lato* in Europe (Korhonen 1978b, Capretti et al. 1990) and two in North America (Otrosina et al. 1993). All intersterile groups have been recognised in the *H. annosum* species complex are now formally described as separate taxonomic species. European groups were described as *H. abietinum*, *H. parviporum* and *H. annosum sensu stricto* (Niemiälä and Korhonen 1998), whereas North American groups were named *H. irregulare* and *H. occidentale* (Otrosina and Garbelotto 2010).

The mating study by Dai et al. (2002) on Asian “*H. insulare*” collections revealed three intersterile groups in China, which were subsequently described as *Heterobasidion linzhiense* (Dai et al. 2007), *H. orientale* and *H. ecrustosum* (Tokuda et al. 2009). *H. australe* related to the *H. insulare* species complex was also described from China by Dai and Korhonen (2009). Chen et al. (2014) described two further *Heterobasidion* species (*H. amyloideum* and *H. tibeticum*) from the eastern Himalayas based on phylogenetic evidence. These species are morphologically closely related to the members of the *H. insulare* species complex, but differ in presence of cystidia and amyloid skeletal hyphae in the context. The recently described *H. amyloideopsis* was collected in the western Himalayas (Pakistan) and formed a monophyletic group with the *H. insulare* species complex, sister to *H. amyloideum* (Zhao et al. 2017).

The main morphological characters which are used for the identification are the resupinate to pileate basidiocarps, the dimitic hyphal system with mostly simple septate generative hyphae, and the asperulate basidiospores showing no reaction in Melzer’s reagent. Besides morphology, host preference, geographical distribution, and DNA sequence data have also been used for species identification (Otrosina and Garbelotto 2010; Chen et al. 2015a).

Molecular based identification and diversity

Heterobasidion has been intensely studied by molecular methods. Sequence data are available for the majority of

taxa, and molecular studies were conducted to understand the evolution (Dalman et al. 2010), mating behaviour (Gonthier and Garbelotto 2011), and pathogenicity (Liu et al. 2018a) of *Heterobasidion* species.

Various marker types were used to resolve the phylogeny of the *H. annosum* species complex, such as isoenzyme (Karlsson and Stenlid 1991a, b), AFLP (Gonthier and Garbelotto 2011) and SSR (Garbelotto et al. 2013) markers. Sequence analyses were carried out initially on nrITS and intergenic spacer regions (Kasuga and Mitchelson 1993a, b; DeScenzo and Harrington 1994), housekeeping genes (Johansson and Stenlid 2003), peroxidase (Maijala et al. 2003) and laccase genes (Asiegbu et al. 2004), with which it was possible to distinguish four lineages (three European and one North American) within the complex (Asiegbu et al. 2005). Later, allowing the differentiation of a larger number of taxa, further nuclear genes were applied, such as the calmodulin (*cam*), translation elongation factor 1- α (*tef1*), glyceraldehydes3-phosphate dehydrogenase (*gapdh*), heat shock protein (*hsp*), glutathione-S-transferase (*gst1*) and transcription factor (*tf*) genes (Johansson and Stenlid 2003; Ota et al. 2006; Dalman et al. 2010), as well as two mitochondrial genes, the mitochondrial ATP synthase subunit 6 (*ATP6*) and mitochondrial rDNA region (Linzer et al. 2008). Dalman et al. (2010) came to the conclusion, that there are two monophyletic sister clades within the *H. annosum* species complex, representing the Eurasian and North American species.

The protein coding largest subunit of RNA polymerase II (*rpb1*) and the second subunit of RNA polymerase II (*rpb2*) genes were used by Chen et al. (2014) and were suitable to differentiate *Heterobasidion* species in the *H. insulare* species complex. The variability of these markers was confirmed by Chen et al. (2015a) and Zhao et al. (2017) who, among other previously mentioned markers, both used the nuclear large ribosomal subunit (nrLSU) and the mitochondrial small subunit (mtSSU) sequences to their studies (Fig. 18).

In this study, we provide a phylogenetic tree (Fig. 19) based on multi-locus phylogenetic analysis of ITS–*gapdh*–*rpb1*–*rpb2*–*tef1* sequence data. Sequences of *H. arbitrarium* and *H. perplexum* could not be analysed as they are unavailable in GenBank. Furthermore, no sequences are available for the type of *H. insulare* hence this species was not included in the analysis. The results provide a similar topology to those obtained by Chen et al. (2015a, b) and Zhao et al. (2017).

Recommended genetic marker (genus level)—nrLSU

Recommended genetic markers (species level)—*rpb1*, *rpb2*

Accepted number of species—There are 33 epithets in Index Fungorum (2020), however only **15 species are accepted**

Table 11 DNA barcodes for accepted species of *Golovinomyces*

Species	Strain no	ITS	LSU
<i>Golovinomyces adenophorae</i>	MUMH < JPN_144	LC516963	AB077632
<i>G. ambrosiae</i> [#]	MUMH345	AB077642	AB077641
<i>G. arabis</i>	HMNWAFU-CF2009256	KR048081	KR048149
<i>G. artemisiae</i> [#]	MUMH175	AB077637	AB077636
<i>G. asperifolii</i>	KUS-F24884	MH189697	MH189696
<i>G. asperifoliorum</i>	MUMH769	AB077684	AB077684
<i>G. asterum</i> [#]	MUMH941	AB769417	AB769418
<i>G. biocellatus</i> [#]	MUMH4293	AB307671	AB307671
<i>G. bolayi</i> [#]	OLM 35939*	LC417106	–
<i>G. calceolariae</i>	MUMH 1934	AB430810	AB430810
<i>G. chrysanthemi</i>	MUMH853	AB077654	AB077653
<i>G. cichoracearum</i> [#]	MUMH623	AB077660	AB077660
<i>G. circumfusus</i> [#]	GLM49501	MK452630	MK452703
<i>G. cucubitarum</i>	HMJAU-PM91761	MK937796	MK937801
<i>G. cynoglossi</i> [#]	VPRI20429	AB769455	–
<i>G. depressus</i>	MUMH696	AB077675	AB077676
<i>G. echinopsis</i>	MUMH1363	AB769414	–
<i>G. euphorbiicola</i>	MUMH3807	AB769460	–
<i>G. fischeri</i>	MUMH1345	AB769451	AB769452
<i>G. glandulariae</i>	BRIP 70490*	NR_166303	MN539541
<i>G. hyoscyami</i>	HMNWAFU-CF2013114	KR048155	KR048155
<i>G. inulae</i>	MUMH1334	AB769428	–
<i>G. leuceriae</i>	MUMH2527	AB246766	–
<i>G. longipes</i> [#]	MUMH2489	AB769440	–
<i>G. macrocarpus</i>	HAL 3153*	NR_154105	–
<i>G. magnicellulatus</i> [#]	MUMH441*	AB077647	AB077646
<i>G. monardae</i> [#]	MUMH936	AB307668	AB077691
<i>G. montagnei</i>	MUMH1082	AB769413	–
<i>G. neosalviae</i> [#]	MUMH4294	AB307673	–
<i>G. ocimi</i>	MUMH<JPN_:1803	LC306656	–
<i>G. oronti</i> [#]	G:00295968	LC417099	–
<i>G. riedlianus</i>	HMNWAFU-CF2012033	KR048088	KR048157
<i>G. reginae</i>	BCRU4645	AB246759	–
<i>G. salviae</i>	MUMH935	AB769437	AB077690
<i>G. sonchicola</i> [#]	MUMH683	AB077673	AB077672
<i>G. sordidus</i> [#]	MUMHn41	AB077658	AB077657
<i>G. spadiceus</i> [#]	MUMH<JPN_:3708	LC306664	–
<i>G. tabaci</i>	BP-1TOB	AF229013	AB022412
<i>G. valerianae</i>	HMNWAFU-CF2011034	KR048090	KR048159
<i>G. verbasci</i> [#]	MUMH958	AB769468	AB769469
<i>G. vincae</i>	MUMH2480	AB769444	–

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold. Species confirmed with pathogenicity studies are marked with [#]

(Table 12). Amongst these, no sequences are available for *H. arbitrarum* and *H. insulare*. *Heterobasidion perplexum* is not accepted in the genus, pending further studies.

References—Dai and Korhonen (2009) (new sp., China, morphology); Tokuda et al. (2009) (new species, East Asia); Dalman et al. (2010) (Evolution, *H. annosum* species

complex, haplotype network); Otrosina and Garbelotto (2010) (new species, North America, biology); Garbelotto and Gonthier (2013) (biology, epidemiology, control); Chen et al. (2014) (new species, China, phylogeny); Chen et al. (2015a) (biogeography, divergence time estimation, phylogeny); Zhao et al. (2017) (new sp., Pakistan, phylogeny).

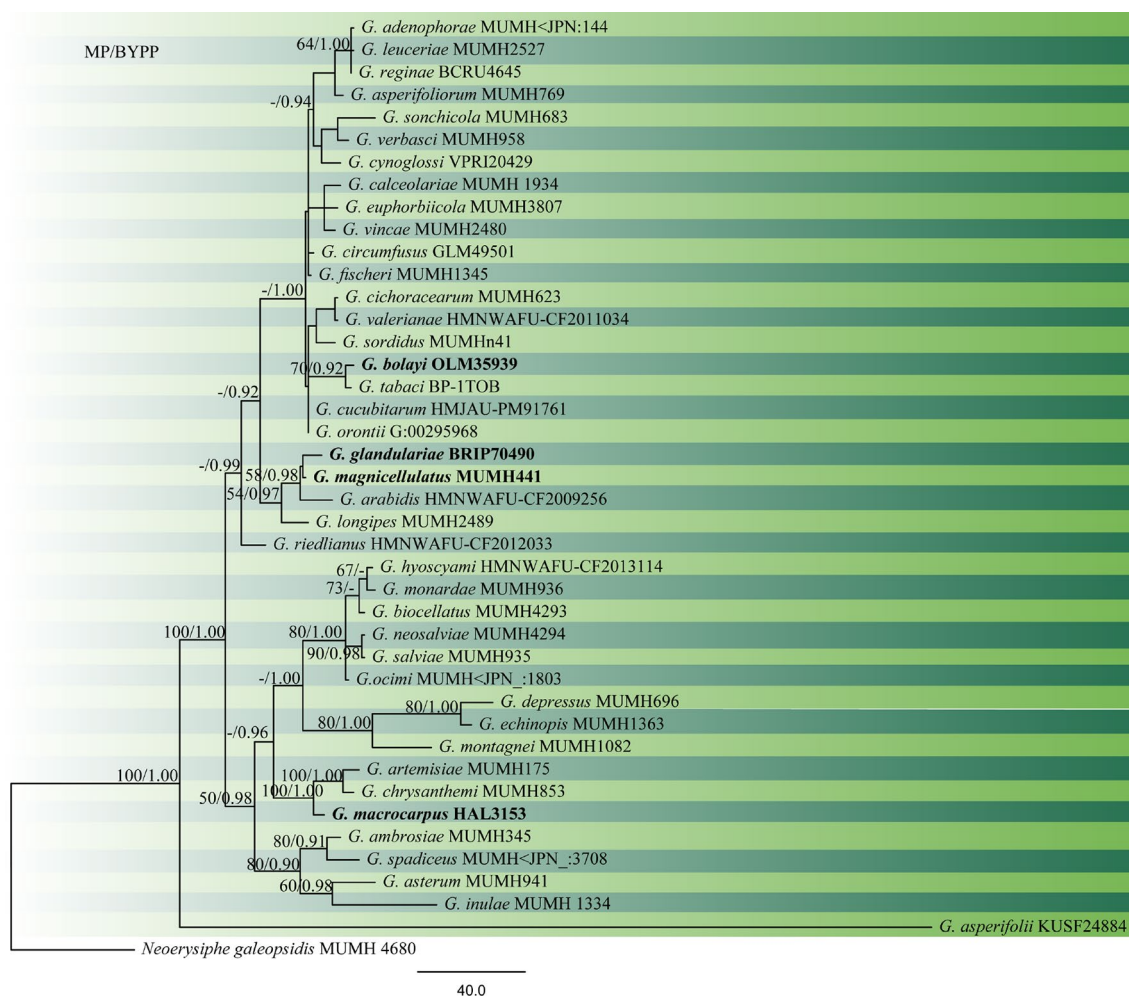


Fig. 17 Phylogram generated from MP analysis based on combined sequences of ITS and LSU sequences of all species of *Golovinomyces* with molecular data. Related sequences were obtained from GenBank. Forty-two taxa are included in the analyses, which comprise 1401 characters including gaps, of which 848 characters are constant, 392 characters are parsimony-uninformative and 161 characters parsimony-informative. The parsimony analysis of the data matrix resulted in the maximum of ten equally most parsimonious trees with a length of 927 steps (CI = 0.740, RI=0.699, RC = 0.517, HI = 0.260) in the second tree. The tree was rooted with *Neoerysiphe galeopsidis* (MUMH 4680). MP bootstrap support value $\geq 50\%$ and BYPP ≥ 0.9 are shown respectively near the nodes. Ex-type strains are in bold

87. *Meliola* Fr., Syst. orb. veg. (Lundae) 1: 111 (1825)

Background

Meliola commonly known as “black mildews” or “dark mildews” is the largest genus of *Meliolaceae* (Hongnan et al. 2015; Zeng et al. 2017). Fries (1825) established this genus, with the type species *M. nidulans*. Species in *Meliola* are mostly biotrophs or pathogens of living leaves and occasionally petioles, twigs, and branches (Hansford 1961; Hosagoudar 1994, 1996, 2008; Mibey and Hawksworth 1997; Old et al. 2003; Hosagoudar and Riju 2013). The phylogenetic placement of *Meliola* was established by using sequence data from fruiting bodies and placed in Sordariomycetes (Gregory and John 1999; Pinho et al. 2012, 2014, Hongnan et al. 2015; Justavino et al. 2015). *Meliola* has been

shown to be polyphyletic (Hyde et al. 2020b; Marasinghe et al. 2020; Zeng et al. 2020). There is little sequence data available in GenBank for clarifying relationships between species and establishing host-specificity (Hongnan et al. 2015; Zeng et al. 2017).

Classification—Ascomycota, Pezizomycotina, Sordariomycetes, Sordariomycetidae, Meliolales, Meliolaceae
Type species—*Meliola nidulans* (Schwein.) Cooke
Distribution—commonly found in tropical and subtropical regions (see Zeng et al. 2017)
Disease symptoms—Black mildews, forming black, radiate velvety colonies on the surface of plants.
Hosts—has a wide range of hosts (see Zeng et al. 2017)

Pathogen biology, disease cycle and epidemiology

For pathogen biology, disease cycle and epidemiology see Hongsanan et al. (2015).

Morphological based identification and diversity

Species in *Meliola* are characterized by forming web-like colonies on the host surface, hyphal setae developed from superficial hyphae, with hyphopodia, 2–4-spored, unitunicate asci, and 3–4-septate pigmented ascospores (Pinho et al. 2012, 2014; Hongsanan et al. 2015, 2020; Justavino et al. 2015; Hyde et al. 2020a, b; Fig. 20). Cannon and Kirk (2007) reported that the asexual morph of the genus develops from the hypha, form ampuliform hyphopodia or flask-shaped which are called “phialides” (Hongsanan et al. 2015). Conidiogenous cells formed from vegetative hyphae and small, hyaline, unicellular conidia (Cannon and Kirk 2007; Hongsanan et al. 2015). Currently, *Meliola* comprises over 1700 species (Zeng et al. 2017), which have mostly been introduced by host association, followed by morphology, and disease distribution (Mibey and Hawksworth 1997). Thus, species identification is almost impossible without a host name. However, the same species can be found in different hosts, but it is not clear if this is widespread (Hongsanan et al. 2015). Therefore, testing of host-specificity in *Meliola* is needed to establish accurate species determination.

Molecular based identification and diversity

Sequence data of species in *Meliola* are from direct sequencing of fruiting bodies and fresh mycelium (Pinho et al. 2012, 2014; Hongsanan et al. 2015; Justavino et al. 2015; Hyde et al. 2016, 2020b). LSU and ITS sequence data placed *Meliola* in Sordariomycetes (Hongsanan et al. 2015, 2020; Maharachchikumbura et al. 2015, 2016; Hyde et al. 2016, 2020a, b). By adding more sequence data, *Meliola* was shown to be polyphyletic (Marasinghe et al. 2020; Zeng et al. 2020). A phylogenetic tree for *Meliola* species is presented in Fig. 21.

Recommended genetic markers (genus level)—LSU, SSU of nrDNA

Recommended genetic marker (species level)—ITS

Accepted number of species—There are 3064 epithets listed in Index Fungorum (2020), however only 25 species have DNA molecular data (Zeng et al. 2017, Table 13).

References—Cannon and Kirk (2007) (morphology); Pinho et al. (2012, 2014), Hongsanan et al. (2015, 2020), Justavino et al. (2015), Zeng et al. (2020) (morphology and phylogeny)

88. *Neoerysiphe* U. Braun, Schlechtendalia 3: 50 (1999)

Background

Neoerysiphe was classified in section Galeopsidis within *Erysiphe*. Phylogenetic analysis, however, showed *Erysiphe* to be polyphyletic, and Galeopsidis was raised to generic rank (Takamatsu et al. 1998; Braun 1999; Saenz and Taylor 1999). Therefore, in the current classification *Neoerysiphe* belongs to the tribe Golovinomyceteae.

Classification—Erysiphaceae, Erysiphales, Leotiomycetidae, Leotiomycetes, Pezizomycotina

Type species—*Neoerysiphe galeopsidis* (DC.) U. Braun

Distribution—Argentina, Australia, Belarus, Brazil, Bulgaria, Canada, China, Denmark, Finland, France, Germany, Hungary, India, Israel, Italy, Japan, Korea, Netherlands, Norway, Poland, Romania, Russia, Slovakia, Sweden, Switzerland, Turkey, UK, Ukraine and USA (Farr and Rossman 2020).

Disease symptoms—powdery mildew

Hosts—*Neoerysiphe* species have a wide host distribution infecting more than 300 species from families including Asteraceae, Acanthaceae, Bignoniaceae, Elaeocarpaceae, Lamiaceae, Rubiaceae and Verbenaceae (Amano 1986; Braun 1999; Bahcecioglu et al. 2006). In general, all species have a specific host range confined to one plant family, except *N. galeopsidis* which affects several species in four families (Takamatsu et al. 2008).

Pathogen biology, disease cycle and epidemiology

Discussed under Erysiphaceae.

Morphological based identification and diversity

Neoerysiphe is in the tribe Golovinomyceteae with *Arthrocladiella* and *Golovinomyces*. These genera share a common asexual morph characterized by catenate conidia without distinct fibrosin bodies (Braun 1999). *Neoerysiphe* is characterized by lobed appressoria and the striate surface of the conidia (Braun 1981; Cook et al. 1997; Braun and Cook 2012). Braun and Cook (2012) mentioned that 15 species of *Neoerysiphe* are described on different hosts belonging to 11 plant families. Of these 15 species, 11 sexual morphs and 14 asexual morphs have been identified (except *N. joerstadii*) (Heluta et al. 2010; Braun and Cook 2012). *Striatodium* is now considered as a synonym of *Neoerysiphe* and three species viz. *N. aloysiae*, *N. baccharidis* and *N. maquii* were transferred to *Neoerysiphe*, while *Striatodium jaborosae* was not transferred as its phylogenetic position are unclear (Wijayawardene et al. 2017a).

Molecular based identification and diversity

The phylogenetic placement of *Neoerysiphe* within Erysiphaceae has been reported in a few papers (Saenz and



Fig. 18 Members of *Heterobasidion annosum* species complex. **a** basidiome on Scots pine, **b** basidiome on European silver fir, **c–e** basidiomes on European spruce, **f** hyphal structure in the trama, **g** hyphal structure in the context, **h–j** basidiospores. Scale bars: **f, g** = 10 μ m, **h, j** = 5 μ m

Taylor 1999; Mori et al. 2000; Cook et al. 2006). However, these treatments used only limited sequence data for the genus. Takamatsu et al. (2008) conducted the first comprehensive study on this genus using ITS sequence data and the divergent domains D1 and D2 of the 28S rDNA for 30 strains. In their study, the 30 taxa, clustered into three monophyletic groups that were represented by *N. galeopsidis* on Lamiaceae, *N. galii* on Rubiaceae and *N. cumminsiana* from Asteraceae. Takamatsu et al. (2008) used an LSU dataset to estimate the timing of divergence of *Neoerysiphe*. *Neoerysiphe* split from other genera ca 35–45 Mya and the three groups of *Neoerysiphe* diverged between 10 and 15 Mya in the Miocene. Heluta et al. (2010) used 65 ITS sequences in their analyses for identifying *Neoerysiphe* species infecting Asteraceae and *Geranium* in Eurasia and introduced three new species, viz. *N. hiratae*, *N. joerstadii* and *N. nevoi*. Gregorio-Cipriano et al. (2020) introduced a new species *N. sechii* causing powdery mildew on *Sechium edule* and *S. mexicanum* in Mexico. The authors mentioned that they were unable to recover DNA in pure form from some samples, as fragments of infected leaves were used during the extraction. Therefore, a specific oligonucleotide for Erysiphales at the 5= region of ITS was designed: ErysiF (5=AGGATCATTACWGAGYGYGAG-3=) was used along with NLP1 (Limkaisang et al. 2006) to amplify a fragment of approximately 1200 bp (that included the ITS1-5.8S-ITS2 region and a section of approximately 680 nucleotides from

28S). Species used in the phylogenetic analyses done in this study are listed in Table 14 and given in Fig. 22.

Recommended genetic marker (genus level)—ITS and LSU

Recommended genetic markers (species level)—ITS

Accepted number of species—There are 16 species epithets in Index Fungorum (2020), for 15 accepted species. However, only 12 species have DNA sequence data (*N. che-lones*, *N. gnaphalii* and *N. rubiae* do not have molecular data) (Table 14).

References—Takamatsu et al. (1998), Braun (1999), Saenz and Taylor (1999) (morphology); Heluta et al. (2010), Braun and Cook (2012), Gregorio-Cipriano et al. (2020) (morphology and phylogeny).

89. Nothophoma Qian Chen & L. Cai, Stud. Mycol. 82: 212 (2015)

Background

Nothophoma was introduced by Chen et al. (2015b) by transferring five *Phoma* species. Species are saprobes and pathogens. In addition, to the phytopathogens, *N. gossypicola* has been isolated from clinical samples of humans in the respiratory secretion of a patient with pneumonia and a human bronchial wash sample (Valenzuela-Lopez et al. 2018). Chethana et al. (2019) showed that the comparative pathogenicity of *Nothophoma* species is low when compared to other opportunistic pathogens. Some species grow on other fungi or occur in soil (Boerema et al. 2004;

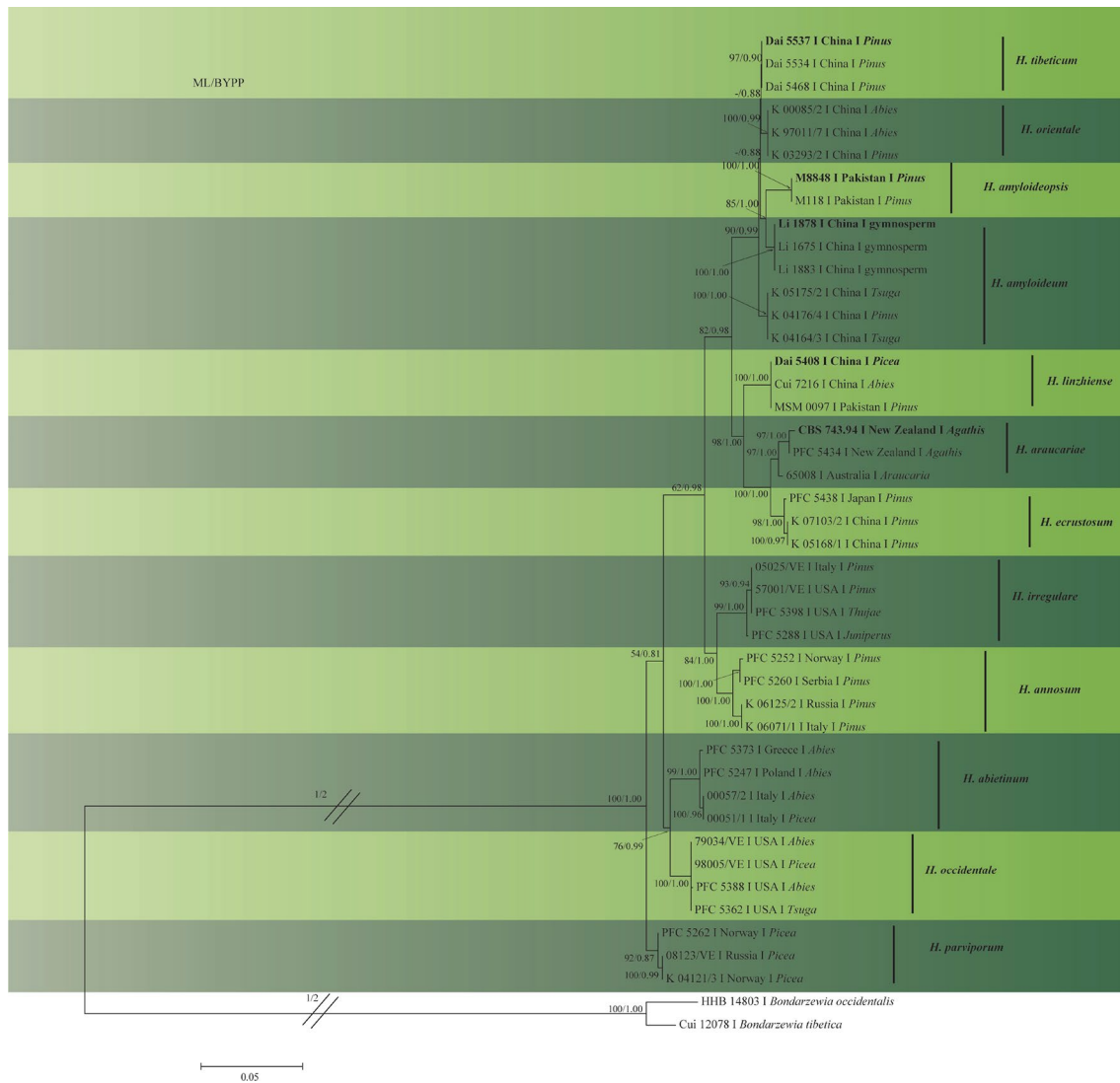


Fig. 19 Phylogram generated from ML analysis based on combined ITS, *rpb1*, *rpb2*, *gapdh* and *tef1* sequence data of *Heterobasidion* species. Related sequences were obtained from GenBank. Forty-four strains are included in the analyses, which comprised 4314 characters

Aveskamp et al. 2009; 2010; Chen et al. 2015b). Some *Nothophoma* species might be host-specific to a single plant genus or family (Aveskamp et al. 2010; Chen et al. 2015b). However, there is no study of host-specificity in *Didymellaceae*. Abdel-Wahab et al. (2017) identified 55 bioactive compounds from an endophyte, *N. multilocularis*. Of these, ten compounds showed strong antimicrobial activity in combination.

Classification—Ascomycota, Pezizomycotina, Dothideomycetes, Pleosporomycetidae, Pleosporales, Didymellaceae
Type species—*Nothophoma infossa* (Ellis & Everh.) Qian Chen & L. Cai

including gaps. The tree was rooted with *Bondarzewia occidentale* (HHB 14803) and *B. tibetica* (Cui 12078). Tree topology of the ML analysis was similar to the Bayesian analysis. ML bootstrap values $> 50\%$ and BYPP > 0.80 are shown respectively near the nodes

Distribution—Argentina, China, Italy, India, Korea, Netherlands, Spain, Tunisia, Ukraine, United States

Disease symptoms—brown spot of fruits, leaf spots, shoot canker, stem cankers

Leaf spot produced by *Nothophoma anigozanthi* is elliptical to circular and black. *Nothophoma pruni* and *N. quercina* develop small, dark red or purple pinpoint lesions (Chethana et al. 2019). Liu et al. (2018b) identified *N. quercina* infection on ornamental crab-apple. Symptoms on the trunk appear as warts, the periderm around warts can become cracked, and the bark is roughened with a scaly periderm. During dry weather, these cankers expand and coalesce (Liu et al. 2018b; Fig. 23). *Nothophoma quercina* develops shoot

Table 12 DNA barcodes for accepted species of *Heterobasidion*

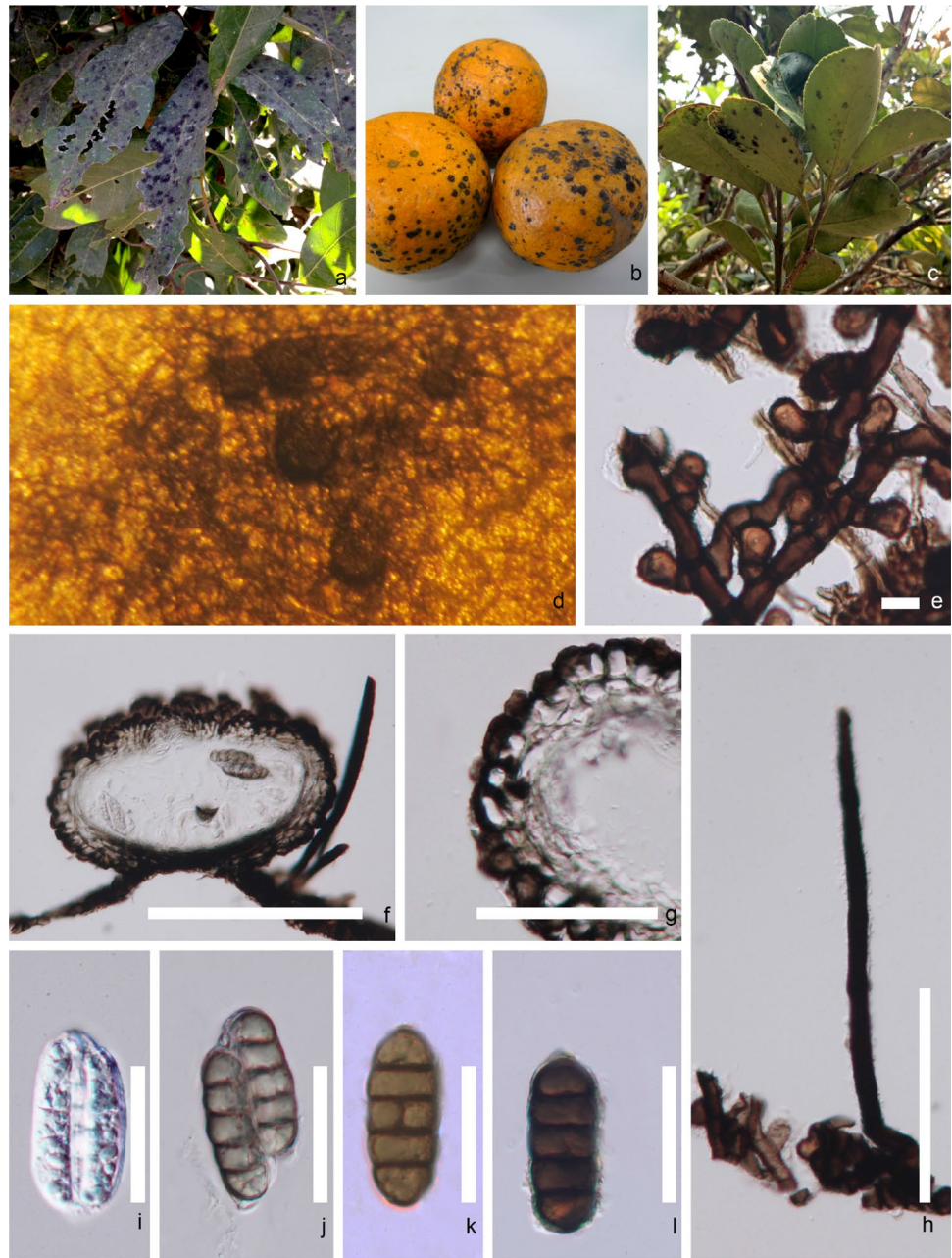
Species	Strain	ITS	<i>rpb1</i>	<i>rpb2</i>	<i>gapdh</i>	<i>tefl</i>
<i>Heterobasidion abietinum</i>	00057/2	KJ651453	KJ651632	KJ651725	KJ651756	–
	00051/1	KJ651450	KJ651629	KJ651722	KJ651753	–
	PFC 5247	KC492895	–	–	KP863657	KC571636
	PFC 5373	KC492956	–	–	KP863664	KC571687
<i>H. amyloideopsis</i>	MS 8848*	KT598384	–	KT598388	–	–
	M 118	KT598385	–	KT598389	–	–
<i>H. amyloideum</i>	Li 1878*	KJ651455	KF033157	KF006538	KJ651758	–
	Li 1675	KJ651454	KF033155	KF006534	KJ651757	–
	Li 1883	KJ651456	KF033156	KF006537	KJ651759	–
<i>H. annosum</i>	K 06125/2	KJ651459	KF453492	KF453498	KJ651762	–
	K 06071/1	KJ651458	KF453491	KF453497	KJ651761	–
	PFC 5252	KC492906	–	–	KP863659	KC571646
	PFC 5260	KC492911	–	–	KP863661	KC571651
<i>H. araucariae</i>	65008	KJ651462	KJ651636	KJ651729	KJ651766	–
	CBS 743.94*	MH862503	–	–	–	–
	PFC 5434	KX130098	–	–	KX130104	KX130101
<i>H. australe</i>	K 05175/2	KJ651467	KF033137	KF006506	KJ651771	–
	K 04167/4	KJ651465	KF033135	KF006502	KJ651769	–
	K 04164/3	KJ651464	KF033134	KF006500	KJ651768	–
<i>H. ecrustosum</i>	K 05168/1	KJ651468	KF033142	KF006513	KJ651772	–
	K 07103/2	KJ651471	KF033145	KF006517	KJ651775	–
	PFC 5438	KX130099	–	–	KX130105	KX130102
<i>H. irregulare</i>	57001/VE	KJ651473	KJ651638	KJ651731	KJ651777	–
	05025/VE	KJ651478	KJ651643	KJ651736	KJ651782	–
	PFC 5398	KP863586	–	–	KP863652	KP863616
	PFC 5288	KP863575	–	–	KP863641	KP863606
<i>H. linzhiense</i>	Dai 5408*	KJ651484	KF033154	KF006533	KJ651788	–
	Cui 7216	KJ651480	KF033148	KF006524	KJ651784	–
	MSM 0097	MH233930	–	–	–	–
<i>H. occidentale</i>	79034/VE	KJ651485	KJ651645	KJ651738	KJ651789	–
	98005/VE	KJ651489	KJ651649	KJ651742	KJ651793	–
	PFC 5362	KP863584	–	–	KP863650	KP863614
	PFC 5388	KP863585	–	–	KP863651	KP863615
<i>H. orientale</i>	K 97011/7	KJ651490	KF033141	KF006512	KJ651794	–
	K 03293/2	KJ651493	KF033140	KF006510	KJ651797	–
	K 00085/2	KJ651492	KF033139	KF006508	KJ651796	–
<i>H. parviporum</i>	K 04121/3	KJ583212	KF453493	KF453499	KJ651800	–
	08123/VE	KJ651500	KF453495	KF453501	KJ651805	–
	PFC 5262	KC492957	–	–	KP863662	KC571688
	<i>H. tibeticum</i>	Dai 5537*	KJ651507	KF033153	KF006531	KJ651812
Dai 5468		KJ651505	KF033151	KF006527	KJ651810	–
Dai 5534		KJ651506	KF033152	KF006529	KJ651811	–

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold

necrosis, stem browning, and wilted leaves on *Chaenomeles sinensis* (Yun and Oh 2016). In Tunisia, shoot blights caused by *N. quercina* were observed with diffuse cankers with gummosis on buds (Triki et al. 2019).

Hosts— Has a wide range of hosts including *Anigozanthos flavidus*, *Anigozanthus maugleisii*, *Arachis hypogaea*, *Chaenomeles sinensis*, *Gossypium* sp., *Fraxinu pennsylvanica*, *Malus micromalus*, *Microsphaera alphitoides*, *Olea europaea*, *Phellodendrona murense*, *Pistacia vera*, *Prunu*

Fig. 20 Morphology of *Meliola* species **a** *Meliola thailandicum* on *Dimocarpus longan*. **b** *Meliola* sp. on *Citrus reticulata*. **c** *Meliola* sp. on *Citrus maxima*. **d** Colony on the host surface. **e** Hyphopodia on mycelium. **f** Section through ascoma. **g** Peridium. **h** Setae. **i** Young ascus. **j** Mature ascus. **k, l** Ascospores. Scale bars: f=50 μ m, g, i–l=30 μ m, h=10 μ m and e=5 μ m



savium, *Prunus dulcis*, *Spiraea salicifolia*, *Quercus* sp. and *Ziziphus jujube* (Babaahmadi et al. 2018; Chen et al. 2015b, 2017; Chethana et al. 2019; Jianyu et al. 2016; Liu et al. 2018b; Moral et al. 2017, 2018; Soleimani et al. 2018; Triki et al. 2019; Valenzuela-Lopez et al. 2018; Yun and Oh 2016; Zhang et al. 2020).

Morphological based identification and diversity

This genus was introduced by Chen et al. (2015b) based on molecular data to delineate a more natural classification for the *Ascochyta-Didymella-Phoma* species complex (Chen et al. 2015b; Fig. 23). Species produce elongate,

barrel-shaped, olivaceous brown chlamydospores in chains (Chen et al. 2015b). However, there is little morphological variation among species (Valenzuela-Lopez et al. 2018).

Molecular based identification and diversity

Species identification is based on multi-locus sequence phylogeny. Phylogenetic analyses of combined LSU, ITS, *tub2* and *rpb2* sequence data resulted in several new species being added to this genus by Chen et al. (2015b), Abdel-Wahab et al. (2017), Valenzuela-Lopez et al. (2018), Chethana et al. (2019), Marin-Felix et al. (2019) and Zhang et al.

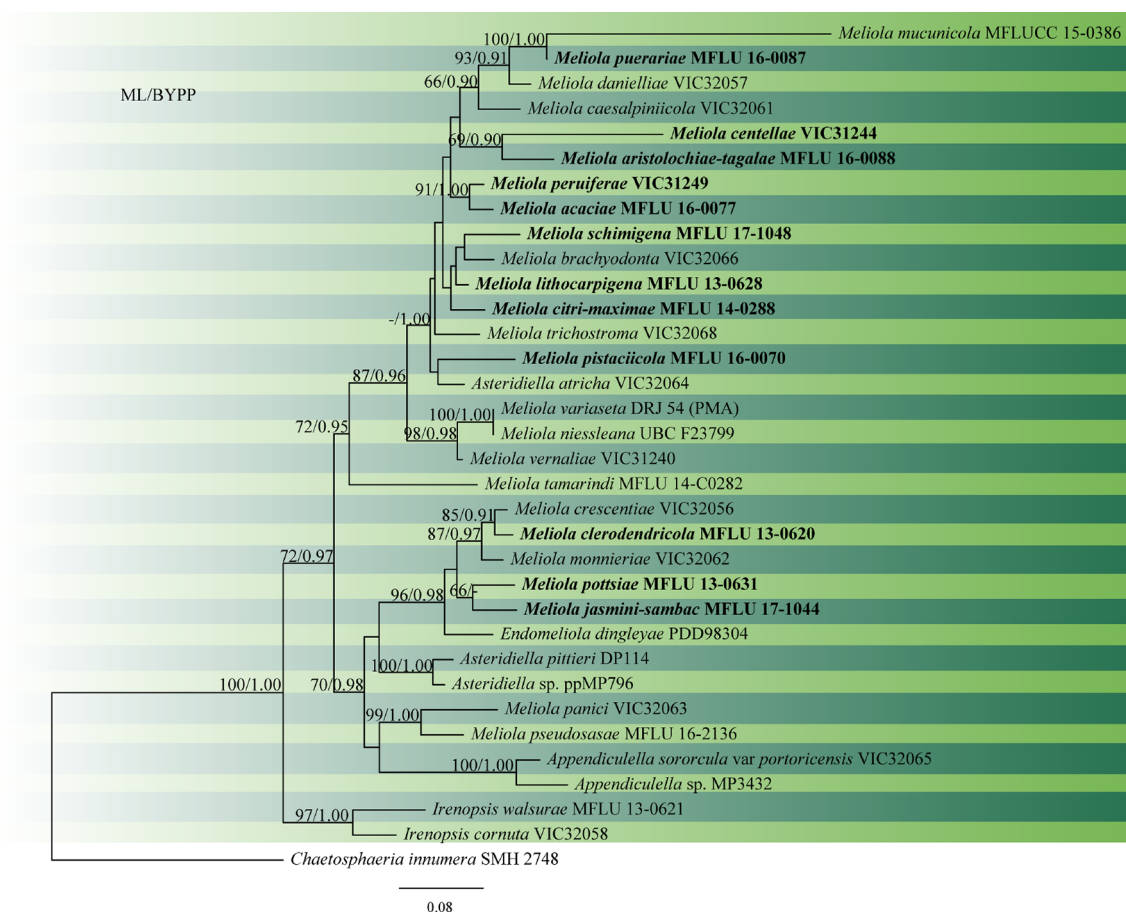


Fig. 21 Phylogram generated from RAxML analysis based on combined ITS and LSU sequence data of *Meliola* species. Related sequences were obtained from GenBank. Thirty-five strains are included in the analyses, which comprised 1655 characters includ-

ing gaps. The tree was rooted with *Chaetosphaeria innumera* (SMH 2748). Tree topology of the ML analysis was similar to the Bayesian analysis. ML bootstrap values $\geq 50\%$ and BYPP ≥ 0.90 are shown respectively near the nodes

(2020). Here we provide an updated phylogenetic tree for this genus (Fig. 24).

Recommended genetic markers (genus level)—LSU, ITS
Recommended genetic markers (species level)—*tub2*, *rpb2*

Since the colony morphology and other morphological features in *Didymellaceae* often overlap, initial species identification is recommended with LSU and ITS sequence data using all type species in *Didymellaceae*. Once the genus is identified as *Nothophoma*, the phylogenetic analysis could be done with LSU, ITS, *tub2*, and *rpb2* sequence data.

Accepted number of species—There are 12 species in Index Fungorum (2020) with DNA sequence data (Table 15).

References—Chen et al. (2015b), Abdel-Wahab et al. (2017), Valenzuela-Lopez et al. (2018), Chethana et al. (2019), Marin-Felix et al. (2019), Zhang et al. (2020) (morphology and phylogeny)

90. *Phellinus* Quél., Enchir. fung. (Paris): 172 (1886)

Background

Phellinus was introduced by Quélet (1886) with *P. igniarius* (\equiv *Boletus igniarius*) as its type species (Murrill 1903) and is placed in Hymenochaetaceae (He et al. 2019). Traditionally, most poroid Hymenochaetaceae were placed in *Phellinus*, which has been characterized by a dimittic hyphal system and perennial habit of the basidiomata (Gilbertson 1979; Larsen and Cobb-Pouille 1990; Ryvarden and Gilbertson 1994; Núñez and Ryvarden 2000). However, phylogenetic studies revealed that the morphologically defined *Phellinus sensu lato* had polyphyletic origins within the Hymenochaetoid clade, and most species previously classified as *Phellinus* are now members of various segregate genera (e.g. Wagner and Fischer 2001, 2002; Jeong et al. 2005; Dai 2010; Rajchenberg et al. 2015; Drechsler-Santos et al. 2016). According to the most narrowly defined generic concept, *Phellinus sensu stricto* is limited to the *P. igniarius* species complex (Fischer and Binder 2004), which includes species causing a delignifying trunk rot mostly on various

Table 13 DNA barcodes available for *Meliola*

Species	Culture/specimen number	LSU	ITS
		MN747479	MN747479
<i>Meliola aristolochiae-tagalae</i>	MFLU 16-0088*	MN747473	–
<i>M. brachyodonta</i>	VIC32066	KC618644	–
<i>M. caesalpiniicola</i>	VIC32061	KC618641	–
<i>M. centellae</i>	VIC31244*	NG042650	NR137799
<i>M. citri-maximae</i>	MFLU 14-0288*	KX458474	–
<i>M. clerodendricola</i>	MFLU 13-0620*	KT021647	–
<i>M. crescentiae</i>	VIC32056	KC618649	–
<i>M. danielliae</i>	VIC32057	KC618648	–
<i>M. jasmini-sambac</i>	MFLU 17-1044*	MN747482	MN747482
<i>M. lithocarpigena</i>	MFLU 13-0628*	MN747474	MN747474
<i>M. monnieriae</i>	VIC32062	KC618647	–
<i>M. mucunicola</i>	MFLU 15-0386	KT157533	KT157534
<i>M. niessleana</i>	UBC F23799	KC833049	–
<i>M. panici</i>	VIC32063	KC618651	–
<i>M. peruiferae</i>	VIC 31249*	NG 060294	–
<i>M. pistaciicola</i>	MFLU 16-0070*	MN747478	MN747478
<i>M. pottsiae</i>	MFLU 13-0631*	MN747475	MN747475
<i>M. puerariae</i>	MFLU 16-0087*	MN747472	–
<i>M. pseudosasae</i>	MFLU 16-2136	KX845434	–
<i>M. schimigena</i>	MFLU 17-1048*	MN747484	MN747484
<i>M. tamarindi</i>	MFLU 14-C0282	KP744489	–
<i>M. trichostroma</i>	VIC32068	KC618643	–
<i>M. variaseta</i>	DRJ 54 (PMA)	EF094840	–
<i>M. vernaliae</i>	VIC 31240	JX096808	–

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*)

deciduous trees in temperate areas (Brazee 2015; Zhou et al. 2016). Based on a wider generic concept, several morphologically similar species described from East Asia, Africa or America are considered as part of *Phellinus sensu stricto* (Decock et al. 2006; Yombiyeni et al. 2011; Cui and Decock 2013; Bian et al. 2016; Campos-Santana et al. 2016; Vlasák and Vlasák 2017; Salvador-Montoya et al. 2018; Zhu et al. 2018). In this study, we follow the broader concept of classification of *Phellinus sensu stricto*, pending further studies.

Classification—Agaricomycotina, Basidiomycota, Agaricomycetes, Incertae sedis, Hymenochaetales, Hymenochaetaceae

Type species—*Phellinus igniarius* (L.) Quél., Enchir. fung. (Paris): 177 (1886)

Distribution—If the wider generic concept of *Phellinus* were accepted it would be a globally distributed genus, with certain species found in East Asia, Europe, North America (Dai 2010; Cui and Decock 2013; Brazee 2015; Zhou et al. 2016; Vlasák and Vlasák 2017; Zhu et al. 2018), Central- and South America (Decock et al. 2006; Campos-Santana et al.

Table 14 DNA barcodes available for *Neoerysiphe*

Species	Strain no	ITS	LSU
<i>Neoerysiphe aloysiae</i>	BCRU 04878	AB329683	–
<i>N. baccharidis</i>	BCRU 01609	AB329685	AB329684
<i>N. cumminsiana</i>	VPRI 20387	GU356539	–
<i>N. galeopsidis</i>	MUMH 4680	AB498949	AB022369
<i>N. galii</i>	MUMH 4682	AB498951	AB103365
<i>N. geranii</i>	HMNWAFU-CF2013083	KR048092	KR048161
<i>N. hiratae</i>	MUMH 3442	AB498962	–
<i>N. joerstadii</i>	MUMH 4668	AB498976	–
<i>N. kerribeeensis</i>	DAR 33493	GU356546	–
<i>N. maquii</i>	MUMH 2460	AB329686	–
<i>N. nevoi</i>	MUMH 4671	AB498975	–

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains and voucher strains are in bold

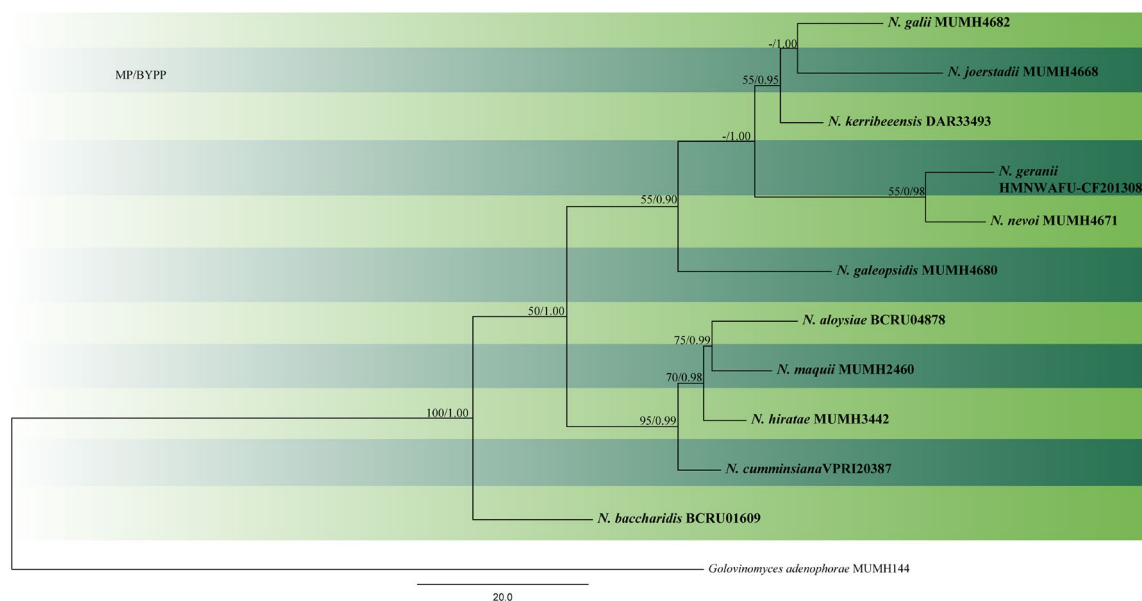


Fig. 22 Phylogram generated from MP analysis based on combined sequences of ITS and LSU sequences of all species of *Neoverysiphia* with molecular data. Related sequences were obtained from GenBank. 12 taxa are included in the analyses, which comprise 2023 characters including gaps, of which 1790 characters are constant, 167 characters are parsimony-uninformative and 66 characters parsimony-informative. The parsimony analysis of the data matrix resulted in the

maximum of four equally most parsimonious trees with a length of 316 steps (CI = 0.848, RI=0.678, RC = 0.575, HI = 0.152) in the first tree. Single gene analyses were carried out and compared with each species, to compare the topology of the tree and clade stability. The tree was rooted with *Golovinomyces adenophorae* (MUMH144). MP bootstrap support value $\geq 50\%$ and BYPP ≥ 0.9 are shown respectively near the nodes. Ex-type strains are in bold

2016; Salvador-Montoya et al. 2018) and Africa (Yombiyeni et al. 2011; Cloete et al. 2016). However, the members of the *P. igniarius* species complex are known only from the Northern Hemisphere (Brazeo 2015; Zhou et al. 2016).

Disease symptoms—Members of *Phellinus* produce white rot, decaying polysaccharides and delignifying the substrata (Niemelä 1974, 1977; Ryvarden and Gilbertson 1994; Wagner and Fischer 2002; Decock et al. 2006; Cui and Decock 2013; Brazeo 2015; Cloete et al. 2016, de Campos-Santana et al. 2016). The rot could be localized in the trunk as a column of decay (Brazeo 2015), in both fallen and in standing dead trunks (Niemelä 1977; Campos-Santana et al. 2016). Branches of living trees (Niemelä 1974; Decock et al. 2006), dead, fallen, corticated branches and logs (Niemelä 1972) and dead stumps (Niemelä 1972; Decock et al. 2006; Campos-Santana et al. 2016) are colonized and decayed. The fungus penetrates the heartwood, causing heartrot (Niemelä 1974; Larsson et al. 2006), sometimes extending into the sapwood (Niemelä 1977; Larsson et al. 2006). Decay characteristics (i.e. colour, fragility and fragmentation) vary between species (Niemelä 1972, 1974, 1977; Yombiyeni et al. 2011; Luna et al. 2012; Campos-Santana et al. 2016). Pathogenic species, such as *P. tremulae* or *P. resupinatus* are usually associated with other basidiomycete species, pathogenic bacteria and basal fungi (Kallio 1972; Cloete et al.

2016). *Phellinus tremulae* is a common and harmful pathogen of aspen (*Populus* species), penetrating the heartwood along dead branches (Niemelä 1974), but is also capable of spreading through the sapwood (Larsson et al. 2006), forming conks around the decayed tissues (Jones 1998; Fig. 25). *Phellinus resupinatus* is also a factor of Esca disease, causing white rot and decline of the cordons in vineyards (Cloete et al. 2016), besides other symptoms caused by this disease (Jayawardena et al. 2019a).

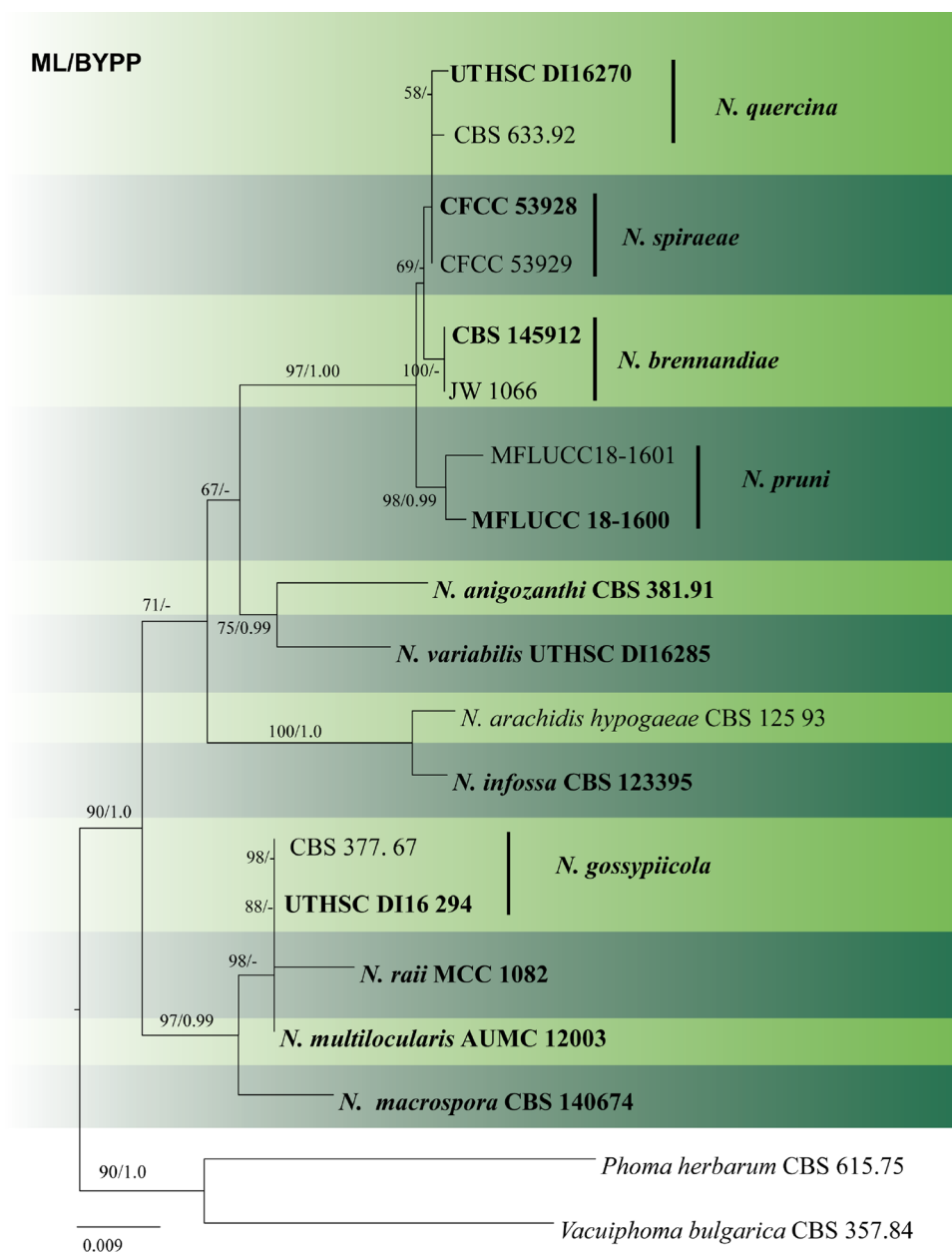
Hosts—Most species in the *P. igniarius* species complex are specialized to a single or few angiosperm genera (Fischer and Binder 1995; Zhou et al. 2016), and only *P. piceicola* has been reported from gymnosperms (Cui and Dai 2012). Species of the *P. igniarius* species complex have been recorded from various host genera, such as *Acer*, *Alnus*, *Arctostaphylos*, *Betula*, *Carpinus*, *Fagus*, *Fraxinus*, *Laburnum*, *Picea*, *Populus*, *Prunus*, *Salix*, *Sorbus* and *Tilia* (Tomšovský et al. 2010; Brazeo 2015; Zhou et al. 2016). The members of other *Phellinus sensu stricto* lineages are known from several additional angiosperm genera, such as *Artemisia*, *Astronium*, *Caesalpinia*, *Carya*, *Castanopsis*, *Dimorphandra*, *Miquartia*, *Morus*, *Sacoglottis*, *Schinopsis*, *Quercus* and *Vitis* (Lombard and Larsen 1985; Decock et al. 2006; Yombiyeni et al. 2011; Cui and Decock 2013;



Fig. 23 *Nothophoma quercina* on *Malus micromalus* **a** *Malus micromalus* (Crab-Apple tree). **b** Canker on the trunk. **c, d** appearance of conidiomata on trunk. **e** longitudinal section through conidiomata. **f**

cross-section of conidiomata **g, h** conidiogenous cells. **i, j** conidia. **k** upper view on PDA. **l** reverse view on PDA. Scale bars: **d**=1000 μm **e, f** = 50 μm **g–j** 10 μm

Fig. 24 Phylogram generated from maximum likelihood analysis based on combined LSU, ITS, *tub2* and *rpb2* sequence data of *Nothophoma* species. Related sequences were obtained from GenBank. Seventeen strains are included in the combined sequence analyses. *Phoma herbarum* (CBS 615.75) and *Vacuiphoma bulgarica* (CBS 357.84) was used as the outgroup taxa. The best scoring RAXML tree with a final likelihood value of -5537.646741 is presented. The matrix had 284 distinct alignment patterns, with 12.23% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.238395, C = 0.241637, G = 0.276596, T = 0.243371; substitution rates AC = 0.975188, AG = 4.004775, AT = 1.500008, CG = 0.519461, CT = 10.843965, GT = 1.000000; gamma distribution shape parameter $\alpha = 1.764918$. ML bootstrap support value $\geq 50\%$ and BYPP ≥ 0.95 are shown respectively near the nodes. Ex-type strains are in bold



de Campos-Santana et al. 2016; Vlasák and Vlasák 2017; Salvador-Montoya et al. 2018).

Morphological based identification and diversity

Phellinus in a wider sense is morphologically heterogeneous. The main features of the *P. igniarius* species complex are the crusted pileal surface (except resupinate species), the hymenial setae arising from the subhymenium (except specimens of “*P. pseudoigniarius*”, see Dai and Yang 2008; Zhou et al. 2016), and the colourless, inamyloid, indextrinoid and weakly cyanophilous basidiospores (Wagner and Fischer 2001; Dai 2010; Zhou et al. 2016). In many cases, the species separation in the complex is difficult when solely based on morphological characters (Sell 2008). Host preference is

also widely used for delimiting species (Tomšovský et al. 2010).

Similar to members of the *P. igniarius* species complex, other *Phellinus* species also have perennial basidiomata, but differ in having distinctive macroscopical features (e.g. size and shape of pores, rimose surface, cracked basidiocarps, absence of pileus crust, see Dai et al. 2008; Bian et al. 2016; Cloete et al. 2016; Vlasák and Vlasák 2017) or microscopic characteristics (e.g. hyphal structure, the shape of setae, basidiospore reaction in chemical solutions). For example, *P. bicuspidatus* is unique in having a monomitic hyphal system with short bicuspid setae (Lombard and Larsen 1985; Cloete et al. 2016). Members of the *P. ellipsoideus* group are

Table 15 DNA barcodes available for *Nothophoma*

Species	Isolate	LSU	ITS	<i>tub2</i>	RPB2
<i>Nothophoma anigozanthi</i>	CBS 381.91*	GU238039	GU237852	GU237580	KT389655
<i>N. arachidis-hypogaeae</i>	CBS 125.93	GU238043	GU237771	GU237583	KT389656
<i>N. brennandiae</i>	CBS 145912*	MN823430	MN823579	MN824753	MN824604
	JW 1066	MN823429	MN823578	MN824752	MN824603
<i>N. gossypicola</i>	CBS 377.67	GU238079	GU237845	GU237611	KT389658
	UTHSC:DI16-294	LN907437	LT592943	LT593012	LT593082
<i>N. infossa</i>	CBS 123395 *	GU238089	FJ427025	FJ427135	KT389659
<i>N. macrospora</i>	CBS 140674 *	LN880537	LN880536	LN880539	LT593073
<i>N. multilocularis</i>	AUMC-12003*	KY996744	–	–	–
<i>N. pruni</i> [#]	MFLUCC 18–1600 *	MH827028	MH827007	MH853671	MH853664
	MFLUCC18–1601	MH827026	MH827005	MH853669	MH853662
<i>N. quercina</i> [#]	CBS 633.92	EU754127	GU237900	GU237609	KT389657
	UTHSC:DI16-270	LN907413	LT592929	LT592998	LT593067
<i>N. raii</i>	MCC 1082 *	–	MF664467	MF664468	–
<i>N. spiraeae</i>	CFCC 53928*	MN737828	MN737833	MN879295	MN879292
	CFCC 53929	MN737829	MN737834	MN879296	MN879293
<i>N. variabilis</i>	UTHSC: DI16-285*	LN907428	LT592939	LT593008	LT593078

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold. Species confirmed with pathogenicity studies are marked with [#]

well-characterised by their weakly dextrinoid basidiospores and hooked hymenial setae (Zhu et al. 2018).

There are several “*Phellinus*” species which have been described solely on morphological features. The status of these species should be critically re-evaluated based on molecular evidence. Amongst these, certain species (e.g. *P. deuteroprunicola*, *P. eugeniae*, *P. formosanus*, *P. livescens*, *P. prunicola*, *P. setulosus*, *P. tenuiculus*, *P. wahlbergii*) may belong to *Phellinus sensu stricto* (Gilbertson 1979; Chang 1995; Chang and Chou 1999, 2000; Robledo et al. 2003; Wang et al. 2011; Rajchenberg et al. 2015; Campos-Santana et al. 2016), but further studies are required to confirm their placements.

Molecular based identification and diversity

In early molecular studies, the restriction fragment length polymorphism (RFLP) data of enzymatically amplified rDNA was used by Fischer (1995) to study the taxonomy of *P. igniarius* and its closest relatives in Europe. Later, single nuclear genes (ITS, Fischer and Binder 2004), or combined datasets (ITS-*tef1*, Tomšovský et al. 2010; Zhou et al. 2016) were used to investigate the species boundaries and phylogenetic relationships within the *P. igniarius* species complex. Phylogenetic analyses by Brazeo (2015) used ITS, LSU, *tef1* and *rpb2*, with isolates representing 13 species-level lineages in the complex. Zhou et al. (2016) distinguished 15 species, five of which are described as new from China and the USA. Based on our multigene analysis (Fig. 26), 16

species can be found in the *P. igniarius* species complex, distributed throughout the Northern Hemisphere. Amongst these, ten species are known from eastern Asia, eight from Europe and seven from North America.

Phellinus caribaeo-quercicola was the first species described from the “*P. ellipsoideus* group” based on molecular evidence (Decock et al. 2006). The nLSU-based phylogenetic analysis of Decock et al. (2006), have shown that *P. caribaeo-quercicola* grouped close to the *P. igniarius* species complex and some other *Phellinus* species (*viz.* *P. bicuspidatus*, *P. chaquensis* and *P. spiculosus*). Later molecular taxonomic studies used combined datasets of various nuclear markers. The combined analyses of nITS, nLSU, *tef1* and *rpb2* have confirmed the phylogenetic position of *P. caribaeo-quercicola* and five morphologically similar species have been accepted in *Phellinus sensu stricto* (Yombiyeni et al. 2011; Cui and Decock 2013; Campos-Santana et al. 2016; Zhu et al. 2018). Currently, this later group consists of six species and mostly has tropical or subtropical distributions (Zhu et al. 2018).

Recommended genetic marker (genus level)—LSU

Recommended genetic markers (species level)—ITS, *tef1*, *rpb2*

Accepted number of species—There are 479 epithets listed in Index Fungorum (2020). However, most of the species belong to other poroid Hymenochaetaceae genera, such as *Fomitiporia*, *Fomitiporella*, *Fulvifomes*, *Fuscoporia*,

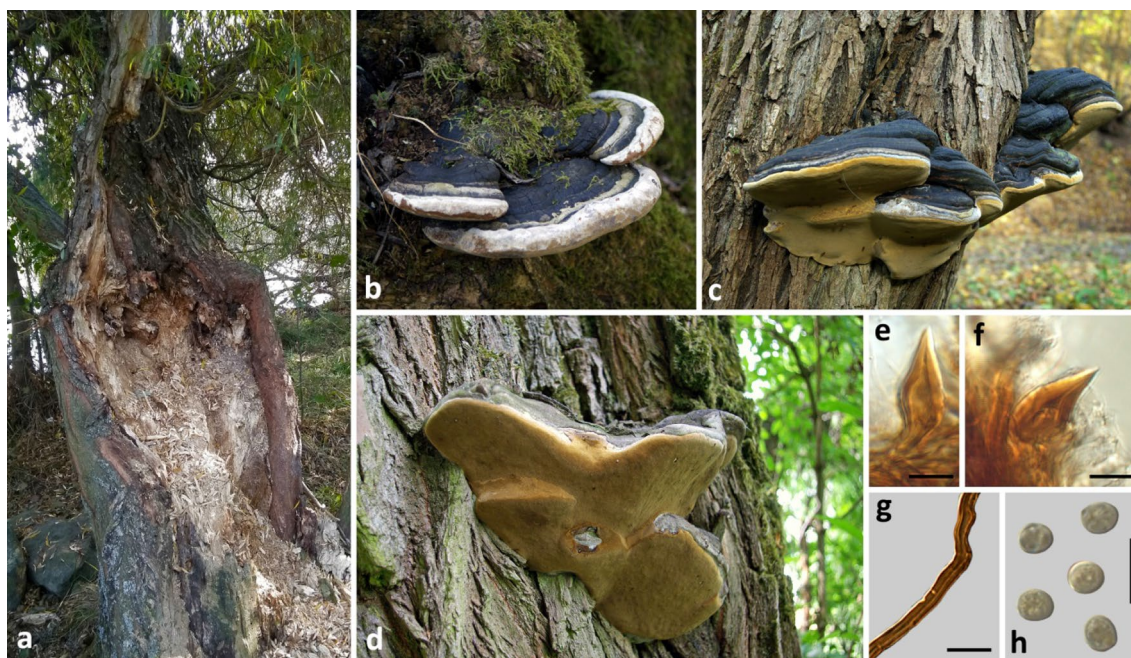


Fig. 25 *Phellinus igniarius*. **a** causing white-rot decay on willow **b–d** basidiomes on living willow **e, f** hymenial setae **g** tramal skeletal hyphae **h** basidiospores, Scale bars: **e–h** = 10 μ m

Nothophellinus, *Phellinidium*, *Phellinopsis*, *Phellinotus*, *Phellopilus*, *Phylloporia*, *Porodaedalea*, *Sanguangporus* and *Tropicoporus* (Wagner and Fischer 2001, 2002; Niemälä et al. 2001; Dai 2010; Drechsler-Santos et al. 2016; Rajchenberg et al. 2015; Zhou et al. 2016). Based on molecular data, **30 species** are accepted in *Phellinus sensu stricto*, from among 16 species in the *P. igniarius* species complex (Table 16; Fig. 26).

References—Tomšovský et al. (2010) (phylogeny, *P. igniarius* species complex, Europe), Brazeo (2015) (phylogeny, *P. igniarius* species complex, North America), Zhou et al. (2016) (phylogeny, *P. igniarius* species complex), Zhu et al. (2018) (phylogeny, *P. ellipsoideus* group)

91. *Pseudoseptoria* Speg., Anal. Mus. nac. B. Aires, Ser. 3 13: 388 (1910) [1911]

Background

Spegazzini (1910) introduced *Pseudoseptoria* as an asexual genus typified with *Pseudoseptoria donacicola*. Wijayawardene et al. (2012) placed the genus under Ascomycota, genera *incertae sedis*. Quaedvlieg et al. (2013) placed the genus in Dothioraceae and this was accepted by Thambugala et al. (2014). With LSU sequence data, Crous et al. (2017) placed *Pseudoseptoria* to Saccoteciaceae. Wijayawardene et al. (2017a, b, 2018, 2020) accepted this placement. Species of *Pseudoseptoria* are recorded as pathogens on Poaceae (Quaedvlieg et al. 2013), impairing the photosynthetic process resulting in yield loss.

Classification—Ascomycota, Pezizomycotina, Dothideomycetes, Dothideomycetidae, Dothideales, Saccoteciaceae
Type species—*Pseudoseptoria donacicola* Speg.

Distribution—Australia, Canada, India, Italy, New Zealand, Poland, Russia, UK and USA (Dennis 1986; Ginns 1986; French 1989; Pennycook 1989; Merezko 1991; Cunnington 2003; Mulyenko et al. 2008; Kamal 2010; Farr and Rossman 2020).

Disease symptoms—halo spot, leaf blotch and stem speckle

Halo spot: Elliptical, tan to brownish-grey spots (<10mm long) with a dark border surrounded by a prominent yellow halo that can be observed on the leaf blade, sometimes covering the entire leaf blade. In older lesions, small pycnidia may be visible (Slopek and Labun 1992; Carmona et al. 1996; Murray et al. 2013).

Leaf blotch: Brown flecks and frog-eye spots on leaf blades can be observed in early spring, which enlarges to straw-coloured blotches scattered with minute pycnidia. These spots may drop out, leaving holes (Horst 2013).

Stem speckle: The disease occurs in the leaves, sheaths, culms, and head spikes. The lesions are rectangular, ash white, (1–2 mm long) with a brown, thin border. The lesion is delimited by leaf veins and becomes distinct with a clear boundary. The conidia formed on the lesions disperse by wind and rain.

Pathogen biology, disease cycle and epidemiology

The pathogen is dispersed through spores in rain splash. Infection requires an extended period of wetness. Spore

germination and infection occur optimally at temperatures between 15 and 25 °C. Spores produced in overwintering crop debris serve as sources of primary inocula (Sinclair and Dhingra 1995). Further studies are needed regarding the disease mechanisms and disease cycle.

Hosts—members of Poaceae are susceptible: *Alopecurus pratensis*, *Arrhenatheru melatius*, *Arundo donax*, *Bromus* species, *Dactylis glomerata*, *Danthonia spicata*, *Elymus alaskanus*, *Festuca carubra*, *Hordeum vulgare*, *Panicum virgatum*, *Phleum* species, *Phragmites australis* and *Poa* species (Ginns 1986; Pennycook 1989; Shivas 1989; Greuter et al. 1991; Merezhko 1991; Roane and Roane 1996; Gravert and Munkvold 2002; Mullenko et al. 2008; Farr and Rossman 2020)

Morphological based identification and diversity

The genus is characterized by immersed, branched, septate, pale brown mycelium, pycnidial, solitary or linearly aggregated, immersed, brown, globose, unilocular, thin-walled conidiomata of walls of pale brown cells of *textura angularis* with distinct, central, circular ostioles. Conidigenous cells are discrete, determinate or indeterminate, hyaline, smooth, ampulliform with a prominent cylindrical papilla and falcate. Conidia are fusoid, hyaline, aseptate, guttulate, smooth and thin-walled, and acutely rounded at each end (Sutton 1980; Quaedvlieg et al. 2013).

Molecular based identification and diversity

Quaedvlieg et al. (2013) revised the *Septoria* and septoria-like genera based on morphology and multi loci analyses and introduced two new species. Phylogenetic analysis conducted by Crous et al. (2017) was based only on LSU sequence data. In our analysis, we used LSU, ITS and *rpb2* and obtained the same topology (Fig. 27).

Recommended genetic marker (genus level)—LSU

Recommended genetic markers (species level)—LSU, ITS and *rpb2*

Accepted number of species—There are eight epithets listed in Index Fungorum (2020). However, only three species have DNA sequence data (*P. collariana*, *P. donacis* and *P. obscura*) (Table 17).

References—Sutton (1980) (morphology); Quaedvlieg et al. (2013), Crous et al. (2017) (morphology and phylogeny)

92. *Stemphylium* Wallr., Flora Cryptogamica Germaniae 2: 300 (1833)

Background

Stemphylium mainly comprises saprobes or weak plant pathogens (Woudenberg et al. 2017). However, some species are primary pathogens causing leaf blight on various crops, resulting in yield and economic losses (Hanse et al. 2015; Brahmanage et al. 2018). The asexual morph is a

dematiaceous hyphomycete while the sexual morph was previously defined as *Pleospora sensu stricto* (Inderbitzin et al. 2009; Woudenberg et al. 2017). Rossman et al. (2015) recommended the use of *Stemphylium* over *Pleospora* which has been followed by various authors (Hongsanan et al. 2017, 2020; Wijayawardene et al. 2018, 2020). *Stemphylium* is one of the most important moulds human allergens in the USA (Gutiérrez-Rodríguez et al. 2011). Brahmanage et al. (2018) discussed the pathogenicity, disease severity, distribution and molecular phylogenetic affinities of pathogenic isolates of *Stemphylium*.

Stemphylium leaf blight caused by *S. versicarium* was identified as an emerging disease in New York, USA. Sharma et al. (2020b) provided two genome resources for two *S. versicarium* isolates from leaf blight of onion. Genomic data allows for an understanding of the population biology, fungicide resistance, as well as development of control strategies against the disease. Pathogenesis related 511 secreted proteins were predicted from *S. lycopersici* by Zeng et al. (2018) which helps in understanding the roles of proteins in host penetration and tissue necrosis. *Stemphylium loti* secretes Tenuazonic acid, inhibiting the plant plasma membrane H⁺-ATPase, which results in membrane potential depolarization and eventually necrosis (Bjørk et al. 2019). Su et al. (2019) fine-mapped the tomato grey spot resistance gene *Sm*, in a 185kb region through a map-based cloning strategy. Leach et al. (2020) identified a relationship between thrips (*Thrips tabaci*) and *S. vesicarium* in the development of *Stemphylium* leaf blight in onion.

Classification—Ascomycota, Pezizomycotina, Dothideomycetes, Pleosporomycetidae, Pleosporales, Pleosporaceae
Type species—*Stemphylium botryosum* Wallr.

Distribution—worldwide

Disease symptoms—Gray spot, *Stemphylium* leaf blight (Leaf spot, defoliation, curling and bending of the leaf margins and stems)

Initial symptoms of the leaves are small, irregular, brown spots. Generally, the spots gradually lighten and eventually become greyish as they become necrotic and dry. When severe, yellow spots can be seen throughout all leaves of the plant and the heavily infected leaves die (Basallote-Ureba et al. 1999, Crous et al. 2016; Brahmanage et al. 2018).

Hosts—Species are pathogenic on a wide range of hosts including Amaryllidaceae, Asparagaceae, Fabaceae, Malvaceae, Poaceae, Rosaceae and Solanaceae

Pathogen biology, disease cycle and epidemiology

Species can survive as saprobes on crop residues, soil, plant debris and on many alternative hosts and ascospores become the primary inocula in the following season. Once the disease is established during favourable conditions, conidial production in primary lesions may occur, dispersing

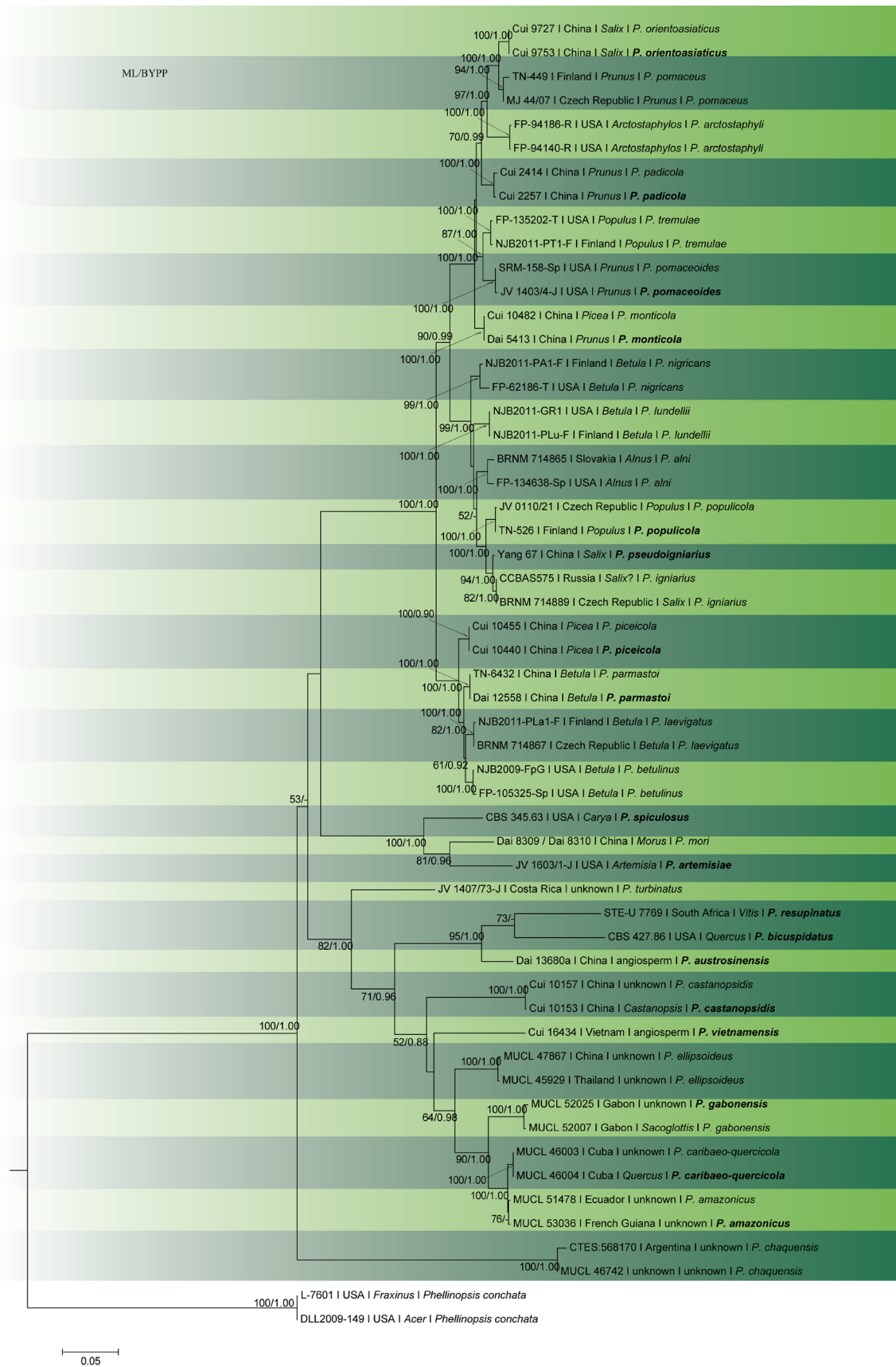


Fig. 26 Phylogram generated from RAxML analysis based on combined ITS, LSU, *Tef1- α* and *rpb2* sequence data of *Phellinus* species. Related sequences were obtained from GenBank. Fifty-five strains are included in the analyses, which comprised 3170 characters including gaps. The tree was rooted with *Phellinopsis conchata* (DLL2009-149 and L-7601). Tree topology of the ML analysis was similar to the Bayesian analysis. ML bootstrap values >50% and BYPP >0.80% are shown respectively near the nodes

spores to healthy plants by wind and rain splashing. Environmental factors such as temperature and moisture are key factors in disease development. Seedlings of plants can transmit the diseases if they become infected in the nursery (Basallote-Ureba et al. 1998, 1999; Boshuizen et al. 2004; Zheng et al. 2010; Blancard 2012). However, to date, diseases and epidemiology such as factors affecting the disease development, interactions with different hosts and genetics of host resistance are poorly studied (Das et al. 2019).

Morphological based identification and diversity

Species can be distinguished from other hyphomycetes in Pleosporaceae forming phaeodictyospores, based on percurrent proliferation of its conidiophores and apically swollen conidiogenous cells (Köhl et al. 2009). Simmons (1967) established criteria for morphological identification of various *Stemphylium* species and introduced *Pleospora herbarum* as the sexual morph of the type species *Stemphylium botryosum*. However, Simmons (1985) subsequently reclassified and reported *Pleospora tarda* as the sexual morph of *Stemphylium botryosum* and *Pleospora herbarum* as the sexual morph of *Stemphylium herbarum* (Moslemi et al. 2017). Morphological features, such as size and time of pseudothecial maturation, conidiophores and conidia and ascospore shape and size can be considered as important characteristics in species identification (Câmara et al. 2002; Fig. 28).

Köhl et al. (2009) and Woudenberg et al. (2017) pointed out that the lack of (ex-) type material of species and morphology-based species identifications without molecular evidence make it difficult in determining correct species nomenclature. Therefore, relying on morphological characters alone in identifying species is not recommended.

Molecular based identification and diversity

ITS (rDNA) and glyceraldehyde-3-phosphate dehydrogenase (*gapdh*) sequences were used by Câmara et al. (2002) to confirm the monophyly of *Stemphylium*. In the extensive study of 110 *Stemphylium* strains from various hosts and DNA sequence data of ITS, *gapdh* and *tef1* loci and the intergenic spacer between *vmaA* and *vpsA*, Inderbitzin et al. (2009) identified 23 representatives derived from type strains, while 40 strains remained unnamed. Woudenberg

et al. (2017) revised the genus and accepted 28 species, synonymizing 22 names and proposing two new combinations based on combined analyses of the ITS, *gapdh* and *cmdA* gene regions. Marin-Felix et al. (2019) introduced three new species (*S. rombunicum*, *S. truncatulae* and *S. waikerianum*), while Brahmanage et al. (2018) introduced *S. dianthi* based on multi loci phylogeny. In this study, we reconstruct the phylogeny based on combined ITS, *gapdh* and *cmdA* sequence data (Fig. 29).

Recommended genetic marker (genus level)—ITS

Recommended genetic markers (species level)—*cmdA*, *gapdh*

Accepted number of species—There are 207 epithets listed in Index Fungorum, however only 32 species have DNA sequence data (Table 18).

References—Simmons (1967), Köhl et al. (2009) (morphology); Câmara et al. (2002), Inderbitzin et al. (2009), Moslemi et al. (2017), Woudenberg et al. (2017), Brahmanage et al. (2019), Marin-Felix et al. (2019) (morphology and phylogeny)

93. *Thyrostroma* Höhn., Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Math.-naturw. Klasse Abt. I 120: 472 (1911)

Background

Thyrostroma belongs to Dothidothiaceae of Pleosporales in Dothideomycetes, Ascomycota (Hongnan et al. 2020). *Thyrostroma* was established by Höhnel (Höhnel 1911) and is typified by *T. compactum*. *Thyrostroma* had been treated as a synonym of *Coryneum*, *Stegonsporium*, *Stigmina*, and *Thyroccoccum*, *Thyrostromella* and *Wilsonomyces* (Höhnel Höhnel 1911; Morgan-Jones 1971; Sutton and Pascoe 1989; Sutton 1997; Index Fungorum 2020). *Thyrostroma* has been reported as the asexual morph of *Dothidothia* based on the production of a hyphomycete state in culture (Ramaley 2005), however, there is no phylogenetic evidence to support this link. With new morphological information and phylogenetic analyses, *Thyrostroma* and *Dothidothia* species were retained in separate genera (Crous et al. 2016; Marin-Felix et al. 2017; Senwana et al. 2019). *Thyrostroma* species are pathogens, saprobes or endophytes associated with canker, dieback and leaf spots in terrestrial habitats (Yuan and Old 1990; Marin-Felix et al. 2017; Senwana et al. 2019). Species of *Thyrostroma* have been recorded from various plants, however, host-specificity and pathogenic capacity of *Thyrostroma* has not yet been clarified.

Classification—Ascomycota, Pezizomycota, Dothideomycetes, Pleosporomycetidae, Pleosporales, Dothidothiaceae

Table 16 DNA barcodes available for *Phellinus*

Species	Strain	ITS	LSU	<i>tefl</i>	<i>rpb2</i>
<i>Phellinus alni</i>	FP-134638-Sp	KU139167	KU139213	KU139330	KU139280
<i>P. alni</i>	BRNM 714865	GQ383730	–	GQ383840	–
<i>P. amazonicus</i>	MUCL 53036*	KU499940	KU376305	KU936772	–
<i>P. amazonicus</i>	MUCL 51478	KU499929	KU376294	KU936769	–
<i>P. arctostaphyli</i>	FP-94186-R	KU139145	KU139252	KU139350	KU139266
<i>P. arctostaphyli</i>	FP-94140-R	KU139143	KU139250	KU139348	KU139264
<i>P. artemisiae</i>	JV 1603/1-J*	KY230518	KY230518	–	–
<i>P. austrosinensis</i>	Dai 13680a*	–	KP027474	–	–
<i>P. betulinus</i>	NJB2009-FpG	KU139153	KU139248	KU139368	KU139311
<i>P. betulinus</i>	FP-105325-Sp	KU139154	KU139239	KU139369	KU139312
<i>P. bicuspidatus</i>	CBS 427.86*	MH861982	MH873674	–	–
<i>P. caribaeo-quercicola</i>	MUCL 46004*	HM635698	DQ127280	HM635726	–
<i>P. caribaeo-quercicola</i>	MUCL 46003	HM635697	DQ127279	HM635725	–
<i>P. castanopsidis</i>	CUI 10153*	JQ837944	JQ837956	KU936783	–
<i>P. castanopsidis</i>	CUI 10157	JQ837945	JQ837957	KU936784	–
<i>P. chaquensis</i>	MUCL 46742	–	DQ122396	–	–
<i>P. chaquensis</i>	CTES568170	MG242440	MG242445	–	–
<i>P. ellipsoideus</i>	MUCL 47867	KU954545	KU954540	KU936786	–
<i>P. ellipsoideus</i>	MUCL 45929	KU954544	DQ127283	KU936785	–
<i>P. gabonensis</i>	MUCL 52025*	HM635708	HM635690	HM635731	–
<i>P. gabonensis</i>	MUCL 52007	HM635718	HM635685	HM635729	–
<i>P. igniarius</i>	BRNM 714889	GQ383709	–	GQ383791	–
<i>P. igniarius</i> ^a	*Yang 67	JQ828880	–	KR013111	–
<i>P. igniarius</i>	CCBAS575	LN714586	–	–	LN714693
<i>P. laevigatus</i>	NJB2011-PLa1-F	KU139148	KU139241	KU139372	KU139305
<i>P. laevigatus</i>	BRNM 714867	GQ383778	–	GQ383856	–
<i>P. lundellii</i>	NJB2011-PLu-F	KU139185	KU139234	KU139337	KU139300
<i>P. lundellii</i>	NJB2011-GR1	KU139182	KU139232	KU139336	KU139301
<i>P. monticola</i>	Dai 5413*	JQ828889	–	KR013087	–
<i>P. monticola</i>	Cui 10482	JQ828888	–	KR013086	–
<i>P. mori</i>	Dai 8309/Dai 8310	FJ627259	HQ328535	–	–
<i>P. nigricans</i>	NJB2011-PA1-F	KU139169	KU139222	KU139340	KU139297
<i>P. nigricans</i>	FP-62186-T	KU139176	KU139227	KU139343	KU139290
<i>P. orientoasiaticus</i>	Cui 9753*	JQ828926	–	KR013079	–
<i>P. orientoasiaticus</i>	Cui 9727	JQ828921	–	KR013076	–
<i>P. padicola</i>	Cui 2257*	JQ828905	–	KR013073	–
<i>P. padicola</i>	Cui 2414	JQ828906	–	–	–
<i>P. parmastoi</i>	Dai 12558*	JQ828900	–	KR013089	–
<i>P. parmastoi</i>	TN-6432	KU139158	KU139245	KU139376	–
<i>P. piceicola</i>	Cui 10440*	JQ828908	–	–	–
<i>P. piceicola</i>	Cui 10455	JQ828910	–	KR013085	–
<i>P. pomaceoides</i>	JV 1403/4-J*	KR013069	–	KR013107	–
<i>P. pomaceoides</i> ^b	SRM-158-Sp	KU139140	KU139210	KU139353	KU139267
<i>P. pomaceus</i>	TN-449	KU139142	KU139254	KU139352	KU139263
<i>P. pomaceus</i>	MJ 44/07	GQ383783	–	GQ383858	–
<i>P. populicola</i>	TN-526*	KU139179	KU139231	KU139333	KU139303
<i>P. populicola</i>	JV 0110/21	KR013062	–	KR013093	–
<i>P. resupinatus</i>	STE-U 7769*	KM523246	KM523251	–	–
<i>P. spiculosus</i>	CBS 345.63*	MH858307	MH869918	–	–
<i>P. tremulae</i>	NJB2011-PT1-F	KU139132	KU139201	KU139357	KU139276
<i>P. tremulae</i>	FP-135202-T	KU139134	KU139207	KU139359	KU139271
<i>P. turbinatus</i>	JV 1407/73-J	KT156687	–	–	–
<i>P. vietnamensis</i>	Cui 16434*	–	MG867716	MG867722	MG867719

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold

^aas *P. pseudoigniarius*

^bas *Phellinus*NA2

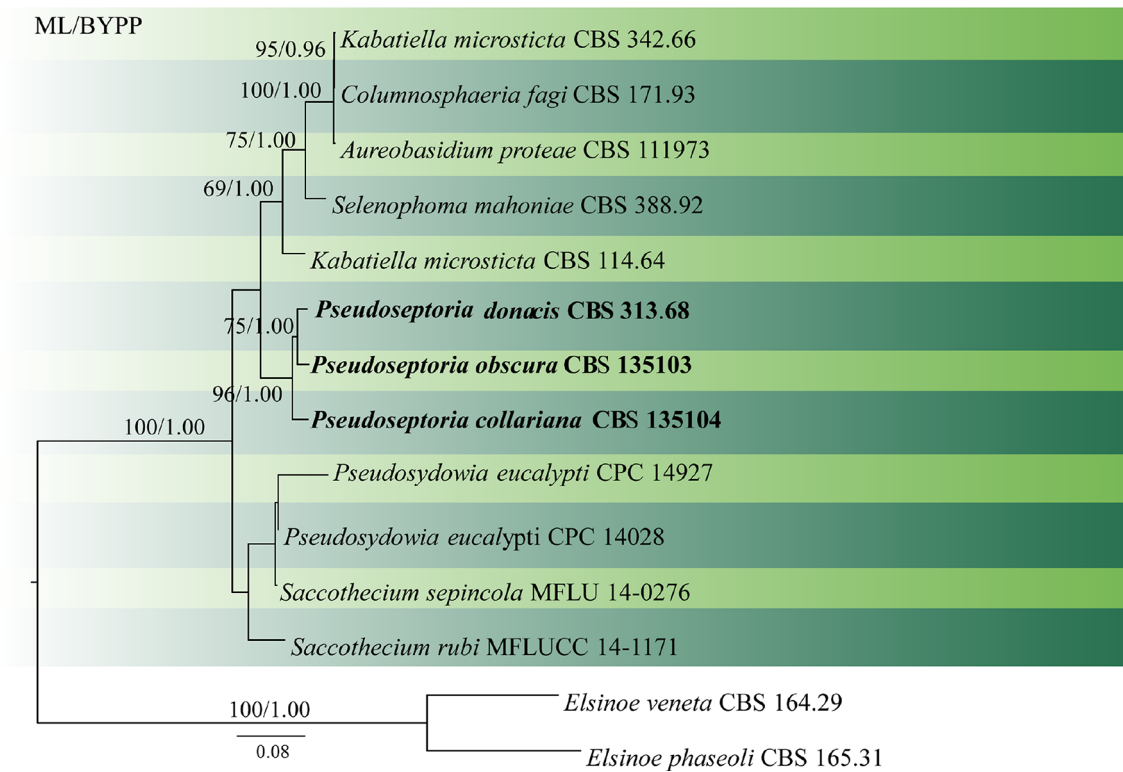


Fig. 27 Phylogenetic tree generated by maximum likelihood analysis of combined LSU, ITS and *rpb2* sequence data. Fourteen strains are included in the analyses, which comprised 2207 characters including gaps. The tree was rooted with *Elsinoe veneta* (CBS 164.29) and *Elsinoe phaseoli* (CBS165.31). Tree topology of the ML analysis was similar to the BYPP analysis. The best scoring RAxML tree with a final likelihood value of -7330.368152 is presented. The

matrix had 500 distinct alignment patterns, with 29.98% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.250948, C = 0.235140, G = 0.278289, T = 0.235623; substitution rates AC = 2.242594, AG = 3.171649, AT = 1.699638, CG = 1.459509, CT = 8.754890, GT = 1.000000; gamma distribution shape parameter $\alpha = 0.601361$ ML bootstrap values $\geq 65\%$ and BYPP ≥ 0.90 are shown respectively near the nodes

Table 17 DNA barcodes available for *Pseudoseptoria*

Species	Isolate	LSU	ITS	<i>rpb2</i>
<i>Pseudoseptoria collariana</i>	CBS 135104*	KF251721	KF251218	KF252223
<i>P. donacis</i> [#]	CBS 313.68	MH870852	MH859141	
<i>P. obscura</i>	CBS 135103	KF251722	KF251219	KF252224

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold. Species confirmed with pathogenicity studies are marked with [#]

Type species—*Thyrostroma compactum* (Sacc.) Höhn

Distribution—Australia, Iran, Korea, Russia, USA, Uzbekistan

Disease Symptoms—Thyrostroma canker, dieback and leaf spots (Fig. 30a, b)

Hosts—Pathogens of *Acanthophyllum* sp., *Astragalus* sp., *Capparis parviflora*, *Celtis occidentalis*, *Cornus officinalis*, *Echinops* sp., *Elaeagnus angustifolia*, *Ephedra equisetina*, *Eucalyptus mannifera* subsp. *maculosa*, *Franseria* sp., *Hali-modendron halodendron*, *Lycium barbarum*, *Morus alba*, *Robinia pseudoacacia*, *Sambucus caerulea*, *Styphnolobium*

japonicum, *Tilia cordata*, *Ulmus pumila* (Farr and Rossman 2020).

Morphological based identification and diversity

Thyrostroma species can be differentiated using conidial dimensions and septation in aged conidia and molecular phylogeny (Crous et al. 2016; Marin-Felix et al. 2017; Senwana et al. 2019; Fig. 30). Senwana et al. (2019) reported the sexual morph of *Thyrostroma* in *T. ulmicola* for the first time. The sexual morph is characterized by pseudothecial, immersed, erumpent or superficial, uniloculate or multiloculate ascostromata, globose to subglobose ascomata, a two-layered peridium, bitunicate, clavate asci, fusiform to ellipsoidal, 1-septate, ascospores.

Molecular based identification and diversity

In the past, there has been no comprehensive phylogenetic study in *Thyrostroma* and consequently, its taxonomy was and still is mostly based on morphological characters. Based on LSU sequence data, *Thyrostroma* clustered in a well-supported clade within the Dothidotiaceae (Marin-Felix et al. 2017; Crous et al. 2019). The asexual morph and sexual morph relationship were resolved by Senwana et al. (2019) by molecular evidence. To achieve correct generic and species identification and taxonomic placement, phylogenetic studies using LSU, SSU, ITS, and *tefl* were performed (Senwana et al. 2019). This study reconstructs the phylogeny using a combined LSU, SSU, ITS, and *tefl* sequence dataset (Fig. 31). The topology is in accordance with Marin-Felix et al. (2017), Senwana et al. (2019) and Hyde et al. (2020b).

Recommended genetic marker (genus level)—LSU

Recommended genetic markers (species level)—ITS, *tefl*, *rpb2* and *tub2*

LSU, ITS and *tefl* are the common genetic markers used in the identification of *Thyrostroma* species. Combined LSU, SSU, ITS and *tefl* genes provide a satisfactory resolution for resolving species. Based on the comparison of ITS and *tefl* gene regions, most species in *Thyrostroma* are not significantly different from one another, therefore, Senwana et al. (2019) suggested that *rpb2*, *tub2* are reliable genes for distinguishing species within *Thyrostroma*.

Accepted number of species—There are 27 epithets in Index Fungorum (2020), however only 13 species have DNA sequence data (Table 19).

References—Höhnelt (1911), Yuan and Old (1990), Ramaley (2005) (morphology); Marin-Felix et al. (2017), Crous et al. (2016, 2019), Senwana et al. (2019) (morphology and phylogeny).

94. *Wojnowiciella* Crous, Hern.-Restr. & M.J. Wingf., Persoonia 34, 201 (2015)

Background

Wojnowiciella was introduced by Crous et al. (2015) to include *Wojnowiciella eucalypti* which exhibited somewhat similar morphological characteristics to *Wojnowicia*, such as setose pycnidia, with ampulliform, enteroblastic, phialidic conidiogenous cells, but differed with apapillate conidiomata lacking setae and having dark brown conidia.

Classification—Ascomycota, Pezizomycota, Dothideomycetes, Pleosporales, Phaeosphaeriaceae

Type species—*Wojnowiciella eucalypti* Crous, Hern.-Restr. & M.J. Wingf

Distribution—Australia (Hernandez-Restrepo et al. 2016), China (Crous et al. 2015, Giraldo et al. 2017), Colombia (Crous et al. 2015, Giraldo et al. 2017), New Zealand (Crous et al. 2019), South Africa and Western Cape (Crous et al. 2016)

Disease symptoms—Leaf spots

Most species are reported as saprobes with the exception of *Wojnowiciella cissampeli*, *W. eucalypti* and *W. vibruni* which were isolated from leaves and twigs of *Cissampelos capensis*, *Eucalyptus* and *Viburnum utile* respectively (Hernandez-Restrepo et al. 2016). Their pathogenicity or disease symptoms are not indicated clearly and there is a need to establish pathogenicity of these species.

Hosts—*Cissampelos capensis*, *Dactylis* sp., *Eucalyptus grandis*, *Rosa* sp., *Leptocarpus* sp., *Lonicera* sp., *Spartium* sp. and *Viburnum utile* (Farr and Rossman 2020).

Morphological based identification and diversity

Wojnowiciella was introduced to include species that were phylogenetically distinct but morphologically similar to *Wojnowicia* (Crous et al. 2015). *Wojnowiciella* is characterized by apapillate conidiomata without setae and dark brown conidia. Some species of *Wojnowiciella* also produce hyaline microconidia. Karunarathna et al. (2017) first reported the sexual morph of *W. dactylidis*. Phookamsak et al. (2019) transferred *Wojnowicia rosicola* to *Wojnowiciella rosicola* based on morphology and phylogenetic analyses.

Molecular based identification and diversity

Wojnowiciella is a well-supported genus in the family Phaeosphaeriaceae (Phookamsak et al. 2019). A combined multiloci phylogeny of LSU, SSU, *tefl* and ITS is used in placing species of *Wojnowiciella* within Phaeosphaeriaceae. To identify species within the genus ITS, LSU, *rpb2* and *tefl* are used (Marin-Felix et al. 2019; Phookamsak et al. 2019). Here we provide an updated phylogenetic tree for this genus (Fig. 32).

Fig. 28 *Stemphylium* sp. **a** Ascomata on host **b** Vertical section through an ascoma **c** immature and mature asci **d** Pseudoparaphyses **e** Ascospores **f** Ascospores in Indian ink. Scale bars: **b** = 50 μ m, **c–f** = 10 μ m



Recommended genetic markers (genus level)—LSU

Recommended genetic markers (species level)—ITS, *rpb2*, *tefl*

Accepted number of species—Nine species are accepted with molecular data (Table 20).

References—Crous et al. (2015), Karunaratna et al. (2017), Marin-Felix et al. (2019), Phookamsak et al. (2019) (morphology and phylogeny)

Updated genera

The following genera are updated due to the addition of many new species during recent years.

95. *Cladosporium* Link, Mag. Gesell. naturf. Freunde, Berlin 7: 37 (1816) [1815]

Cladosporium Link, Mag. Gesell. naturf. Freunde, Berlin 7: 37 (1816) [1815]

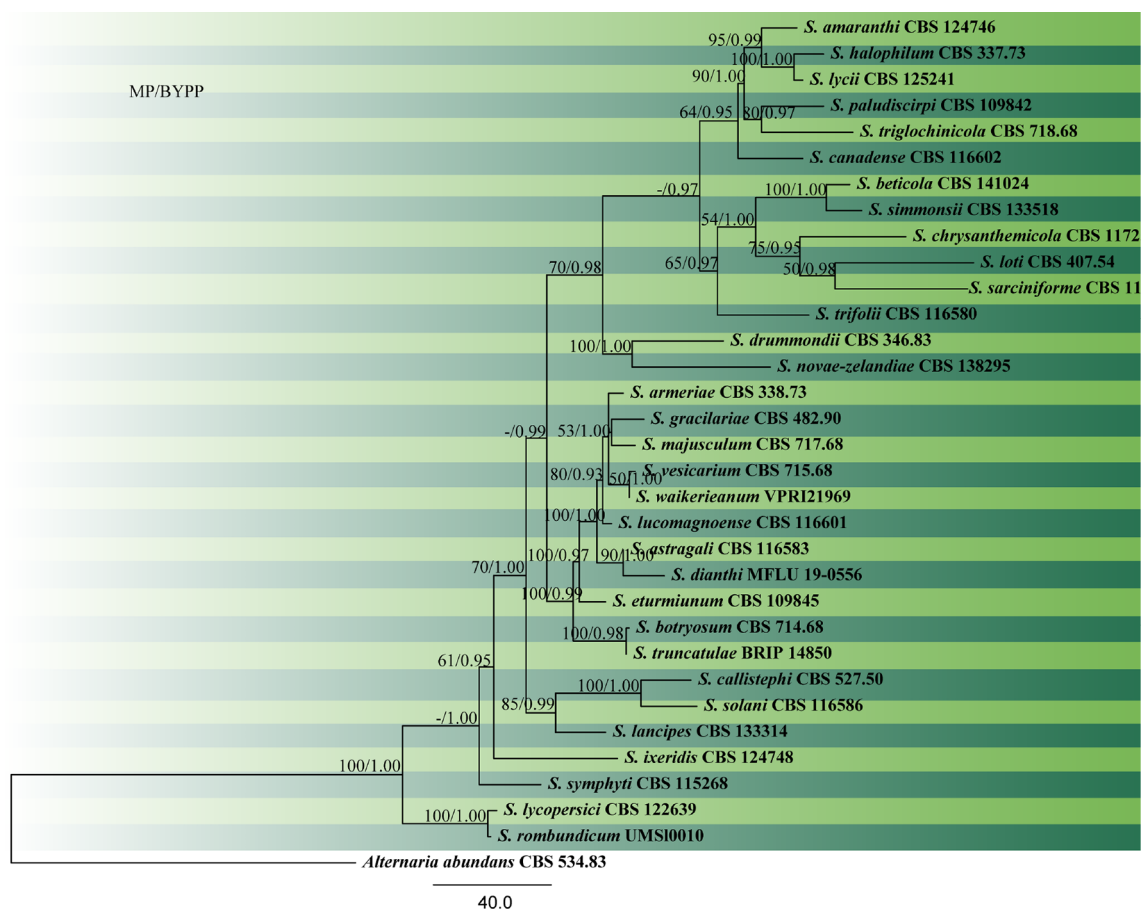


Fig. 29 Phylogram generated from MP analysis based on combined sequences of ITS, *gapdh* and *cmdA* sequences of all species of *Stemphylium*. Related sequences were obtained from GenBank. Thirty three taxa are included in the analyses, which comprise 1936 characters including gaps, of which 1355 characters are constant, 271 characters are parsimony-uninformative and 310 characters parsimony-informative. The parsimony analysis of the data matrix resulted in the

maximum of four equally most parsimonious trees with a length of 1112 steps (CI = 0.660, RI=0.721, RC = 0.476, HI = 0.340) in the first tree. Single gene analyses were carried out and compared with each species, to compare the topology of the tree and clade stability. The tree was rooted with *Alternaria abundans* (CBS 534.83). MP bootstrap support value $\geq 50\%$ and BYPP ≥ 0.9 are shown respectively near the nodes. Ex-type strains are in bold

Background

Cladosporium belongs to Cladosporiaceae in the order Capnodiales (Hyde et al. 2013). Established in 1816 with *C. herbarum* as type species, *Cladosporium* is one of the largest genera of dematiaceous hyphomycetes. *Davidiella* was erected by Braun et al. (2003) to accommodate the sexual morph of *Cladosporium sensu stricto*. *Davidiella* was therefore recognized as a synonym of *Cladosporium* as *Cladosporium* has priority over *Davidiella* at generic rank, and is also the more commonly used name in literature (Bensch et al. 2012). Therefore, Cladosporiaceae took preference over Davidiellaceae (Bensch et al. 2012). *Cladosporium* species have a worldwide distribution and can be easily spread in the environment, because of their small conidia. *Cladosporium* includes many important pathogens causing leaf spots and stem rots of many plant hosts. For

example, *Cladosporium fulvum* is the causal agent of tomato leaf mold (van Kan et al. 1991). *Cladosporium* species have been recorded as endophytes and may have a positive effect, for example, *C. sphaerospermum* was isolated from the roots of *Glycine max* which can promote its growth (Hamayun et al. 2009). Some species, such as *C. herbarum*, are also known as common contaminants in clinical laboratories and cause allergic lung disease (de Hoog et al. 2000). Several species were also isolated from human respiratory samples (Sandoval-Denis et al. 2016). Thirteen species are fungicolous (Heuchert et al. 2005; Sun et al. 2019) and have the potential for biological control in agriculture and forestry (Torres et al. 2017).

There have been studies towards understanding the genetic components of *Cladosporium*. *Cladosporium fulvum* is an important model species in the plant pathology study.

Table 18 DNA barcodes available for *Stemphylium*

Species name	Isolate/specimen no	ITS	<i>gapdh</i>	<i>cmdA</i>
<i>Stemphylium amaranthi</i>	CBS 124746*	KU850505	KU850652	KU850793
<i>S. armeriae</i>	CBS 338.73	KU850511	KU850658	KU850799
<i>S. astragali</i> [#]	CBS 116583*	KU850512	KU850659	KU850800
<i>S. beticola</i> [#]	CBS 141024*	KU850520	KU850667	KU850808
<i>S. botryosum</i> [#]	CBS 714.68*	KC584238	AF443881	KU850826
<i>S. callistephi</i>	CBS 527.50*	KU850539	KU850686	KU850828
<i>S. canadense</i>	CBS 116602*	KU850641	KU850782	KU850932
<i>S. chrysanthemicola</i> [#]	CBS 117255*	KU850640	KU850781	KU850931
<i>S. dianthi</i>	MFLU 19-0556*	MK500718	–	MK500734
<i>S. drummondii</i>	CBS 346.83*	GQ395365	KU850687	KU850829
<i>S. eturmiunum</i> [#]	CBS 109845*	KU850541	KU850689	KU850831
<i>S. gracilariae</i>	CBS 482.90*	KU850549	AF443883	KU850839
<i>S. halophilum</i>	CBS 337.73*	KU850553	KU850700	KU850843
<i>S. ixeridis</i>	CBS 124748*	KU850590	KU850737	KU850881
<i>S. lancipes</i>	CBS 133314*	KU850596	KU850742	KU850887
<i>S. loti</i>	CBS 407.54*	KU850597	KU850743	KU850888
<i>S. lucomagnoense</i>	CBS 116601*	KU850629	KU850770	KU850920
<i>S. lycii</i>	CBS 125241*	KU850602	KU850748	KU850893
<i>S. lycopersici</i>	CBS 122639*	KU850611	KU850756	KU850902
<i>S. majusculum</i>	CBS 717.68*	KU850618	AF443891	KU850909
<i>S. novae-zelandiae</i>	CBS 138295*	KU850631	KU850772	KU850922
<i>S. paludiscirpi</i>	CBS 109842*	KU850620	KU850762	KU850911
<i>S. rombuncicum</i>	BRIP 27486*	MK336819	MK336865	MK336842
<i>S. sarciniforme</i>	CBS 110049*	KU850591	KU850738	KU850882
<i>S. simmonsii</i> [#]	CBS 133518*	KU850637	KU850778	KU850928
<i>S. solani</i> [#]	CBS 116586*	KU850627	KU850768	KU850918
<i>S. symphyti</i>	CBS 115268*	KU850643	KU850784	KU850934
<i>S. trifolii</i>	CBS 116580*	KU850647	KU850788	KU850938
<i>S. triglochinicola</i>	CBS 718.68*	KU850648	KU850789	KU850939
<i>S. truncatulae</i>	BRIP 14850*	MK336815	MK336861	MK336838
<i>S. vesicarium</i> [#]	CBS 715.68*	KU850565	KU850712	KU850855
<i>S. waikerianum</i>	VPRI 21969*	MK336832	MK336878	MK336855

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold. Species confirmed with pathogenicity studies are marked with [#]

Iakovidis et al. (2020) reported classical mapping strategies for loci of tomato that response to sequence-monomorphic effector Ecp5. Convergent evolution could be used for choosing different functional genes according to individual plant breeding needs. Ge et al. (2019) showed that *Cladosporium* species have the potential to be used in industrial processes. They identified a new glucose oxidase gene *CtgoxB* from *C. tianshanense* and suggested this could be a candidate for the aquatic feed and detergent industries. Transcriptome and proteome analyses of *C. fulvum* showed that 14 out of 59 predicted proteases are expressed during *in vitro* and *in planta*, of which nine belong to serine proteases and the rest belong to metallo and aspartic proteases (Jashni et al. 2019). This study also confirmed the presence of six proteases at proteome level during the infection.

Grinn-Gofroń et al. (2019) developed and evaluated the models of forecasting possibilities of airborne spore concentrations in 18 sites in six countries across Europe. The study revealed the possibility of reliable prediction of fungal spore levels using gridded meteorological data. They concluded that these forecasting models can be used in the more timely and efficient management of phytopathogenic and of human allergic diseases. An environmentally isolated strain of *C. sphaerospermum* substantially enhanced plant growth, early flowering and increase in crop yield after exposure *in vitro* (Li et al. 2019). Pan et al. (2020) identified four new hybrid polyketides (Cladosin L-O) from *C. shaerospermum* which showed strong cytotoxicity, antifungal activity and moderate antibacterial activity.



Fig. 30 **a, b** Symptoms on *Ulmus pumila* caused by *Thyrostroma ulmicola* (MFLU 16-1622); **c, d** Sporodochia on the host surface. **e** Section of sporodochium. **f** Conidiogenesis and conidiogenous cells.

g–l Conidia. **m** Germinated conidium. Scale bars: **d** = 1000 μ m, **e** = 200 μ m, **f–m** = 30 μ m

Classification: Ascomycota, Pezizomycotina, Dothideomycetes, Pleosporomycetidae, Capnodiales, Cladosporiaceae
Type species–*Cladosporium herbarum* (Pers.) Link
Distribution– Worldwide

Disease symptoms–Leaf spots, leaf blight, discolourations, necrosis, or shot-hole symptoms, on stems and fruits, rots
Hosts– *Cladosporium* species occur on a wide range of host plants including Asparagaceae, Asteraceae, Fabaceae, Myrtaceae, Orchidaceae, Poaceae, Solanaceae and Vitaceae (Farr and Rossman 2020). Some species can be hyperparasites of insects and fungi (Heuchert et al. 2005; Islam et al.

2019; Sun et al. 2019; Abdel-Baky 2000). These species can cause allergies in humans such as sneezing, hives and also can cause eye, ear and sinus infections (de Hoog et al. 2000).

Pathogen biology, disease cycle and epidemiology

Cladosporium survives in the soil or on plant debris and produce spores during humid weather. Fungal spores germinate under high humidity and cool to warm temperatures. Wind, rain and irrigation splash, workers, tools, and insects readily disseminate spores (Jordan et al. 1990; Lan and Scherm 2003; Liu et al. 2019).

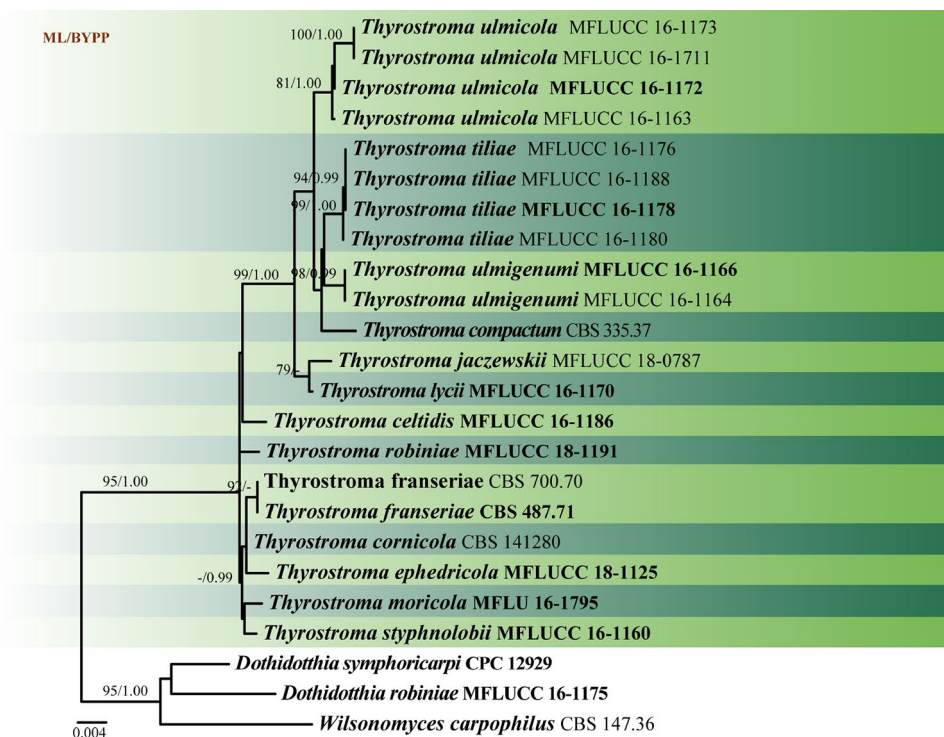


Fig. 31 Phylogenetic tree generated by maximum likelihood analysis of LSU, SSU, ITS and *tef1* sequence data of *Thyrostroma* species. Related sequences were obtained from GenBank. The tree was rooted with *Dothidothia robiniae* (MFLUCC 16-1175), *D. symphoricarpi* (CPC 12929) and *Wilsonomyces carpophilus* CBS 147.36). Tree topology of the ML analysis was similar to the Bayesian analysis. The best scoring RAXML tree with a final likelihood value of -5556.187049 is presented. The matrix had 170 distinct alignment

patterns, with 18.30% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.243922, C = 0.240705, G = 0.270231, T = 0.245142; substitution rates AC = 3.570314, AG = 6.771467, AT = 4.177691, CG = 1.603201, CT = 31.935571, GT = 1.000000; gamma distribution shape parameter $\alpha = 0.602378$. Maximum likelihood bootstrap support values greater than 60% and Bayesian posterior probabilities ≥ 0.95 (BYPP) are indicated above the nodes. Ex-type (ex-epitype) and voucher strains are in bold

Morphological based identification and diversity

The asexual morph of *Cladosporium* species is characterized by a unique coronate structure of the conidiogenous loci and conidia, consisting of the central convex dome surrounded by a raised periclinal rim (Bensch et al. 2012; Fig. 33), while ascomata of sexual morphs are identical to those of *Mycosphaerella* (sect. *Tassiana*) (Braun et al. 2003). Historically, all types of dematiaceous hyphomycetes with amero- to phragmosporous conidia formed in acropetal chains had been assigned to *Cladosporium sensu lato*, resulting in the complication to resolve a natural classification of *Cladosporium*. Various mycologists proposed natural genetic circumscriptions of *Cladosporium* (David 1997; Braun et al. 2003; Aptroot 2006). David (1997) found the unique structure of conidiogenous loci and conidial hila using scanning electron microscopy. Based on the genetic circumscriptions, some cladosporioid groups, such as *Fusicladium* being non-coronate (Schubert et al. 2003), have been excluded from *Cladosporium s. str.* Various *Cladosporium* species have been re-examined based on the new generic concepts (Schubert and Braun 2004, 2005a, b, 2007;

Schubert 2005; Schubert et al. 2006; Braun and Schubert 2007; Braun et al. 2008). A polyphasic approach revealed three major species complexes within *Cladosporium*, viz. *C. cladosporioides*, *C. herbarum* and *C. sphaerospermum* (Schubert et al. 2007; Dugan et al. 2008; Bensch et al. 2010; Bensch et al. 2015). A modern monograph of the genus treated 993 names of *Cladosporium sensu lato*, of which 169 were recognized in *Cladosporium sensu stricto* and others remain doubtful (Bensch et al. (2012).

Molecular based identification and diversity

The first molecular examination of *Cladosporium*-like hyphomycetes based on ITS and SSU was carried out by Braun et al. (2003), who confirmed the strong heterogeneity. A new genus *Davidiella* was established to accommodate the sexual morphs of *Cladosporium sensu stricto* species which were previously assigned in *Mycosphaerella*. Aptroot (2006) made a better circumscription of *Davidiella* after he found species of *Davidiella* have ascospores with irregular cellular inclusions, which are absent in *Mycosphaerella*. Schoch et al. (2006) studied the phylogenetic relationships

Table 19 DNA barcodes available for *Thyrostroma*

Species	Isolate/Voucher no	LSU	SSU	ITS	<i>tefl</i>
<i>Thyrostroma compactum</i>	CBS 335.37	KY905664	–	KY905670	KY905681
<i>T. cornicola</i>	CBS 141280*	KX228300	–	KX228248	KX228372
<i>T. ephedricola</i>	MFLUCC 18-1125*	MK765854	MK765853	MK765855	–
<i>T. franseriae</i>	CBS 487.71*	KX228301	–	KX228249	KY905680
	CBS 700.70	KX228302	–	KX228250	KY905682
<i>T. jaczewskii</i>	MFLUCC 18-0787	MK765857	MK765858	MK765856	–
<i>T. celtidis</i>	MFLUCC 16-1186*	MK751822	MK751767	MK751732	MK908022
<i>T. moricola</i>	MFLU 16-1795*	MK751823	MK751768	MK751733	MK908023
<i>T. lycii</i>	MFLUCC 16-1170*	MK751824	MK751769	MK751734	MK908024
<i>T. robiniae</i>	MFLUCC 18-1191*	MK751825	MK751770	MK751735	MK908025
<i>T. styphnolobii</i>	MFLUCC 16-1160*	MK751826	MK751771	MK751736	MK908026
<i>T. tiliae</i>	MFLUCC 16-1176	MK751827	MK751772	MK751737	MK908027
	MFLUCC 16-1178*	MK751828	MK751773	MK751738	MK908028
	MFLUCC 16-1180	MK751829	MK751774	MK751739	MK908029
	MFLUCC 16-1188	MK751830	MK751775	MK751740	MK908030
<i>T. ulmicola</i>	MFLUCC 16-1172*	MK751840	MK751785	MK751750	MK908040
	MFLUCC 16-1173	MK751841	MK751786	MK751751	MK908041
	MFLUCC 16-1163	MK751834	MK751779	MK751744	MK908034
	MFLUCC 16-1711	MK751839	MK751784	MK751749	MK908039
<i>T. ulmigenum</i>	MFLUCC 16-1166*	MK751846	MK751791	MK751756	MK908046
	MFLUCC 16-1164	MK751845	MK751790	MK751755	MK908045

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold

of 96 taxa of the Dothideomycetes using LSU, SSU, *tefl* and *rpb2* gene data. *Davidiella* and its *Cladosporium* asexual morphs were assigned to the family Cladosporiaceae in the order Capnodiales, together with Mycosphaerellaceae. Crous et al. (2007) delimited *Cladosporium* from morphologically similar genera using their morphology and DNA phylogeny based on LSU. Several species were transferred to new genera such as *Hyalodendriella*, *Ochrocladosporium*, *Rachicladosporium*, *Rhizocladosporium*, *Toxicocladosporium* and *Verrucocladosporium*. Furthermore, *C. castellanii* was confirmed as a synonym of *Stenella araguata*, while the type species of *Stenella* resided in Teratosphaeriaceae instead of Mycosphaerellaceae. Schubert et al. (2007) performed a comprehensive study of the *C. herbarum* species complex based on both morphology and phylogenetic analysis with five combined genes. Bensch et al. (2010) carried out species and ecological diversity within the *C. cladosporioides* species complex. More than 200 isolates belonging to the *C. cladosporioides* species complex were examined and analyzed on the basis of ITS, *act* and *tefl* gene regions. A comprehensive monograph of *Cladosporium sensu lato* was provided by Bensch et al. (2012) based on morphology and combined ITS, *act* and *tefl* sequence data. In their study, 993 names assigned to *Cladosporium sensu lato* are treated and 169 names were recognized in *Cladosporium sensu stricto*. Bensch et al. (2015) introduced the three major species

complexes in *Cladosporium*, i.e. *C. cladosporioides*, *C. herbarum* and *C. sphaerospermum*, and 19 new species were described. Razafinarivo et al. (2016) introduced a new species *C. lebrasiae* from milk bread rolls in France, Ma et al. (2017) introduced six new soil-inhabiting *Cladosporium* species from plateaus in China. Bensch et al. (2018) studied *Cladosporium* species from indoor environments and introduced 16 new species. Several new *Cladosporium* species including *Cladosporium omanense* (Halo et al. 2019), *C. passiflorae* and *C. passifloricola* (Rosado et al. 2019) have been introduced more recently. In this study, we reconstruct the phylogeny of *Cladosporium* based on ITS, *tefl* and *act* sequenced data (Table 21; Fig. 34).

Recommended genetic marker (genus level)—ITS and LSU
Recommended genetic markers (species level)—*act* and *tefl* (in a few cases *tub2*)

Accepted number of species—There are 844 epithets listed in Index Fungorum (2020), however, 138 species have DNA sequence data.

References—David (1997), Aptroot (2006), Schubert and Braun (2004, 2005a, b, 2007), Schubert (2005), Schubert et al. (2006), Braun and Schubert (2007), Braun et al. (2008) (morphology), Braun et al. (2003), Schoch et al. (2006), Bensch et al. (2010, 2012, 2015), Ma et al. (2017) (morphology and phylogeny)

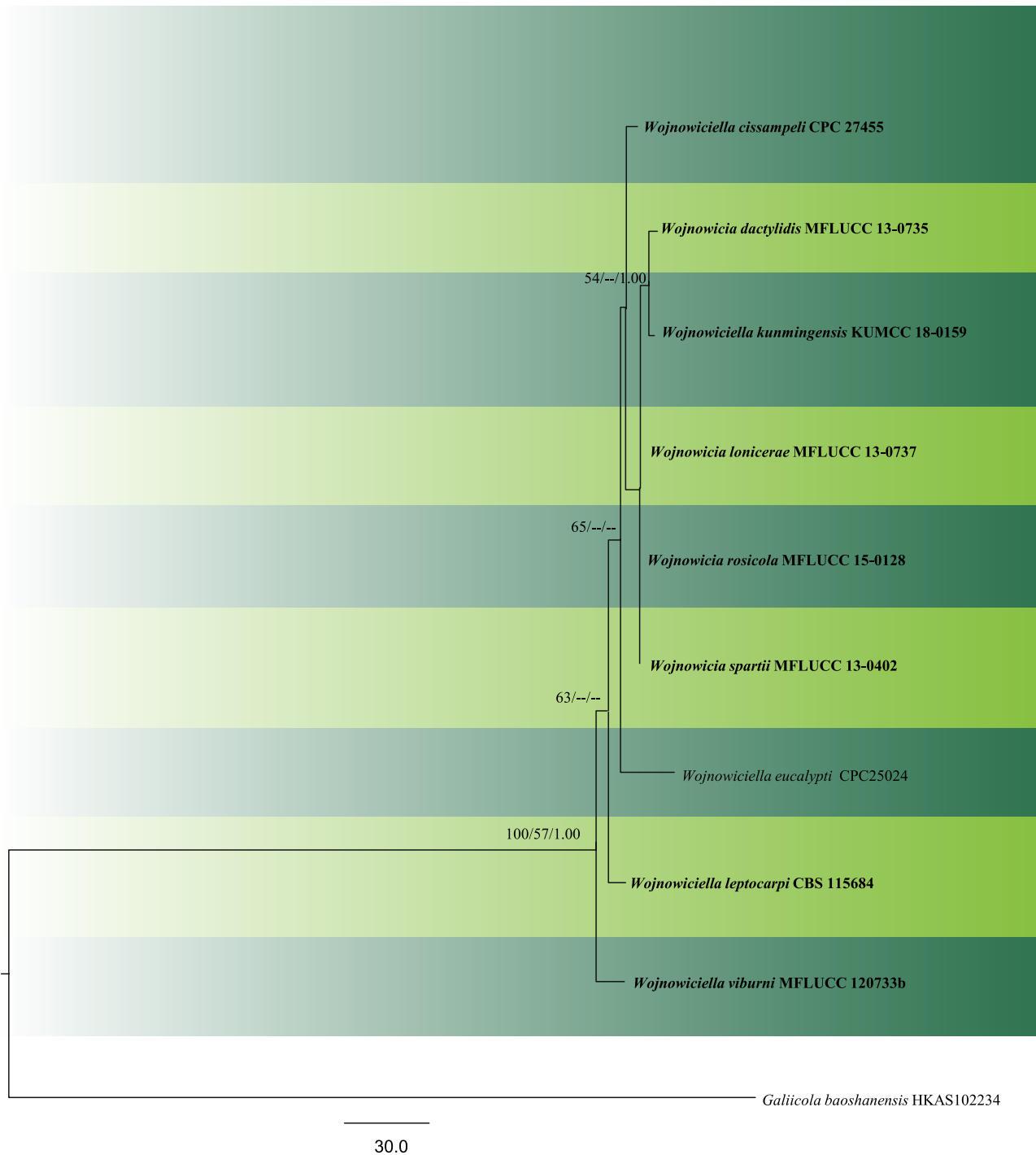


Fig. 32 Phylogram generated from MP analysis based on combined sequences of ITS, LSU and *tefl* sequences of all the accepted species of *Wojnowiciella*. Related sequences were obtained from GenBank. Ten taxa are included in the analyses, which comprise 2460 characters including gaps. Single gene analyses were carried out and compared with each species, to compare the topology of the tree and clade stability. The tree was rooted with *Galiicola baoshanensis* (HKAS102234). The best scoring RAxML tree with a final likeli-

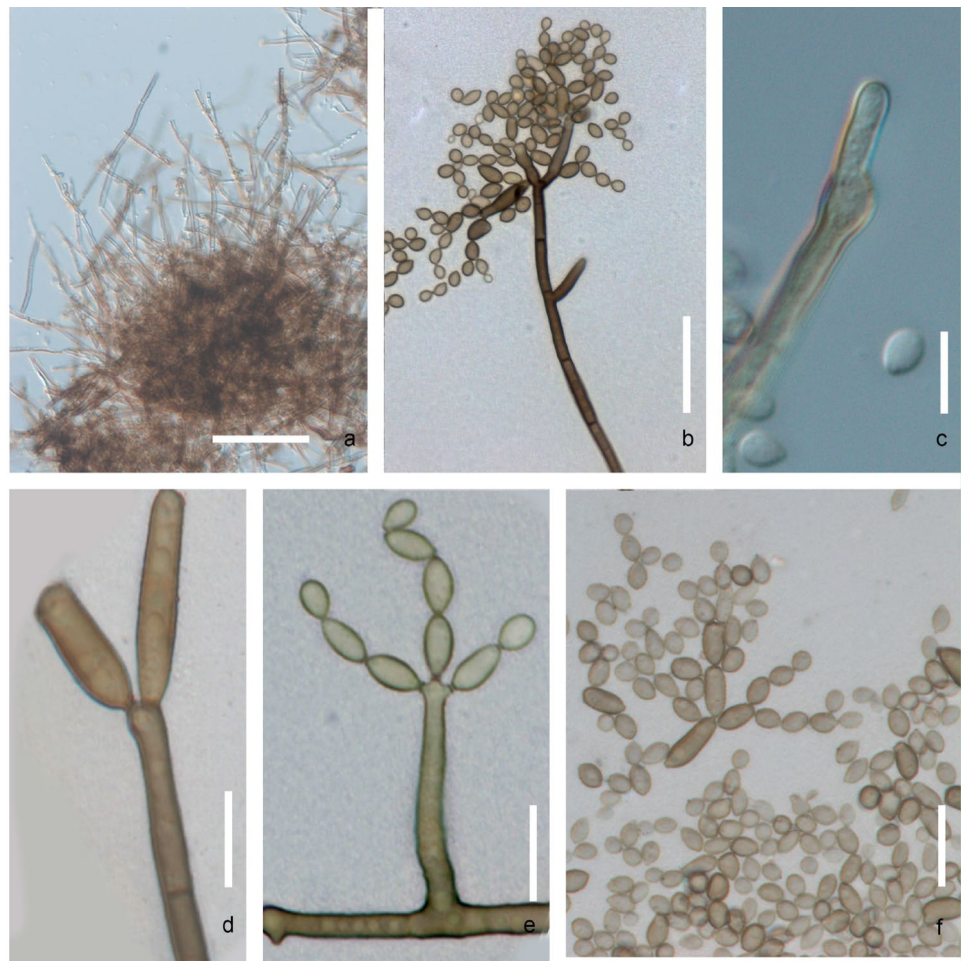
hood value of -6772.195394 is presented. The matrix had 261 distinct alignment patterns, with 0.96% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.230657, C = 0.279364, G = 0.252128, T = 0.237852; substitution rates AC = 1.388608, AG = 2.845402, AT = 2.389715, CG = 0.838197, CT = 7.220493, GT = 1.000000; gamma distribution shape parameter $\alpha = 0.650385$. ML and MP bootstrap support value $\geq 50\%$ are shown respectively near the nodes. Ex-type strains are in bold

Table 20 Details of *Wojnowiciella*, isolates used in the phylogenetic analyses

Species	Isolates	ITS	LSU	<i>tefl</i>	References
<i>Wojnowiciella cissampeli</i>	CBS 141297*	KX228272	KX228323	LT990616	Crous et al. (2016)
<i>W. dactylidis</i>	MFLUCC 13-0735*	KP744470	KP684149	–	Liu et al. (2015)
<i>W. eucalypti</i>	CBS 139904*	KR476741	KR476774	LT990617	Crous et al. (2015)
<i>W. kunmingensis</i>	KUMCC18-0159*	MK356380	MK356354	MK359071	Phookamsak et al. (2019)
<i>W. leptocarpi</i>	CBS 115684*	KX306775	KX306800	LT990615	Hernandez-Restrepo et al. (2016)
<i>W. loniceræ</i>	MFLUCC 13-0737*	KP744471	KP684151	–	Liu et al. (2015)
<i>W. rosicola</i>	MFLUCC 15-0128*	MG828979	MG829091	–	Phookamsak et al. (2019)
<i>W. spartii</i>	MFLUCC 13-0402*	KU058719	KU058729	–	Li et al. (2015)
<i>W. viburni</i>	MFLUCC 12-0733*	KC594286	KC594287	–	Wijayawardene et al. (2013)

Ex-type (or ex-epitype) strains are in bold and marked with an asterisk* and voucher strains are in bold

Fig. 33 *Cladosporium clad-
osporioides*. **a** Conidiomata. **b**,
c, **e** Macro- and micronematous
conidiophores and conidia
chains. **d**. Secondary ramoco-
nidia. **f**. Conidia. Scale bars: **b**,
c, **e**, **f** = 50 μ m, **d**–**g**=10 μ m



96. *Colletotrichum* Corda, in Sturm, Deutschl. Fl., 3 Abt. (Pilze Deutschl.) 3(12): 41 (1831)

Background

Colletotrichum was introduced by Corda (1831), belonging to *Glomerellaceae* (Glomerellales, Sordariomycetes), and is the sole member of this family (Maharachchikumbura et al. 2015, 2016; Hyde et al. 2020b). Species may occupy different lifestyles, ranging from necrotrophy to hemibiotrophy as well

as endophytism (Crouch et al. 2014). *Colletotrichum* species are important plant pathogens in both tropical and temperate regions on many economically important crops (Hyde et al. 2009a, b, 2014; Cannon et al. 2012; Jayawardena et al. 2016b, c). Based on recognized scientific and economic importance this genus was voted the eighth most important plant pathogenic group in the world (Dean et al. 2012). *Colletotrichum* species have been identified as endophytes (Manamgoda

et al. 2013; Tao et al. 2013; Hyde et al. 2014; Jayawardena et al. 2016c) and some are saprobes on dead plant material (Photita et al. 2005; Jayawardena et al. 2016b). A few species have been identified to be pathogenic to humans (*C. coccodes*, *C. dematium*, *C. gloeosporioides* (Natarajan et al. 2013)) and on insects (*C. fioriniae* (Damm et al. 2012b)). *Colletotrichum* species are cosmopolitan in distribution and show a diverse hosts association (Sharma et al. 2015). A host plant genus can be infected by many *Colletotrichum* species (Silva et al. 2012; Jayawardena et al. 2016c), and on the contrary, a single species of *Colletotrichum* can infect many host plants (Damm et al. 2012a, b; Weir et al. 2012).

Correct species identification is important to understand the species diversity, plant pathology and quarantine, concerning human infections, agriculture, bio-control, plant breeding, whole-genome sequencing, developing and maintaining knowledge databases, bioprospecting and understanding the evolutionary history (Jayawardena et al. 2016a). Due to a small number of distinctive morphological characters available for identification, misidentification of these species is frequent. Misapplication and misidentification of species are also due to the misunderstanding of their host-specific nature, ambiguous species boundaries and incorrect sequences (Cannon et al. 2012; Hyde et al. 2014; Jayawardena et al. 2016a). Therefore, having a stable taxonomy for the identification of these species is a significant practical concern (Shenoy et al. 2007). To establish a natural classification system, researchers strongly recommend the use of geographical, ecological, morphological and genetic data (Cai et al. 2009; Sharma and Shenoy 2016).

Species of *Colletotrichum* are extensively studied as model organisms (Cannon et al. 2012; Hyde et al. 2014). This enables the researchers to understand the pathogen variation, infection mechanism, evolution and population dynamics. Pathogenicity genes of *C. graminicola*, *C. higginsianum* and *C. orbiculare* have been studied (Huser et al. 2009; O'Connell et al. 2012). Asakura et al. (2009) discovered the importance of the pexophagy factor ATG26 for appressorium formation. A total of 28 genome projects that include 25 different *Colletotrichum* species can be found; 15 of these strains are still at the annotation stage and 13 are now at the 'Fungal Standard Draft' stage (Carbú et al. 2019). These genomes will allow further analysis of species diversity and evolutionary mechanisms and may serve as a foundation for genetic analysis that leads to a greater understanding of interactions between plants and fungal pathogens (Meng et al. 2020). Baroncelli et al. (2016) studied four strains of *C. acutatum* and illustrated the plasticity of *Colletotrichum* genomes and showed that major changes in host range are associated with relatively recent changes in gene content. A genome of *C. fruticola* from apple in China was compared with its reference genome, which identified a number of strong duplication/loss events at key phylogenetic nodes (Liang et al. 2018). Gan et al. (2019)

provided the updated genome for *C. orbiculare* and also provided three draft genomes for *C. trifolii*, *C. sidae* and *C. spinosum*. *Colletotrichum higginsianum* has a compartmentalized genome consisting of gene-sparse, transposable elements dense regions with more effector candidate genes and gene-dense, TE-sparse regions harbouring conserved genes which help the pathogen to generate genomic diversity (Tsushima et al. 2019). Comparative genome analysis indicated that there is a rapid evolution of pathogenicity genes in *C. tanacetii* (Lelwala et al. 2019).

Species of *Colletotrichum* can be used as biocontrol agents and as biocatalysts (*C. dematium*, *C. gloeosporioides*, *C. graminicola*, *C. lindemuthianum*, *C. orbiculare*, *C. theobromicola*, *C. trifoli* (Jayawardena et al. 2016b)). Jayawardena et al. (2016b) discussed the importance of secondary metabolites produced by species with relation to pathogenesis, medicines, disease control and toxins.

Classification—Ascomycota, Pezizomycotina Sordariomycetes, Hypocreomycetidae, Glomerellales, Glomerellaceae
Type species—*Colletotrichum lineola* Corda, in Sturm, *Deutschl. Fl.*, 3 Abt. (Pilze Deutschl.) 3(12): 41 (1831)

Distribution—Worldwide

Disease symptoms—Anthracnose disease, red rot, crown and stem rots, ripe rot, seedling blights and brown blotch.

Anthracnose disease symptoms include defined, often sunken necrotic spots on leaves, stems, flowers or fruits and may show a lot of variation depending on the host (35a–e).

Hosts—Pathogens on many host families including, Amaryllidaceae, Amaranthaceae, Anacardiaceae, Annonaceae, Apiaceae, Apocynaceae, Araceae, Araliaceae, Arecaceae, Asparagaceae, Asteraceae, Bignoniaceae, Campanulaceae, Caricaceae, Crassulaceae, Cucurbitaceae, Euphorbiaceae, Fabaceae, Iridaceae, Lamiaceae, Lauraceae, Malvaceae, Melastomataceae, Menispermaceae, Moraceae, Myrtaceae, Oleaceae, Olivaceae, Orchidaceae, Passifloraceae, Pinaceae, Piperaceae, Plumbaginaceae, Poaceae, Podocarpaceae, Polemoniaceae, Proteaceae, Ranunculaceae, Rosaceae, Rubiaceae, Rutaceae, Solanaceae, Theaceae and Vitaceae.

Pathogen biology, disease cycle and epidemiology

For *Colletotrichum* biology, disease cycle and epidemiology see Cannon et al. (2012) and De Silva et al. (2017).

Morphological based identification and diversity

Due to the overlapping morphological characters, species delimitation based on morphology alone is hardly possible (Jayawardena et al. 2016b; Marin-Felix et al. 2017; Fig. 35f–l).

Molecular based identification and diversity

Cai et al. (2009) proposed the use of a polyphasic approach with multi-loci sequence analyses combined with

Table 21 DNA barcodes available for *Cladosporium*

Species	Isolate	ITS	<i>tefl</i>	<i>act</i>
<i>Cladosporium acalyphae</i>	CBS 125982*	HM147994	HM148235	HM148481
<i>C. aciculare</i>	CBS 140488*	KT600411	KT600509	KT600607
<i>C. aerium</i>	CBS 143356*	MF472897	MF473324	MF473747
<i>C. aggregatocicatricatum</i> [#]	CBS 140493*	KT600448	KT600547	KT600645
<i>C. alboflavescens</i>	CBS 140690*	LN834420	LN834516	LN834604
<i>C. allicinum</i>	CBS 121624*	EF679350	EF679425	EF679502
<i>C. allii</i>	CBS 101.81	JN906977	JN906983	JN906996
<i>C. angulosum</i>	CBS 140692*	LN834425	LN834521	LN834609
<i>C. angustiterbarum</i>	CBS 140479*	KT600378	KT600475	KT600574
<i>C. angustisporum</i>	CBS 125983*	HM147995	HM148236	HM148482
<i>C. angustiterminale</i>	CBS 140480*	KT600379	KT600476	KT600575
<i>C. antarcticum</i>	CBS 690.92*	EF679334	EF679405	EF679484
<i>C. anthropophilum</i>	CBS 140685*	LN834437	LN834533	LN834621
<i>C. aphidis</i>	CBS 132182*	JN906978	JN906984	JN906997
<i>C. arthropodii</i>	CBS 124043*	JN906979	JN906985	JN906998
<i>C. asperulatum</i> [#]	CBS 126340*	HM147998	HM148239	HM148485
<i>C. australiense</i>	CBS 125984*	HM147999	HM148240	HM148486
<i>C. austroafricanum</i>	CBS 140481*	KT600381	KT600478	KT600577
<i>C. austrohemisphaericum</i>	CBS 140482*	KT600382	KT600479	KT600578
<i>C. basiinflatum</i> [#]	CBS 822.84*	HM148000	HM148241	HM148487
<i>C. chalastosporoides</i>	CBS 125985*	HM148001	HM148242	HM148488
<i>C. chasmanthicola</i>	CBS 142612*	KY646221	KY646227	KY646224
<i>C. chubutense</i>	CBS 124457*	FJ936158	FJ936161	FJ936165
<i>C. cladosporioides</i> [#]	CBS 112388*	HM148003	HM148244	HM148490
<i>C. colocasiae</i> [#]	CBS 386.64*	HM148067	HM148310	HM148555
<i>C. colombiae</i>	CBS 274.80B*	FJ936159	FJ936163	FJ936166
<i>C. coloradense</i>	CBS 143357*	MF472945	MF473372	MF473795
<i>C. crousii</i>	CBS 140686*	LN834431	LN834527	LN834615
<i>C. cucumerinum</i> [#]	CBS 171.52*	HM148072	HM148316	HM148561
<i>C. cycadicola</i>	CBS 137970*	KJ869122	KJ869236	KJ869227
<i>C. delicatulum</i>	CBS 126344*	HM148081	HM148325	HM148570
<i>C. domesticum</i>	CBS 143358*	MF472955	MF473382	MF473805
<i>C. dominicanum</i>	CBS 119415*	DQ780353	JN906986	EF101368
<i>C. echinulatum</i> [#]	CBS 123191	JN906980	JN906987	JN906999
<i>C. endophyticum</i>	MFLUCC 17-0599*	MG646956	MG646988	
<i>C. entadae</i>	MFLUCC 17-0919*	MK347728		
<i>C. europaeum</i>	CBS 134914*	HM148056	HM148298	HM148543
<i>C. exasperatum</i>	CBS 125986*	HM148090	HM148334	HM148579
<i>C. exile</i>	CBS 125987*	HM148091	HM148335	HM148580
<i>C. fildesense</i>	ChFC-554*	JX845290	MN233633	MN233632
<i>C. flabelliforme</i>	CBS 126345*	HM148092	HM148336	HM148581
<i>C. flavovirens</i>	CBS 140462*	LN834440	LN834536	LN834624
<i>C. floccosum</i> [#]	CBS 140463*	LN834416	LN834512	LN834600
<i>C. funiculosum</i>	CBS 122129*	HM148094	HM148338	HM148583
<i>C. fusiforme</i>	CBS 119414*	DQ780388	JN906988	EF101372
<i>C. gamsianum</i>	CBS 125989*	HM148095	HM148339	HM148584
<i>C. globisporum</i> [#]	CBS 812.96*	HM148096	HM148340	HM148585
<i>C. grevilleae</i>	CBS 114271*	JF770450	JF770472	JF770473
<i>C. halotolerans</i>	CBS 119416*	DQ780364	JN906989	EF101397
<i>C. hebeiense</i> [#]	JZB390001*	MG516597	MG516595	MG516593
<i>C. herbaroides</i> [#]	CBS 121626*	EF679357	EF679432	EF679509

Table 21 (continued)

Species	Isolate	ITS	<i>tefl</i>	<i>act</i>
<i>C. herbarum</i> [#]	CBS 121621*	EF679363	EF679440	EF679516
<i>C. hillianum</i>	CBS 125988*	HM148097	HM148341	HM148586
<i>C. inversicolor</i>	CBS 401.80*	HM148101	HM148345	HM148590
<i>C. ipereniae</i>	CBS 140483*	KT600394	KT600491	KT600589
<i>C. iranicum</i> [#]	CBS 126346*	HM148110	HM148354	HM148599
<i>C. iridis</i> [#]	CBS 138.40*	EF679370	EF679447	EF679523
<i>C. kenpeggii</i> [#]	CBS 142613*	KY646222	KY646228	KY646225
<i>C. langeronii</i>	CBS 189.54*	DQ780379	JN906990	EF101357
<i>C. lebrasiae</i>	CBS 138283*	KJ596568	KJ596583	KJ596631
<i>C. licheniphilum</i>	CBS 125990*	HM148111	HM148355	HM148600
<i>C. limoniforme</i> [#]	CBS 140484*	KT600397	KT600494	KT600592
<i>C. longicatenatum</i>	CBS 140485*	KT600403	KT600500	KT600598
<i>C. longissimum</i>	CBS 300.96*	DQ780352	EU570259	EF101385
<i>C. lycoperdinum</i>	CBS 126347	HM148112	HM148356	HM148601
<i>C. macrocarpum</i> [#]	CBS 121623*	EF679375	EF679453	EF679529
<i>C. magnoliigena</i>	MFLUCC 18-1559*	MK347813	MK340864	
<i>C. michoacanense</i>	CBS 143588*	LT907958	LT907945	LT907961
<i>C. montecillanum</i>	CBS 140486*	KT600406	KT600504	KT600602
<i>C. myrtacearum</i>	CBS 126350*	HM148117	HM148361	HM148606
<i>C. needhamense</i>	CBS 143359*	MF473142	MF473570	MF473991
<i>C. neerlandicum</i>	CBS 143360*	KP701887	KP701764	KP702010
<i>C. neolangeronii</i>	CBS 797.97*	MF473143		MF473992
<i>C. neopsychrotolerans</i>	CGMCC 3.18031*	KX938383	KX938400	KX938366
<i>C. omanense</i>	SQUCC 13165*	MH725789	MH716047	MH716046
<i>C. ossifragi</i>	CBS 842.91*	EF679381	EF679459	EF679535
<i>C. oxysporum</i> [#]	CBS 125991	HM148118	HM148362	HM148607
<i>C. paracladosporioides</i>	CBS 171.54*	HM148120	HM148364	HM148609
<i>C. parahalotolerans</i>	CBS 139585*	KP701955	KP701832	KP702077
<i>C. paralimoniforme</i>	CGMCC 3.18103*	KX938392	KX938409	KX938375
<i>C. parapendielloides</i>	CBS 140487*	KT600410	KT600508	KT600606
<i>C. parasubtilissimum</i>	CBS 143361*	MF473170	MF473593	MF474018
<i>C. passiflorae</i> [#]	COAD 2135*	MH682175	MH724943	MH729795
<i>C. passifloricola</i>	COAD 2140*		MH724948	MH729800
<i>C. penidielloides</i>	CBS 140489*	KT600412	KT600510	KT600608
<i>C. perangustum</i> [#]	CBS 125996*	HM148121	HM148365	HM148610
<i>C. phaenocomae</i>	CBS 128769*	JF499837	JF499875	JF499881
<i>C. phlei</i> [#]	CBS 358.69*	JN906981	JN906991	JN907000
<i>C. phyllactiniicola</i>	CBS 126352*	HM148150	HM148394	HM148639
<i>C. phyllophilum</i>	CBS 125992*	HM148154	HM148398	HM148643
<i>C. pini-ponderosae</i>	CBS 124456*	FJ936160	FJ936164	FJ936167
<i>C. prolongatum</i>	CGMCC 3.18036*	KX938394	KX938411	KX938377
<i>C. pseudiridis</i>	CBS 116463*	EF679383	EF679461	EF679537
<i>C. pseudochalastosporoides</i>	CBS 140490*	KT600415	KT600513	KT600611
<i>C. pseudocladosporioides</i> [#]	CBS 125993*	HM148158	HM148402	HM148647
<i>C. psychrotolerans</i>	CBS 119412*	DQ780386	JN906992	EF101365
<i>C. pulvericola</i>	CBS 143362*	MF473226	MF473648	MF474075
<i>C. puyae</i>	CBS 274.80A*	KT600418	KT600516	KT600614
<i>C. ramotenellum</i> [#]	CBS 121628*	EF679384	EF679462	EF679538
<i>C. rectoides</i>	CBS 125994*	HM148193	HM148438	HM148683
<i>C. rhusicola</i>	CBS 140492*	KT600440	KT600539	KT600637
<i>C. ruguloflabelliforme</i>	CBS 140494*	KT600458	KT600557	KT600655

Table 21 (continued)

Species	Isolate	ITS	<i>tef1</i>	<i>act</i>
<i>C. rugulovarians</i>	CBS 140495*	KT600459	KT600558	KT600656
<i>C. salinae</i>	CBS 119413*	DQ780374	JN906993	EF101390
<i>C. scabrellum</i>	CBS 126358*	HM148195	HM148440	HM148685
<i>C. silenes</i>	CBS 109082*	EF679354	EF679429	EF679506
<i>C. sinense</i>	CBS 143363*	MF473252	MF473675	MF474102
<i>C. sinuatum</i>	CGMCC 3.18096*	KX938385	KX938402	KX938368
<i>C. sinuosum</i>	CBS 121629*	EF679386	EF679464	EF679540
<i>C. sloanii</i>	CBS 143364*	MF473253	MF473676	MF474103
<i>C. soldanellae</i>	CBS 132186*	JN906982	JN906994	JN907001
<i>C. sphaerospermum</i> [#]	CBS 193.54*	DQ780343	EU570261	EF101380
<i>C. spinulosum</i>	CBS 119907*	EF679388	EF679466	EF679542
<i>C. subcinereum</i>	CBS 140465*	LN834433	LN834529	LN834617
<i>C. subinflatum</i>	CBS 121630*	EF679389	EF679467	EF679543
<i>C. subtilissimum</i> [#]	CBS 113754*	EF679397	EF679475	EF679551
<i>C. subuliforme</i> [#]	CBS 126500*	HM148196	HM148441	HM148686
<i>C. succulentum</i>	CBS 140466*	LN834434	LN834530	LN834618
<i>C. tenellum</i> [#]	CBS 121634*	EF679401	EF679479	EF679555
<i>C. tenuissimum</i> [#]	CBS 125995*	HM148197	HM148442	HM148687
<i>C. tianshanense</i>	CGMCC 3.18033*	KX938381		KX938364
<i>C. tuberosum</i>	CBS 140693*	LN834417	LN834513	LN834601
<i>C. uredinicola</i>	ATCC 46649	AY251071	HM148467	HM148712
<i>C. uwebraunianum</i>	CBS 143365*	MF473306	MF473729	MF474156
<i>C. variabile</i> [#]	CBS 121635*	EF679402	EF679480	EF679556
<i>C. varians</i>	CBS 126362*	HM148224	HM148470	HM148715
<i>C. velox</i>	CBS 119417*	DQ780361	JN906995	EF101388
<i>C. verrucocladosporioides</i>	CBS 126363*	HM148226	HM148472	HM148717
<i>C. verruculosum</i>	CGMCC 3.18099*	KX938388	KX938405	KX938371
<i>C. versiforme</i>	CBS 140491*	KT600417	KT600515	KT600613
<i>C. vicinum</i>	CBS 143366*	MF473311	MF473734	MF474161
<i>C. vignae</i> [#]	CBS 121.25	HM148227	HM148473	HM148718
<i>C. welwitschiicola</i>	CBS 142614*	KY646223	KY646229	KY646226
<i>C. westerdijkiae</i>	CBS 113746*	HM148061	HM148303	HM148548
<i>C. wyomingense</i>	CBS 143367*	MF473315	MF473738	MF474165
<i>C. xanthochromaticum</i>	CBS 140691*	LN834415	LN834511	LN834599
<i>C. xylophilum</i>	CBS 125997*	HM148230	HM148476	HM148721
<i>Toxicocladosporium banksiae</i>	CBS 128215*	HQ599598		LT821371

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold. Species confirmed with pathogenicity studies are marked with [#]

geographical, ecological and morphological data for reliable species delimitation. Application of this polyphasic approach resulted in the delimitation of almost 200 species, most of them belonging to species complexes such as acutatum, boninense and gloeosporioides. There is no universal set of loci to use when identifying *Colletotrichum* species. Cannon et al. (2012), Damm et al. (2012a, b, 2013, 2014, 2019, Liu et al. 2016) used ITS, *gapdh*, *chs*, *act*, *his* and *tub2* (with some also *gs* or *cal*) for studying species within the acutatum, boninense, dematium, destructivum, gigasporum, orbiculare, spaethianum and truncatum species complexes, while Weir et al. (2012) additionally applied *gs*, *cal* and *sod2*

within the gloeosporioides species complex. Hyde et al. (2014), Jayawardena et al. (2016b), Marin-Felix et al. (2017) used ITS, *gapdh*, *chs*, *act* and *tub2* to differentiate the species. Using five loci for the whole genus gave similar results to 6–7 loci used for the whole genus. In contrast, Crouch et al. (2009b) applied ITS, *sod2*, *apn2* and *mat1/apn2*, to study the graminicola and caudatum species complexes. Use of *ApMat* locus to delimit the species within gloeosporioides species complex was emphasized by Silva et al. (2012) and Sharma et al. (2015) as it provides a higher resolution when compared to previously used loci. However, studies by Liu et al. (2015, 2016) revealed that using this locus with other

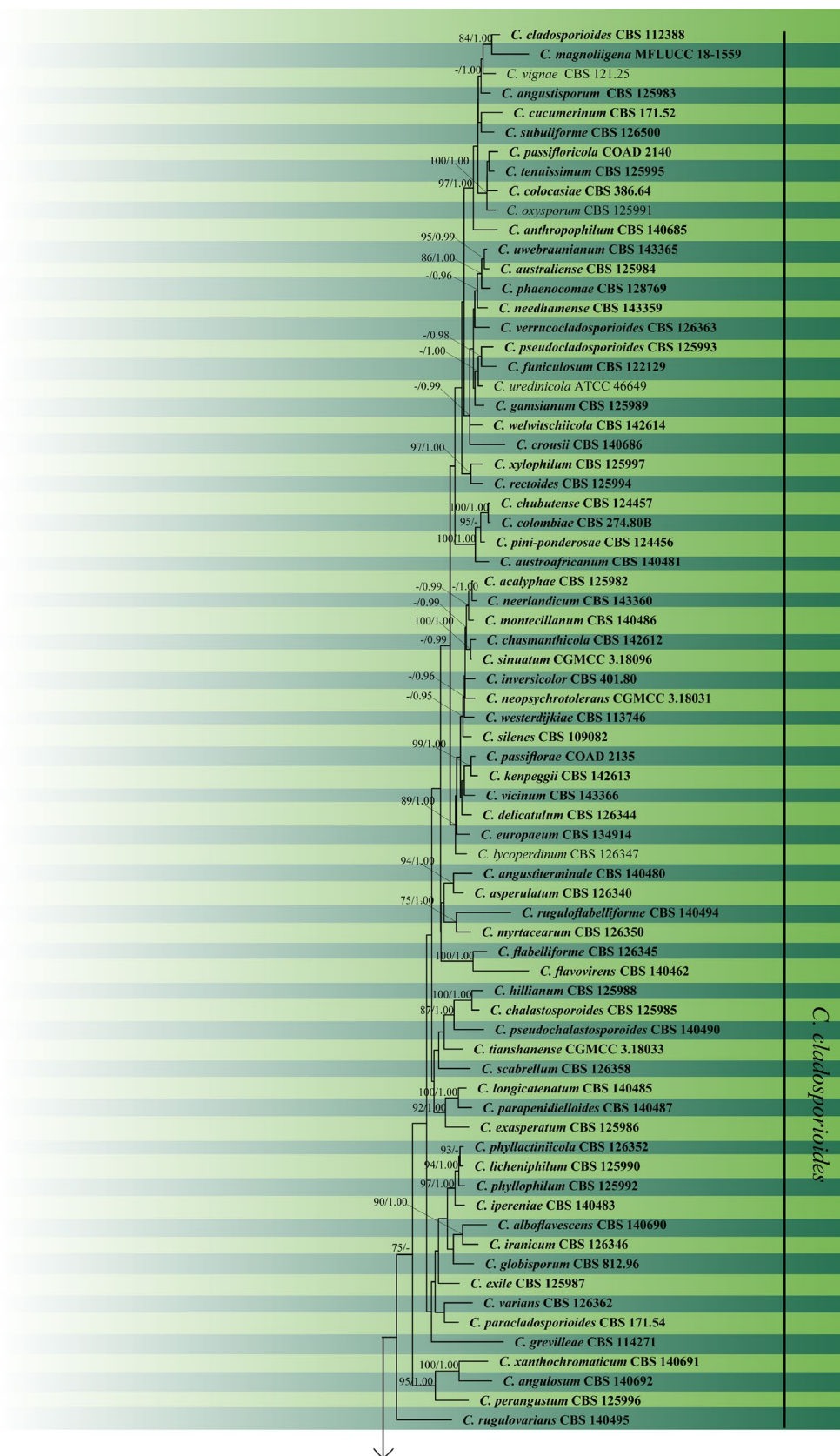


Fig. 34 Phylogram generated from Maximum Likelihood analysis based on ITS, *tef1* and *act* sequenced data. Bootstrap support values $\geq 75\%$ and Bayesian posterior probabilities ≥ 0.95 are given near the

nodes. The ex-type (ex-epitype) and voucher strains are in bold. The tree is rooted with *Toxicocladosporium banksiae* CBS 128215

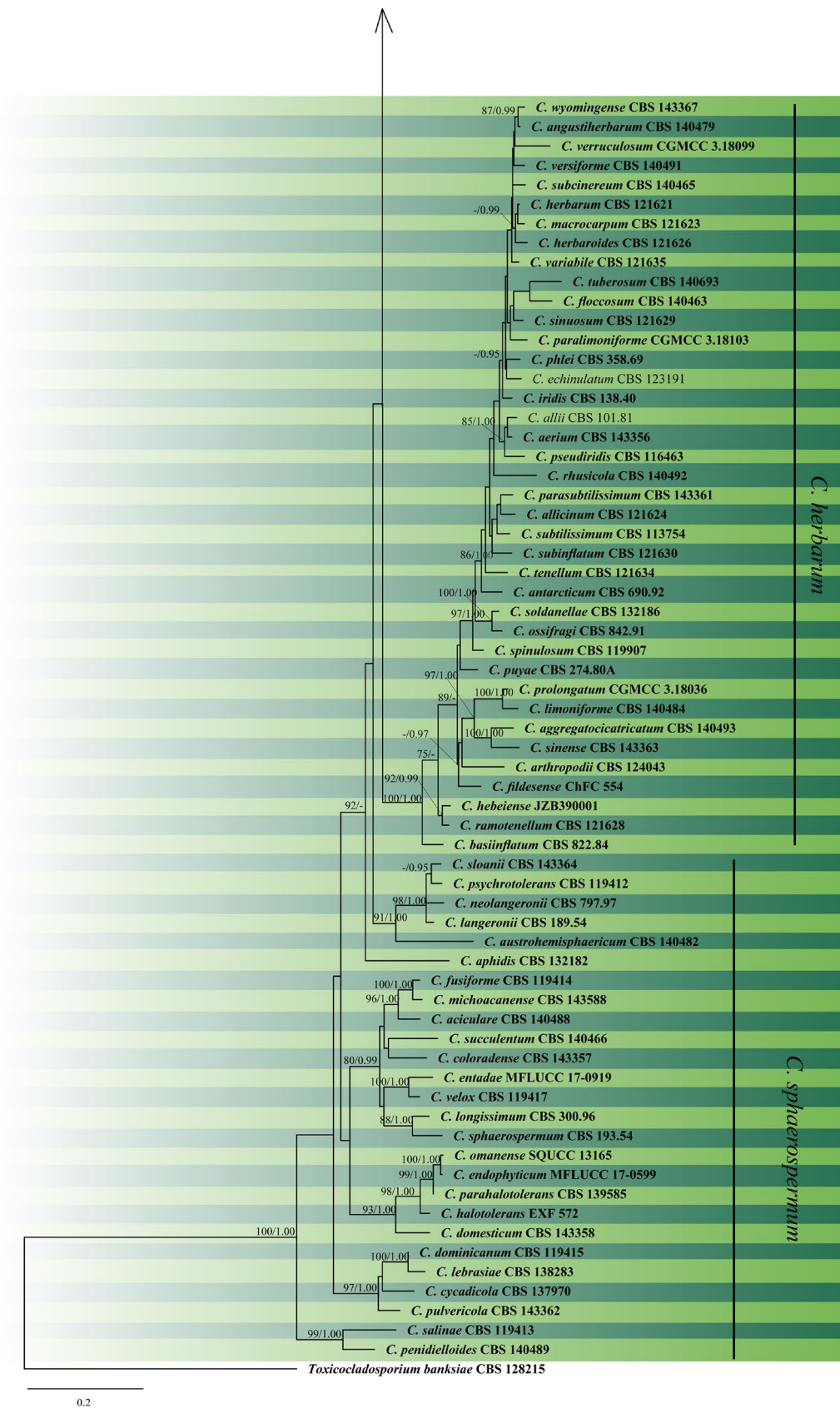


Fig. 34 (continued)

loci would provide a satisfactory species delimitation within the gloeosporioides species complex. For species delimitation, application of the Genealogical Concordance Phylogenetic Species Recognition (GCPSR) has proven to be a powerful tool (Cai et al. 2009). Coalescent-based species delimitation methods can also be used to infer the dynamic of divergence, evolutionary process and the relationships among species (McCormack et al. 2009, Liu et al. 2016).

Jayawardena et al. (2016b) provided the accepted species for the genus with backbone trees for each species complex and with notes for each accepted species. De Silva et al. (2017) reviewed the lifestyles and how this can be applied to plant biosecurity. Ariyawansa et al. (2015), Yan et al. (2015), Li et al. (2016), De Silva et al. (2017), Hyde et al. (2020a, b), Marin-Felix et al. (2017), Tibpromma et al. (2017, 2018), Samarakoon et al. (2018), Bhunjun et al. (2019) have introduced new species based on morphology, phylogeny and GCPSR evidence. Damm et al. (2019) introduced three new species complexes namely, dracaenophilum, magnum and orchidearum based on morphology and phylogeny. Cabral et al. (2020) based on pathological, morphological, cytogenomic, biochemical and molecular data, assigned the previously known *C. kahawae* subsp. *ciggaro* as a new species, *C. ciggaro*. At present, based on multi-loci phylogeny there are 14 species complexes. With 59 new species having been added since the last treatment (Marin-Felix et al. 2017), here we present an analysis using five loci (Table 21) for all *Colletotrichum* species (Fig. 36). From the studies conducted on this genus, it is clear that the resolution of species differs depending on both locus and species. Therefore, to select a better genetic marker and the best secondary barcoding gene/genes is still an ongoing process.

Recommended genetic marker (genus level)—ITS

Recommended genetic markers (species level)—*act*, *apmat*, *apn2*, *cal*, *chs-1*, *gapdh*, *gs*, *his*, *mat1/apn2*, *sod2*, and *tub2*.

Accepted number of species—There are 903 epithets listed in Index Fungorum (2020), however, 247 species with molecular data are treated as accepted (Table 22).

References—Cai et al. (2009) (polyphasic approach); Hyde et al. (2009a, b) (morphology and accepted species); Cannon et al. (2012) (A review and an updated account of the genus); Crouch et al. (2009a, b, c, 2014), Damm et al. (2009, 2012a, b, 2013, 2014, 2019), Weir et al. (2012) (morphology and phylogeny); Hyde et al. (2014), Jayawardena et al. (2016b), Marin-Felix et al. (2017) (accepted number of species).

97. *Mucor* Fresen., Beitr. Mykol. 1: 7 (1850)

Background

Mucor belongs to the order Mucorales, which is among one of the most studied groups of early diverging lineages of fungi. The genus has the largest number of species within the order and half of the sequences submitted to GenBank for Mucorales are of *Mucor* (Hoffmann et al. 2013; Spatafora et al. 2016; Hyde et al. 2014; Nguyen and Lee 2018).

Mucor belongs to the phylum Mucoromycota, subphylum Mucoromycotina, class Mucoromycetes, order Mucorales and family Mucoraceae (Wijayawardene et al. 2018, 2020). It was described by Fresenius in 1850 and the type species is *Mucor mucedo*. Recent molecular studies of mucoralean species have indicated that *Mucor* is polyphyletic (Nguyen et al. 2017). However, even with definite results showing the polyphyly of *Mucor*, few clear lineages within *Mucor* are recognized. Some of these lineages share innate characteristics, such as sporangium size and branching of tall sporangiophores and the morphology is still widely used in current taxonomy (Walther et al. 2013). Analysis of internal transcribed spacer (ITS) and large subunit (LSU) rDNA sequence data of several mucoralean species, showed that some *Mucor* species with curved sporangiophores grouped with species of *Backusella* and hence was transferred to *Backusella* (Walther et al. 2013; Nguyen et al. 2017). *Mucor* species are commonly isolated from soil, dung, insect, and fruits (Benny 2008). Some species are of biotechnological importance such as biofuel, enzyme, terpenoid production and biotransformation while other species cause mucoromycosis in immunosuppressed humans (Nguyen et al. 2017; Steve et al. 2018; Morin-Sardin et al. 2017). Comparative analyses of five *Mucor* species based on their lifestyles (*M. fuscus* and *M. lanceolatus* (used for cheese production), *M. circinelloides* and *M. racemosus* (opportunistic pathogens) and *M. endophyticus* (an endophyte)) revealed the core transcriptome comprising 5566 orthogroups included genes potentially involved in secondary metabolism. Due to the wide taxonomic range investigated, the five transcriptomes also displayed specificities that can be linked to the different lifestyles, such as differences in the composition of transcripts identified as virulence factors or carbohydrate transporters. Research on this genus has changed its course to identify the link between genetic and biological data, especially in terms of lifestyle and adaptations to a given habitat (Lebreton et al. 2019) (Figs. 37, 38).

Classification—Zygomycota, Mucoromycotina, Mucoromycetes, Mucorales, Mucorineae, Mucoraceae

Type species—*Mucor mucedo* Fresen.

Distribution—Worldwide

Disease symptoms—Mucor rot and soft rot

Mucor species especially *M. fragilis*, *M. irregularis*, *M. piriformis* and *M. racemosus* often cause postharvest diseases such as Mucor rot and soft rot. The initial symptoms of Mucor rot are similar to plant diseases caused by green mold, blue mold, and sour mold. The infected tissue becomes soft and watery. The lesions turn light to dark brown and as the infection progresses, white or shiny grey sporangiophores form at the lesions. Fungal growth spreads across the whole host and masses of sporangiophores bearing black to pale brown sporangia are observed. Decaying fruits become “juicy” within which are abundant spores of

the fungus (Li et al. 2014; Saito et al. 2016). Ito et al. (1979) found that three species of fruit flies namely *Certitis capitata*, *Dacus cucurbitae* and *D. dorsalis*, can transmit *Mucor* rot in guava.

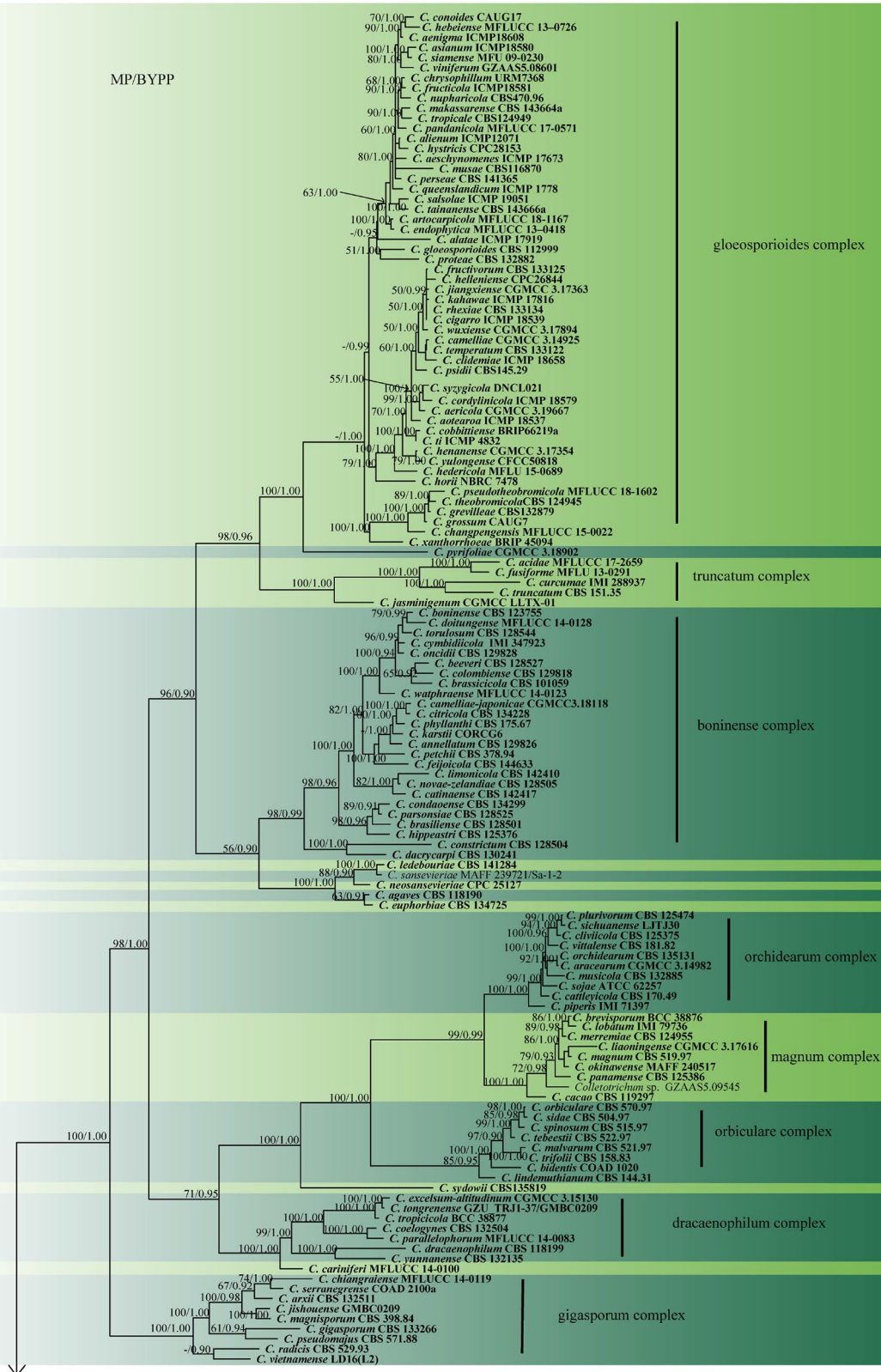
Soft rot caused by *Mucor racemosus* results in water-soaked appearance followed by a softening of the infected part. When the disease progresses growth of white mycelium and brownish to grey sporangia can be observed. Finally, the infected tissue is broken down and disintegrates in a watery rot (Kwon and Hong 2005; López et al. 2016).

Fig. 36 Phylogram generated from MP analysis based on combined sequences of ITS, *gapdh*, *chs*, *act* and *tub2* sequences of all species of *Colletotrichum* with molecular data. Related sequences were obtained from GenBank. Two hundred and forty nine taxa are included in the analyses, which comprise 2296 characters including gaps, of which 868 characters are constant, 295 characters are parsimony-uninformative and 1133 characters parsimony-informative. The parsimony analysis of the data matrix resulted in the maximum of ten equally most parsimonious trees with a length of 10088 steps (CI = 0.283, RI=0.840, RC = 0.237, HI = 0.717) in the third tree. Single gene analyses were carried out and compared with each species, to compare the topology of the tree and clade stability. The tree was rooted with *Monilochaetes infuscans* (CBS 869.96) and *M. populi* (CBS 139623). MP bootstrap support value $\geq 50\%$ and BYPP ≥ 0.9 are shown respectively near the nodes. Ex-type strains are in bold



Fig. 35 *Colletotrichum* sp. **a** Chilli anthracnose symptoms **b** Crown rot of strawberry **c** Leaf blight of *Cannas* sp. **d, e** strawberry anthracnose symptoms **f, g** Conidiomata and spore mass **h** Conidiophore **i** Setae **j** Conidiogenous cells and curved conidia **k** Conidia of *C. gloeosporioides* **l** Appressoria. Phylogram generated from RAxML analysis based on combined sequences of ITS and LSU of *Mucor* and *Backusella* species. Eighty-one taxa were used for the analysis, which consisted 1256 characters including gaps. The tree is rooted using *Backusella lamprospora* (CBS 195.28), and *B. grandis* (CBS 186.87). Likelihood of the best scoring ML tree was -16174.718247. The

concatenated matrix contained 657 distinct alignment patterns with 22.27% of undetermined characters or gaps. Estimated base frequencies were as follows; A = 0.302146, C = 0.168433, G = 0.219872, T = 0.309549; substitution rates AC = 0.776817, AG = 3.154911, AT = 1.674079, CG = 0.632500, CT = 4.808262, GT = 1.000000; gamma distribution shape parameter $\alpha = 0.291909$. Type species in the dataset are indicated using T. Maximum likelihood RAxML bootstrap support value $\geq 70\%$ and Bayesian posterior probabilities ≥ 0.70 are shown near the nodes (ML/BYPP). – indicates bootstrap support values lower than 70% and * shows unrecovered branching



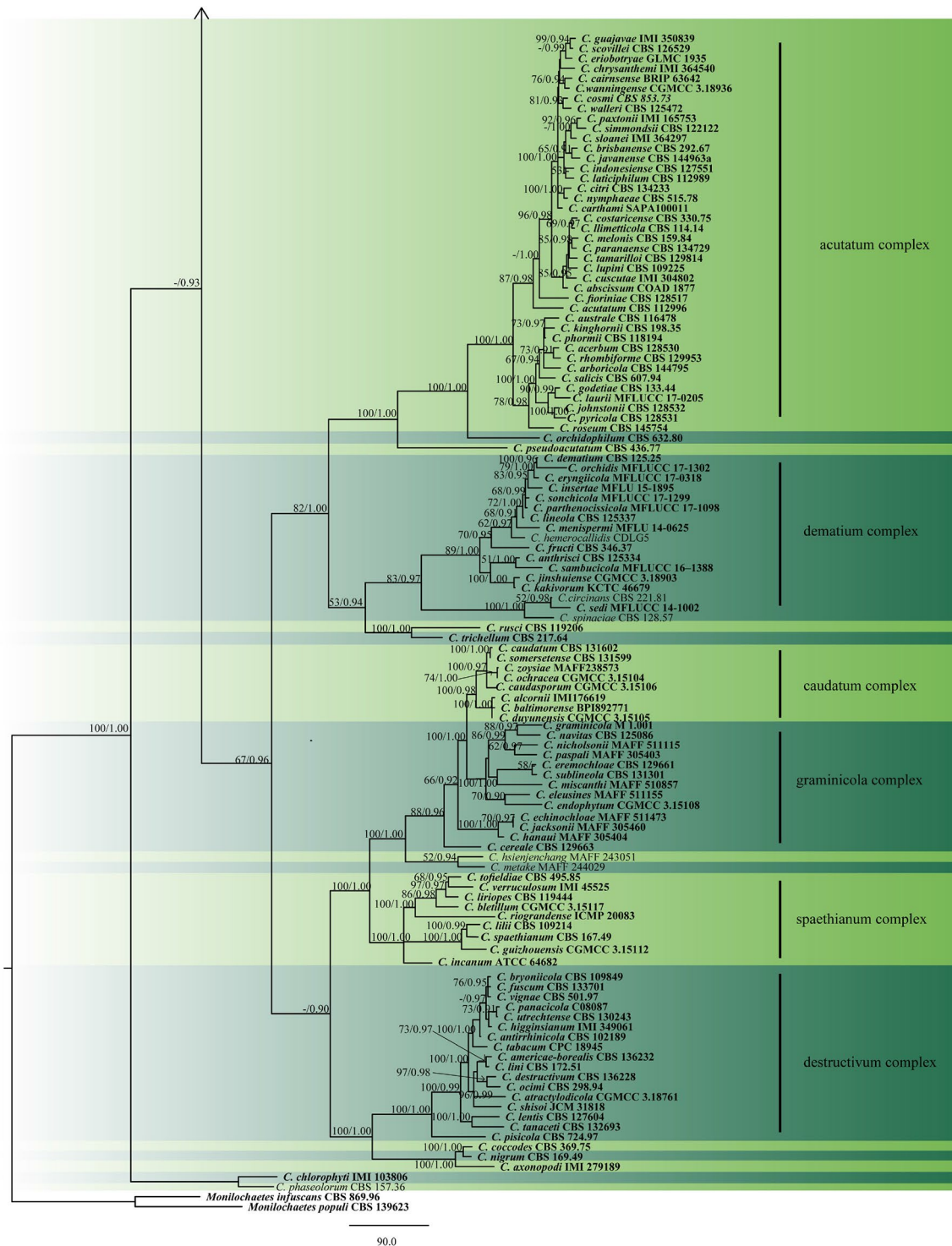


Fig. 36 (continued)

Hosts—Wide host range including, *Actinidia deliciosa*, *Citrus reticulata*, *Dioscorea* species, *Fragaria* × *ananassa*, *Mangifera indica*, *Manihot esculenta*, *Prunus* species, *Psidium guajava*, *Solanum melongena*, *Solanum lycopersicum* and *Vitis* species (Farr and Rossman 2020).

Pathogen biology, disease cycle and epidemiology

The pathogen reproduces asexually. Mucor rot often develops by infecting punctured wounds and cracks on the surface of the fruit, stem end or calyx of the host. In the early stages of the infection, the fruit becomes soft and

Table 22 DNA barcodes available for *Colletotrichum*, isolates used in the phylogenetic analyses

Species name	Isolate no	ITS	<i>gapdh</i>	<i>chs-1</i>	<i>act</i>	<i>tub2</i>	Complex
<i>Colletotrichum abscissum</i> [#]	COAD 1877*	KP843126	KP843129	KP843132	KP843141	KP843135	acutatum
<i>C. acerbum</i>	CBS 128530*	JQ948459	JQ948790	JQ949120	JQ949780	JQ950110	acutatum
<i>C. acidiae</i>	MFLUCC 17-2659*	MG996505	MH003691	MH003694	MH003697	MH003700	truncatum
<i>C. acutatum</i> [#]	CBS 112996*	JQ005776	JQ948677	JQ005797	JQ005839	JQ005860	acutatum
<i>C. aenigma</i> [#]	ICMP 18608*	JX010244	JX010044	JX009774	JX009443	JX010389	gloeosporioides
<i>C. aericola</i> [#]	CGMCC 3.19667*	MK914635	MK935455	MK935541	MK935374	MK935498	gloeosporioides
<i>C. aeshynomene</i> [#]	ICMP 17673	JX010176	JX009930	JX009799	JX009483	JX010392	gloeosporioides
<i>C. agaves</i>	CBS 118190*	DQ286221					singleton
<i>C. alcornii</i>	IMI176619*	JX076858					caudatum
<i>C. alatae</i> [#]	CBS 304.67*	JX010190	JX009990	JX009837	JX009471	JX010383	gloeosporioides
<i>C. alienum</i> [#]	ICMP 12071*	JX010251	JX010028	JX009882	JX009572	JX010411	gloeosporioides
<i>C. americanae-borealis</i> [#]	CBS 136232*	KM105224	KM105579	KM105294	KM105434	KM105504	destructivum
<i>C. annellatum</i>	CBS 129826*	JQ005222	JQ005309	JQ005396	JQ005570	JQ005656	boninense
<i>C. anthrisci</i>	CBS 125334*	GU227845	GU228237	GU228335	GU227943	GU228139	dematium
<i>C. antirrhinicola</i>	CBS 102189*	KM105180	KM105531	KM105250	KM105390	KM105460	destructivum
<i>C. aotearoa</i>	ICMP 18537*	JX010205	JX010005	JX009853	JX009854	JX010420	gloeosporioides
<i>C. araceaerum</i>	CGMCC 3.14982*	KX853166	KX893585		KX893577	KX893581	singleton
<i>C. arboricola</i> [#]	CBS 144795*	MH817944	MH817950		MH817956	MH817962	acutatum
<i>C. artocarpicola</i> [#]	MFLUCC 18-1167*	MN415991	MN435568	MN435569	MN435570	MN435567	gloeosporioides
<i>C. arxii</i>	CBS 132511*	KF687716	KF687843	KF687780	KF687802	KF687881	gigasporum
<i>C. asianum</i> [#]	ICMP 18580*	JX010196	JX010053	JX009867	JX009584	JX010406	gloeosporioides
<i>C. atractylodiolica</i>	CGMCC 3.18761*	KR149280	KR259334	KR259333	KR132243	KU058178	destructivum
<i>C. australe</i>	CBS 116478*	JQ948455	JQ948786	JQ949116	JQ949776	JQ950106	acutatum
<i>C. axonopodi</i>	IMI 279189/279189AA	EU554086					singleton
<i>C. beeveri</i>	CBS 128527*	JQ005171	JQ005258	JQ005345	JQ005519	JQ005605	boninense
<i>C. baltimorense</i>	BPI892771*	JX076866					caudatum
<i>C. bidentis</i>	COAD 1020*	KF178481	KF178506	KF178530	KF178578	KF178602	orbiculare
<i>C. bletillum</i>	CGMCC 3.15117*	JX625178	KC843506		KC843542	JX625207	spathianum
<i>C. boninense</i> [#]	CBS 123755*	JQ005153	JQ005240	JQ005327	JQ005501	JQ005588	boninense
<i>C. brasiliense</i>	CBS 128501*	JQ005235	JQ005322	JQ005409	JQ005583	JQ005669	boninense
<i>C. brassicicola</i>	CBS 101059*	JQ005172	JQ005259	JQ005346	JQ005520	JQ005606	boninense
<i>C. brevisporum</i> [#]	BCC 38876*	JN050238	JN050227		JN050216	JN050244	magnum
<i>C. brisbanense</i>	CBS 292.67*	JQ948291	JQ948621	JQ948952	JQ949612	JQ949942	acutatum
<i>C. bryoniicola</i>	CBS 109849*	KM105181	KM105532	KM105251	KM105391	KM105461	destructivum
<i>C. cacao</i> [#]	CBS 119297*	MG600772	MG600832	MG600878	MG600976	MG601039	magnum
<i>C. cairnsense</i> [#]	BRIP 63642*	KU923672	KU923704	KU923710	KU923716	KU923688	acutatum
<i>C. camelliae</i> [#]	CGMCC3.14925*	KJ955081	KJ954782		KJ954363	KJ955230	gloeosporioides
<i>C. camelliae-japonicae</i>	CGMCC3.18118*	KX853165	KX893584		KX893576	KX893580	boninense
<i>C. carthami</i> [#]	SAPA100011*	AB696998				AB696992	acutatum
<i>C. catinaense</i> [#]	CBS 142417*	KY856400	KY856224	KY856136	KY855971	KY856482	boninense
<i>C. cattleyicola</i>	CBS 170.49*	MG600758	MG600819	MG600866	MG600963	MG601025	orchidearum
<i>C. cariniferi</i>	MFLUCC 14-0100*	MF448521				MH351274	singleton
<i>C. caudatum</i>	CBS 131602*	JX076860					caudatum
<i>C. caudasporum</i>	CGMCC 3.15106*	JX625162	KC843512		KC843526	JX625190	caudatum
<i>C. cereale</i> [#]	CBS 129663*	JQ005774		JQ005795	JQ005837	JQ005858	graminicola
<i>C. changpingense</i> [#]	MFLUCC 15-0022*	KP683152	KP852469	KP852449	KP683093	KP852490	gloeosporioides
<i>C. chlorophyti</i> [#]	IMI 103806*	GU227894	GU228286	GU228384	GU227992	GU228188	singleton
<i>C. chiangraiese</i>	MFLUCC 14-0119*	MF448522			MH376383	MH351275	gigasporum
<i>C. chrysanthem</i> [#]	IMI 364540*	JQ948273	JQ948603	JQ948934	JQ949594	JQ949924	acutatum
<i>C. chrysophillum</i>	URM7368*	KX094252	KX094183	KX094083	KX093982	KX094285	gloeosporioides

Table 22 (continued)

Species name	Isolate no	ITS	<i>gapdh</i>	<i>chs-1</i>	<i>act</i>	<i>tub2</i>	Complex
<i>C. ciggaro</i> [#]	ICMP 18539*	JX010230	JX009966	JX009800	JX009523	JX010434	gloeosporioides
<i>C. circinans</i>	CBS 221.81	GU227855	GU228247	GU228345	GU227953	GU228149	dematium
<i>C. citri</i>	CBS 134233*	KC293581	KC293741	KY856138	KY855973	KC293661	acutatum
<i>C. citricola</i> [#]	CBS 134228*	KC293576	KC293736	KC293792	KC293616	KC293656	boninense
<i>C. clidemiae</i>	ICMP 18658*	JX010265	JX009989	JX009877	JX009537	JX010438	gloeosporioides
<i>C. cliviicola</i> [#]	CBS 125375*	MG600733	MG600795	MG600850	MG600939	MG601000	orchidearum
<i>C. cobbittiense</i>	BRIP 66219a*	MH087016	MH094133	MH094135	MH094134	MH094137	gloeosporioides
<i>C. coccodes</i> [#]	CBS 369.75*	HM171679	HM171673	JQ005796	HM171667	JQ005859	singleton
<i>C. coelogyne</i>	CBS 132504*	MG600713	MG600776	MG600836	MG600920	MG600980	dracaenophilum
<i>C. colombiense</i>	CBS 129818*	JQ005174	JQ005261	JQ005348	JQ005522	JQ005608	boninense
<i>C. condaoense</i>	CBS 134299*	MH229914	MH229920	MH229926		MH229923	boninense
<i>C. conoides</i> [#]	CAUG17*	KP890168	KP890162	KP890156	KP890144	KP890174	gloeosporioides
<i>C. constrictum</i>	CBS 128504*	JQ005238	JQ005325	JQ005412	JQ005586	JQ005672	boninense
<i>C. cordylinicola</i> [#]	MFU 09-0551*	JX010226	JX009975	JX009864	HM470234	JX010440	gloeosporioides
<i>C. cosmi</i>	CBS 853.73*	JQ948274	JQ948604	JQ948935	JQ949595	JQ949925	acutatum
<i>C. costaricense</i>	CBS 330.75*	JQ948180	JQ948510	JQ948841	JQ949501	JQ949831	acutatum
<i>C. curcumae</i> [#]	IMI 288937*	GU227893	GU228285	GU228383	GU227991	GU228187	truncatum
<i>C. cuscutae</i>	IMI 304802*	JQ948195	JQ948525	JQ948856	JQ949516	JQ949846	acutatum
<i>C. cymbidiicola</i> [#]	IMI 347923*	JQ005166	JQ005253	JQ005340	JQ005514	JQ005600	boninense
<i>C. dacrycarpi</i>	CBS 130241*	JQ005236	JQ005323	JQ005410	JQ005584	JQ005670	boninense
<i>C. dematium</i> [#]	CBS 125.25*	GU227819	GU228211	GU228309	GU227917	GU228113	dematium
<i>C. destructivum</i> [#]	CBS 136228*	KM105207	KM105561	KM105277	KM105417	KM105487	destructivum
<i>C. doitungense</i>	MFLUCC 14-0128*	MF448524	MH049480		MH376385	MH351277	boninense
<i>C. dracaenophilum</i> [#]	CBS 118199*	JX519222	JX546707	JX519230	JX519238	JX519247	dracaenophilum
<i>C. duyunensis</i>	CGMCC 3.15105*	JX625160	KC843515		KC843530	JX625187	caudatum
<i>C. echinochloae</i>	MAFF 511473*	AB439811					graminicola
<i>C. eleusines</i>	MAFF 511155*	JX519218		JX519226	JX519234	JX519243	graminicola
<i>C. endophytica</i> [#]	MFLUCC 13-0418*	KC633854	KC832854		KF306258		gloeosporioides
<i>C. endophytum</i>	CGMCC 3.15108 *	JX625177	KC843521		KC843533	JX625206	graminicola
<i>C. eremochloae</i> [#]	CBS 129661*	JX519220		JX519228	JX519236	JX519245	graminicola
<i>C. eriobotryae</i> [#]	GLMC 1935*	MF772487	MF795423	MN191653	MN191648	MF795428	acutatum
<i>C. eryngicola</i>	MFLUCC 17-0318*	KY792726	KY792723	KY792720	KY792717	KY792729	dematium
<i>C. excelsum-altitudinum</i>	CGMCC 3.15130*	HM751815	KC843502		KC843548	JX625211	dracaenophilum
<i>C. euphorbiae</i>	CBS 134725*	KF777146	KF777131	KF777128	KF777125	KF777247	singleton
<i>C. falcatum</i> [#]	CBS 147945*	JQ005772		JQ005793	JQ005835	JQ005856	graminicola
<i>C. feijoicola</i>	CBS 144633 *	MK876413	MK876475		MK876466	MK876507	boninense
<i>C. fioriniae</i> [#]	CBS 128517*	JQ948292	JQ948622	JQ948953	JQ949613	JQ949943	acutatum
<i>C. fructi</i>	CBS 346.37*	GU227844	GU228236	GU228334	GU227942	GU228138	dematium
<i>C. fructicola</i> [#]	ICMP 18581*	JX010165	JX010033	JX009866	FJ907426	JX010405	gloeosporioides
<i>C. fructivorum</i> [#]	CBS 133125*	JX145145				JX145196	gloeosporioides
<i>C. fuscum</i> [#]	CBS 133701*	KM105174	KM105524	KM105244	KM105384	KM105454	destructivum
<i>C. fusiforme</i>	MFLU 13-0291*	KT290266	KT290255	KT290253	KT290251	KT290256	truncatum
<i>C. gigasporum</i> [#]	CBS 133266*	KF687715	KF687822	KF687761		KF687866	gigasporum
<i>C. gloeosporioides</i> [#]	CBS 112999*	JQ005152	JQ005239	JQ005326	JQ005500	JQ005587	gloeosporioides
<i>C. godetiae</i> [#]	CBS 133.44*	JQ948402	JQ948733	JQ949063	JQ949723	JQ950053	acutatum
<i>C. graminicola</i> [#]	M 1.001*	JQ005767		JQ005788	JQ005830	JQ005851	graminicola
<i>C. grevilleae</i>	CBS 132879*	KC297078	KC297010	KC296987	KC296941	KC297102	gloeosporioides
<i>C. grossum</i> [#]	CAUG7*	KP890165	KP890159	KP890153	KP890141	KP890171	gloeosporioides
<i>C. guajavae</i>	IMI 350839*	JQ948270	JQ948600	JQ948931	JQ949591	JQ949921	acutatum
<i>C. guizhouensis</i>	CGMCC 3.15112*	JX625158	KC843507		KC843536	JX625185	spathianum

Table 22 (continued)

Species name	Isolate no	ITS	<i>gapdh</i>	<i>chs-1</i>	<i>act</i>	<i>tub2</i>	Complex
<i>C. hanau</i>	MAFF 305404*	JX519217		JX519225		JX519242	graminicola
<i>C. hebeiense</i> [#]	MFLUCC13–0726*	KF156863	KF377495	KF289008	KF377532	KF288975	gloeosporioides
<i>C. hedericola</i>	MFLU 15-0689*	MN631384		MN635794	MN635795		gloeosporioides
<i>C. helleniense</i> [#]	CBS 142418*	KY856446	KY856270	KY856186	KY856019	KY856528	gloeosporioides
<i>C. henanense</i> [#]	CGMCC 3.17354*	KJ955109	KJ954810		KM023257	KJ955257	gloeosporioides
<i>C. hemerocallidis</i>	CDLG5	JQ400005	JQ400012	Q399998	JQ399991	JQ400019	dematium
<i>C. higginsianum</i> [#]	IMI 349061*	KM105184	KM105535	KM105254	KM105394	KM105464	destructivum
<i>C. hippeastri</i>	CBS 125376*	JQ005231	JQ005318	JQ005405	JQ005579	JQ005665	boninense
<i>C. horii</i> [#]	NBRC 7478*	GQ329690	GQ329681	JX009752	JX009438	JX010450	gloeosporioides
<i>C. hystricis</i> [#]	CBS 142411*	KY856450	KY856274	KY856190	KY856023	KY856532	gloeosporioides
<i>C. hsienjenchang</i>	MAFF 243051	AB738855		AB738846	AB738845		singleton
<i>C. incanum</i>	ATCC 64682*	KC110789	KC110807		KC110825	KC110816	spaethianum
<i>C. indonesiense</i>	CBS 127551*	JQ948288	JQ948618	JQ948949	JQ949609	JQ949939	acutatum
<i>C. insertae</i>	MFLU 15-1895*	KX618686	KX618684	KX618683	KX618682	KX618685	dematium
<i>C. jacksonii</i>	MAFF 305460*	JX519216		JX519224	JX519233	JX519241	graminicola
<i>C. jasminigenum</i>	CGMCC LLTX-01*	HM131513	HM131499		HM131508	HM153770	truncatum
<i>C. javanense</i> [#]	CBS 144963a*	MH846576	MH846572	MH846573	MH846575	MH846574	acutatum
<i>C. jiangxiense</i>	CGMCC 3.17363*	KJ955201	KJ954902		KJ954471	KJ955348	gloeosporioides
<i>C. jinshuiense</i> [#]	CGMCC 3.18903*	MG748077	MG747995	MG747913	MG747767	MG748157	dematium
<i>C. jishouense</i>	GMBC0209*	MH482929	MH681658		MH708135	MH727473	gigasporum
<i>C. johnstonii</i>	CBS 128532*	JQ948444	JQ948775	JQ949105	JQ949765	JQ950095	acutatum
<i>C. kahawae</i> [#]	IMI 319418*	JX010231	JX010012	JX009813	JX009452	JX010444	gloeosporioides
<i>C. kakivorum</i> [#]	KCTC 46679*	LC324781	LC324787	LC324783	LC324785	LC324791	dematium
<i>C. karstii</i> [#]	CORCG6*	HM585409	HM585391	HM582023	HM581995	HM585428	boninense
<i>C. kinghornii</i>	CBS 198.35*	JQ948454	JQ948785	JQ949115	JQ949775	JQ950105	acutatum
<i>C. laticiphilum</i> [#]	CBS 112989*	JQ948289	JQ948619	JQ948950	JQ949610	JQ949940	acutatum
<i>C. lauri</i>	MFLUCC 17-0205*	KY514347	KY514344	KY514341	KY514338	KY514350	acutatum
<i>C. ledebouriae</i>	CBS 141284*	KX228254			KX228357		singleton
<i>C. lentis</i> [#]	CBS 127604*	JQ005766	KM105597	JQ005787	JQ005829	JQ005850	destructivum
<i>C. liaoningense</i> [#]	CGMCC 3.17616*	KP890104	KP890135	KP890127	KP890097	KP890111	magnum
<i>C. lili</i>	CBS 109214/BBA 62147*	GU227810	GU228202	GU228300	GU227908	GU228104	spaethianum
<i>C. lini</i>	CBS 172.51*	JQ005765	KM105581	JQ005786	JQ005828	JQ005849	destructivum
<i>C. limetticola</i>	CBS 114.14*	JQ948193	JQ948523	JQ948854	JQ949514	JQ949844	acutatum
<i>C. limonicola</i> [#]	CBS 142410*	KY856472	KY856296	KY856213	KY856045	KY856554	boninense
<i>C. lindemuthianum</i> [#]	CBS 144.31*	JQ005779	JX546712	JQ005800	JQ005842	JQ005863	orbiculare
<i>C. lineola</i> [#]	CBS 125337*	GU227829	GU228221	GU228319	GU227927	GU228123	dematium
<i>C. liriopes</i> [#]	CBS 119444*	GU227804	GU228196	GU228294	GU227902	GU228098	spaethianum
<i>C. lobatum</i>	IMI 79736*	MG600768	MG600828	MG600874	MG600972	MG601035	magnum
<i>C. lupini</i> [#]	CBS 109225*	JQ948155	JQ948485	JQ948816	JQ949476	JQ949806	acutatum
<i>C. magnisporum</i>	CBS 398.84*	KF687718	KF687842	KF687782	KF687803	KF687882	gigasporum
<i>C. makassarensis</i> [#]	CBS 143664a*	MH728812	MH728820	MH805850	MH781480	MH846563	gloeosporioides
<i>C. magnum</i>	CBS 519.97*	MG600769	MG600829	MG600875	MG600973	MG601036	magnum
<i>C. malvarum</i>	CBS 521.97*	KF178480	KF178504	KF178529	KF178577	KF178601	orbiculare
<i>C. melonis</i> [#]	CBS 159.84*	JQ948194	JQ948524	JQ948855	JQ949515	JQ949845	acutatum
<i>C. menispermii</i>	MFLU 14-0625*	KU242357	KU242356	KU242355	KU242353	KU242354	dematium
<i>C. metake</i>	MAFF 244029	AB738859					singleton
<i>C. merremiae</i>	CBS 124955*	MG600765	MG600825	MG600872	MG600969	MG601032	magnum
<i>C. miscanthi</i>	MAFF 510857*	JX519221		JX519229	JX519237	JX519246	graminicola
<i>C. musae</i> [#]	CBS 116870*	HQ596292	HQ596299	JX009896	HQ596284	HQ596280	gloeosporioides
<i>C. musicola</i> [#]	CBS 132885*	MG600736	MG600798	MG600853	MG600942	MG601003	orchidearum

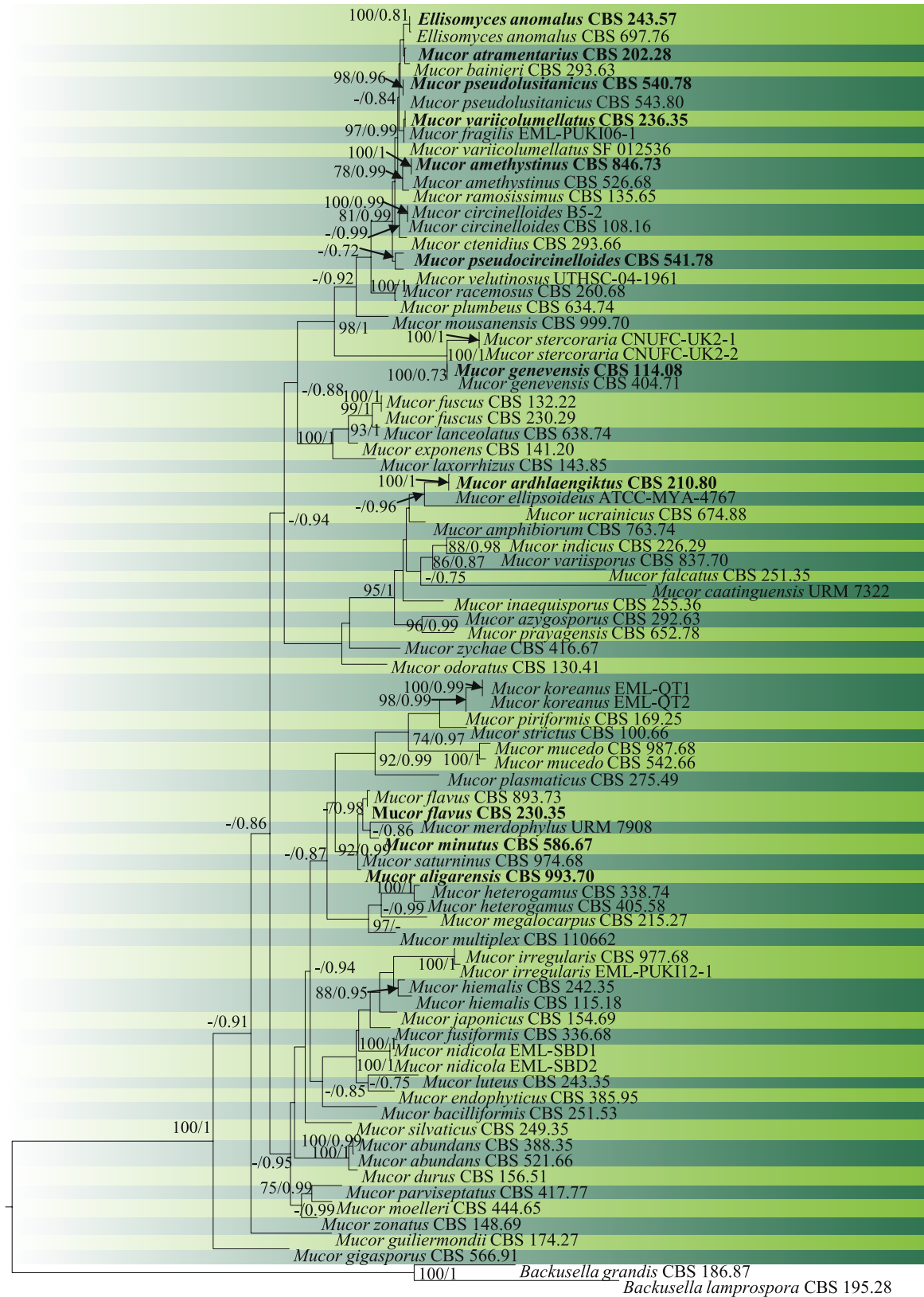
Table 22 (continued)

Species name	Isolate no	ITS	<i>gapdh</i>	<i>chs-1</i>	<i>act</i>	<i>tub2</i>	Complex
<i>C. navitas</i>	CBS 125086*	JQ005769		JQ005790	JQ005832	JQ005853	graminicola
<i>C. neosansevieraiae</i>	CPC 25127*	KR476747	KR476791		KR476790	KR476797	singleton
<i>C. nicholsonii</i>	MAFF 511115*	JQ005770		JQ005791	JQ005833	JQ005854	graminicola
<i>C. nigrum</i> [#]	CBS 169.49*	JX546838	JX546742	JX546693	JX546646	JX546885	singleton
<i>C. novae-zelandiae</i> [#]	CBS 128505*	JQ005228	JQ005315	JQ005402	JQ005576	JQ005662	boninense
<i>C. nupharicola</i> [#]	CBS 470.96*	JX010187	JX009972	JX009835	JX009437	JX010398	gloeosporioides
<i>C. nymphaeae</i> [#]	CBS 515.78*	JQ948197	JQ948527	JQ948858	JQ949518	JQ949848	acutatum
<i>C. ocimi</i>	CBS 298.94*	KM105222	KM105577	KM105292	KM105432	KM105502	destructivum
<i>C. ochracea</i>	CGMCC 3.15104*	JX625156	KC843513		KC843527	JX625183	caudatum
<i>C. okinawense</i> [#]	MAFF 240517*	MG600767	MG600827		MG600971	MG601034	magnum
<i>C. oncidii</i>	CBS 129828*	JQ005169	JQ005256	JQ005343	JQ005517	JQ005603	boninense
<i>C. orbiculare</i> [#]	CBS 570.97*	KF178466	KF178490	KF178515	KF178563	KF178587	orbiculare
<i>C. orchidearum</i> [#]	CBS 135131*	MG600738	MG600800	MG600855	MG600944	MG601005	orchidearum
<i>C. orchidophilum</i> [#]	CBS 632.80*	JQ948151	JQ948481	JQ948812	JQ949472	JQ949802	singleton
<i>C. orchidis</i>	MFLUCC 17-1302*	MK502144	MK496857	MK496855	MK496853	MK496859	dematium
<i>C. panacicola</i>	C08087*	GU935869	GU935849		GU944758	GU935889	destructivum
<i>C. pandanicola</i>	MFLUCC 17-0571*	MG646967	MG646934	MG646931	MG646938	MG646926	gloeosporioides
<i>C. panamense</i>	CBS 125386*	MG600766	MG600826	MG600873	MG600970	MG601033	magnum
<i>C. paranaense</i> [#]	CBS 134729*	KC204992	KC205026	KC205043	KC205077	KC205060	acutatum
<i>C. parallelophorum</i>	MFLUCC 14-0083*	MF448525	MK165695			MH351280	singleton
<i>C. parsonsiae</i>	CBS 128525*	JQ005233	JQ005320	JQ005407	JQ005581	JQ005667	boninense
<i>C. parthenocissicola</i>	MFLUCC 17-1098*	MK629452	MK639362	MK639356	MK639358	MK639360	dematium
<i>C. paspali</i>	MAFF 305403*	JX519219		JX519227	JX519235	JX519244	graminicola
<i>C. paxtonii</i>	IMI 165753*	JQ948285	JQ948615	JQ948946	JQ949606	JQ949936	acutatum
<i>C. petchii</i>	CBS 378.94*	JQ005223	JQ005310	JQ005397	JQ005571	JQ005657	boninense
<i>C. perseae</i> [#]	CBS 141365*	KX620308	KX620242		KX620145	KX620341	gloeosporioides
<i>C. phaseolorum</i> [#]	CBS 157.36	GU227896	GU228288	GU228386	GU227994	GU228190	dematium
<i>C. phormii</i>	CBS 118194*	JQ948446	JQ948777	JQ949107	JQ949767	JQ950097	acutatum
<i>C. phyllanthi</i> [#]	CBS 175.67*	JQ005221	JQ005308	JQ005395	JQ005569	JQ005655	boninense
<i>C. piperis</i> [#]	IMI 71397*	MG600760	MG600820	MG600867	MG600964	MG601027	orchidearum
<i>C. pisicola</i>	CBS 724.97*	KM105172	KM105522	KM105242	KM105382	KM105452	destructivum
<i>C. plurivorum</i> [#]	CBS 125474*	MG600718	MG600781	MG600841	MG600925	MG600985	orchidearum
<i>C. pseudoacutatum</i> [#]	CBS 436.77*	JQ948480	JQ948811	JQ949141	JQ949801	JQ950131	singleton
<i>C. pseudomajus</i>	CBS 571.88*	KF687722	KF687826	KF687779	KF687801	KF687883	gigasporum
<i>C. pseudotheobromicola</i> [#]	MFLUCC 18-1602*	MH817395	MH853675	MH853678	MH853681	MH853684	gloeosporioides
<i>C. psidii</i>	CBS 145.29*	JX010219	JX009967	JX009901	JX009515	JX010443	gloeosporioides
<i>C. proteae</i>	CBS 132882*	KC297079	KC297009	KC296986	KC296940	KC297101	gloeosporioides
<i>C. pyricola</i>	CBS 128531*	JQ948445	JQ948776	JQ949106	JQ949766	JQ950096	acutatum
<i>C. pyrifoliae</i> [#]	CGMCC 3.18902*	MG748078	MG747996	MG747914	MG747768	MG748158	singleton
<i>C. queenslandicum</i> [#]	ICMP 1778*	JX010276	JX009934	JX009899	JX009447	JX010414	gloeosporioides
<i>C. radialis</i>	CBS 529.93*	KF687719	KF687825	KF687762	KF687785	KF687869	gigasporum
<i>C. rhexiae</i>	CBS 133134*	JX145128				JX145179	gloeosporioides
<i>C. rhombiforme</i> [#]	CBS 129953*	JQ948457	JQ948788	JQ949118	JQ949778	JQ950108	acutatum
<i>C. riograndense</i>	ICMP 20083*	KM655299	KM655298	KM655297	KM655295	KM655300	spaethianum
<i>C. roseum</i>	CBS 145754*	MK903611	MK903603		MK903604	MK903607	acutatum
<i>C. rusci</i>	CBS 119206*	GU227818	GU228210	GU228308	GU227916	GU228112	singleton
<i>C. salicis</i> [#]	CBS 607.94*	JQ948460	JQ948791	JQ949121	JQ949781	JQ950111	acutatum
<i>C. salsolae</i> [#]	ICMP 19051*	JX010242	JX009916	JX009863	JX009562	JX010403	gloeosporioides
<i>C. sambucicola</i>	MFLUCC 16-1388*	KY098781	KY098780	KY098779	KY098778	KY098782	dematium
<i>C. sansevieraiae</i> [#]	MAFF 239721/Sa-1-2	LC179806	LC180130	LC180129	LC180127	LC180128	singleton

Table 22 (continued)

Species name	Isolate no	ITS	<i>gapdh</i>	<i>chs-1</i>	<i>act</i>	<i>tub2</i>	Complex
<i>C. scovillei</i> [#]	CBS 126529*	JQ948267	JQ948597	JQ948928	JQ949588	JQ949918	acutatum
<i>C. sedi</i>	MFLUCC14-1002*	KM974758	KM974755	KM974754	KM974756	KM974757	dematium
<i>C. serranegrense</i>	COAD 2100a*	KY400111		KY407894	KY407892	KY407896	gigasporum
<i>C. shisoii</i> [#]	JCM 31818*	MH660930	MH660931	MH660929	MH660928	MH660932	destructivum
<i>C. siamense</i> [#]	MFU 090230*	FJ972613	FJ972575	JX009865	FJ907423	FJ907438	gloeosporioides
<i>C. sidae</i>	CBS 504.97*	KF178472	KF178497	KF178521	KF178569	KF178593	orbiculare
<i>C. simmondsii</i> [#]	CBS 122122*	JQ948276	JQ948606	JQ948937	JQ949597	JQ949927	acutatum
<i>C. sloanei</i>	IMI 364297*	JQ948287	JQ948617	JQ948948	JQ949608	JQ949938	acutatum
<i>C. somersetense</i>	CBS 131599*	JX076862					caudatum
<i>C. sonchicola</i>	MFLUCC 17-1299*	KY962757	KY962754	KY962751	KY962748		dematium
<i>C. sojae</i>	ATCC 62257*	MG600749	MG600810	MG600860	MG600954	MG601016	orchidearum
<i>C. spaethianum</i> [#]	CBS 167.49*	GU227807	GU228199	GU228297	GU227905	GU228101	spaethianum
<i>C. spinaciae</i> [#]	CBS 128.57	GU227847	GU228239	GU228337	GU227945	GU228141	dematium
<i>C. spinosum</i>	CBS 515.97*	KF178474	KF178498	KF178523	KF178571	KF178595	orbiculare
<i>C. sublineola</i> [#]	CBS 131301*	JQ005771		JQ005792	JQ005834	JQ005855	graminicola
<i>C. sydowii</i>	CBS135819*	KY263783	KY263785	KY263787	KY263791	KY263793	singleton
<i>C. syzygiicola</i>	MFLUCC 10-0624*	KF242094	KF242156		KF157801	KF254880	gloeosporioides
<i>C. tabacum</i>	CPC 18945*	KM105204	KM105557	KM105274	KM105414	KM105484	destructivum
<i>C. tainanense</i>	CBS 143666a*	MH728818	MH728823	MH805845	MH781475	MH846558	gloeosporioides
<i>C. tanacetii</i> [#]	CBS 132693*	JX218228	JX218243	JX259268	JX218238	JX218233	destructivum
<i>C. tamarilloi</i> [#]	CBS 129814*	JQ948184	JQ948514	JQ948845	JQ949505	JQ949835	acutatum
<i>C. tebeesti</i>	CBS 522.97*	KF178473	KF178505	KF178522	KF178570	KF178594	orbiculare
<i>C. theobromicola</i> [#]	ICMP 18649*	JX010294	JX010006	JX009869	JX009444	JX010447	gloeosporioides
<i>C. temperatum</i>	CBS 133122*	JX145159				JX145211	gloeosporioides
<i>C. ti</i> [#]	ICMP 4832*	JX010269	JX009952	JX009898	JX009520	JX010442	gloeosporioides
<i>C. tofieldiae</i>	CBS 495.85*	GU227801	GU228193	GU228291	GU227899	GU228095	spaethianum
<i>C. tongrenense</i>	GZU_TRJ1-37/ GMBC0209*	MH482933	MH705332		MH717074	MH729805	dracaenophilum
<i>C. torulosum</i>	CBS 128544*	JQ005164	JQ005251	JQ005338	JQ005512	JQ005598	boninense
<i>C. trichellum</i>	CBS 217.64*	GU227812	GU228204	GU228302	GU227910	GU228106	singleton
<i>C. trifolii</i> [#]	CBS 158.83*	KF178478	KF178502	KF178527	KF178575	KF178599	orbiculare
<i>C. tropicale</i> [#]	CBS 124949*	JX010264	JX010007	JX009870	JX009489	JX010407	gloeosporioides
<i>C. tropicicola</i>	BCC 38877*	JN050240	JN050229		JN050218	JN050246	dracaenophilum
<i>C. truncatum</i> [#]	CBS 151.35*	GU227862	GU228254	GU228352	GU227960	GU228156	truncatum
<i>C. utrechtense</i>	CBS 130243*	KM105201	KM105554	KM105271	KM105411	KM105481	destructivum
<i>C. verruculosum</i>	IMI 45525*	GU227806	GU228198	GU228296	GU227904	GU228100	spaethianum
<i>C. vietnamense</i>	LD16(L2)*	KF687721	KF687832	KF687769	KF687792	KF687877	gigasporum
<i>C. vignae</i>	CBS 501.97*	KM105183	KM105534	KM105253	KM105393	KM105463	destructivum
<i>C. viniferum</i> [#]	GZAAS5.08601*	JN412804	JN412798		JN412795	JN412813	gloeosporioides
<i>C. vittalense</i>	CBS 181.82*	MG600734	MG600796	MG600851	MG600940	MG601001	orchidearum
<i>C. walleri</i>	CBS 125472*	JQ948275	JQ948605	JQ948936	JQ949596	JQ949926	acutatum
<i>C. wanningense</i> [#]	CGMCC 3.18936*	MG830462	MG830318	MG830302	MG830270	MG830286	acutatum
<i>C. watphaense</i>	MFLUCC 14-0123*	MF448523	MH049479		MH376384	MH351276	boninense
<i>C. wuxiense</i> [#]	CGMCC 3.17894*	KU251591	KU252045	KU251939	KU251672	KU252200	gloeosporioides
<i>C. xanthorrhoeae</i>	BRIP 45094*	JX010261	JX009927	JX009823	JX009478	JX010448	gloeosporioides
<i>C. yulongense</i>	CFCC 50818*	MH751507	MK108986	MH793605	MH777394	MK108987	gloeosporioides
<i>C. yunnanense</i>	CBS 132135*	JX546804	JX546706	JX519231	JX519239	JX519248	dracaenophilum
<i>C. zoysiae</i>	MAFF238573*	JX076871					caudatum

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains in bold and marked with an asterisk (*). Voucher strains are also in bold. Species confirmed with pathogenicity studies are marked with [#]



0.2

Fig. 37 Phylogram generated from RAxML analysis based on combined sequences of ITS and LSU of *Mucor* and *Backusella* species. Eighty-seven taxa were used for the analysis, which consisted of 1264 characters including gaps. The tree is rooted using *Backusella lamprospora* (CBS 195.28), and *B. grandis* (CBS 186.87). Likelihood of the best-scoring ML tree was -17553.567209 . The concatenated matrix contained 716 distinct alignment patterns with 21.98% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.302082, C = 0.168706, G = 0.219403, T = 0.309809; substitution rates AC = 0.749467, AG = 2.977575, AT = 1.651634, CG = 0.631954, CT = 4.647089, GT = 1.000000; gamma distribution shape parameter $\alpha = 0.302610$. The type species are in bold. Scale bar indicates the number of substitutions per site. ML bootstrap support values greater than 70% are shown near the nodes

appears water-soaked. The lesions formed are quasicircular or irregular, light to dark brown and the sporangiophores protrude through the wounds (Kwon and Hong 2005; Saito et al. 2016; Michailides and Spotts 1990). As the infection advances, the infected part disintegrates into a watery rot and the infection spreads and extends to all extremities of the fruit or even the surface of the container. The infected part is covered with a large mass of mycelium with erect sporangiophores and sporangia (Saito et al. 2016; Michailides and Spotts 1990). When tested, rotten apple and pear by some *Mucor* species release an alcoholic odour while *Mucor* rot in peaches and nectarines caused by *M. piriformis* emits a pleasant aromatic odour. At an advanced stage, *Mucor* rot can be distinguished from other rots caused by *Rhizopus* or *Gilbertella*. Differences are observed in the mycelial character, growth, sporangiophores and sporangia. For *Mucor* rot, erect, white or yellowish sporangiophore with grey to black sporangia is observed which covers the decay lesion densely. However, for *Rhizopus* rot, the mycelia are interwoven with stolons with dark sporangiophores and black sporangia. The sporangial wall eventually dries and falls apart while in *Mucor* rot, the sporangia absorb water from the sporangial wall which dissolves (Michailides and Spotts 1990).

Morphology-based identification and diversity

Mucor is characterized by fast-growing colonies. The sporangiophores are simple or branched without basal rhizoids. However, under some conditions, they form rhizoids. These species normally form globose sporangia, containing the columella and spores. The sporangium is non-apophysate with pigmented and ornamented zygosporangial walls. Arthrospores, chlamydospores, and zygosporangia may be produced by some species. The zygosporangia lack appendaged suspenders and broad aseptate or sparsely septate hyphae are commonly found in *Mucor* species (Nguyen et al. 2016). When spores from sporangia are released, a remaining collarette is observed. The sporangiospores are round or slightly elongated (Larone 1995; Sutton et al. 1998; de Hoog et al. 2000). With 76 accepted species, the genus is the largest and most studied group in Mucorales (Walther et al. 2019).

Molecular identification and diversity

The present taxonomy of *Mucor* is mostly based on morphological characters and interfertility tests. The genus was previously diagnosed using biological species recognition and morphological species recognition (Schipper 1973; Hermet et al. 2012). However, identification often fails with only morphology hence phylogenetic species recognition has been used to resolve species (Taylor et al. 2000). The use of multi-gene (ITS, *tefl* and *act*) phylogenetic analysis showed that *Mucor* is not monophyletic (Nguyen et al. 2017). An extensive study by Walther et al. (2013), using about 400 *Mucor* strains, led to a refinement in the classification of *Mucor* species. Phylogeny-based on 28S rDNA led to the transfer of some species to different groups and it was shown that some of these groups intermingled with other genera, such as *Chaetocladium* and *Helicostylum*, which do not belong to Mucoraceae. The use of five markers (ITS, *rpb1*, *tsr1*, *mcm7* and *cfs*) phylogeny by Wagner et al. (2019), combined with phenotypic studies, mating tests and the determination of the maximum growth temperatures revealed 16 phylogenetic species of which 14 showed distinct phenotypic traits and were recognized as discrete species.

Recommended genetic markers (genus level)—LSU and SSU

Recommended genetic markers (species level)—ITS and *rpb 1*

Accepted number of species—There are 735 species epithets in Index Fungorum (2020), however only 76 species have DNA sequence data (Table 23) (Walther et al. 2019).

References—Larone (1995), Sutton et al. (1998), de Hoog et al. (2000) (morphology), Nguyen et al. (2016, 2017), Walther et al. (2013, 2019), Wagner et al. (2019) (morphology and phylogeny).

98. *Phytophthora* de Bary, J. Roy. Agric. Soc. England, ser. 2 12: 240 (1876)

Background

Phytophthora is classified in the kingdom Straminipila within the diploid, alga-like Oomycetes in the Stramenopile clade of the Kingdom Chromista (Cavalier-Smith 1986; Dick 1995; Yoon et al. 2002; Wijayawardene et al. 2020). *Phytophthora* consists of about 130 described species with many important plant pathogens. The Oomycota are biologically different from main fungal groups within the Kingdom Fungi (Corliss 1994; Cavalier-Smith 1998). For example, their cell walls are made primarily of cellulose instead of chitin as in most fungi and they cannot synthesize β -hydroxysterols, which is vital for synthesizing hormones that regulate sexual reproduction (Hyde et al. 2014). Another important difference is that oomycetes are diploid throughout their life cycle. One similarity between *Phytophthora* species and Eumycotan fungi is that they both produce hyphae.

Classification—Oomycota, Peronosporales, Peronosporaceae

Type species—*Phytophthora infestans* (Mont.) de Bary

Distribution—worldwide

Disease symptoms—blight, canker, dieback, root rots and wilt

Species can have a large impact on agriculture (e.g. *Phytophthora infestans*, potato late blight), arboriculture (e.g. *Phytophthora ramorum*, sudden oak death) and whole ecosystems (e.g. *Phytophthora cinnamomi* in Australia). *Phytophthora* species damage plants by killing the tissues and resulting necrosis can be seen in leaves, stems or roots. Some species can cause multiple symptoms on a single host, or cause different symptoms on different hosts (Jung and Blaschke 1996).

Blight: Initial symptom is the development of a “water-soaked” appearance, which progresses into brown or black irregular-shaped spots or wedge-shaped lesions. These lesions are usually not surrounded by a yellow halo (Babadoost 2004; Pande et al. 2011; Ali et al. 2017).

Canker: A dark discoloured necrotic lesion in the inner bark of a tree can be seen often on the stem or branches. However, generally, cankers are visible once the outer bark is removed. Cankers are often seen with a reddish-brown liquid that oozes through the bark (Davidson et al. 2002; Jung et al. 2018).

Dieback: Death of shoot tips, twigs and branch tips can be observed. The infection progresses towards the main stem accompanied by a loss of foliage (Kuske and Benson 1983; Akilli et al. 2013).

Decline and Death: This is a gradual process that will take place over several years. Plants fail to grow and the canopy becomes thin due to loss of foliage. Then the whole canopy or sections of the canopy may die (Marais 1980; Belisario et al. 2004; González et al. 2020).

Rot: Dark discoloured rotten tissues that are common on roots, but sometimes extend above the soil surface. However, collar rot occurs at the base of the trunk and extends just below the soil line (Jung and Blaschke 1996; Graham et al. 2011; Summerell and Liew 2020).

Wilting: This is the first above-ground symptom of root rot. Foliage becomes flaccid due to lack of water intake (Vettraino et al. 2009; Xiong et al. 2019).

Phytophthora causes disease in important agricultural and ecological plants. *Phytophthora infestans* was responsible for the Irish potato famine from 1845 to 1852, causing the death of over 1 million people. *Phytophthora ramorum* has resulted in the death of millions of coast live oak, tanoak and Japanese larch trees, thus altering the forest ecosystems in California and Oregon, USA (Goheen et al. 2002; Rizzo et al. 2002, 2005).

Hosts—*Phytophthora agathidicida* (commonly known as kauri dieback), which causes kauri death, is considered as one of the world’s most feared fungi (Hyde et al. 2018a). An extensive survey in previously unexplored ecosystems such as natural forests (Rea et al. 2010; Vettraino et al. 2011; Jung et al. 2011, 2017; Reeser et al. 2013), streams (Reeser et al. 2007; Bezuidenhout et al. 2010; Yang et al. 2016; Braze

et al. 2017), riparian ecosystems (Brasier et al. 2003, 2004; Hansen et al. 2012), and irrigation systems (Hong et al. 2010, 2012; Yang et al. 2014a, b) has led an exponential increase in the number of species.

Pathogen biology, disease cycle and epidemiology

Morphological based identification and diversity

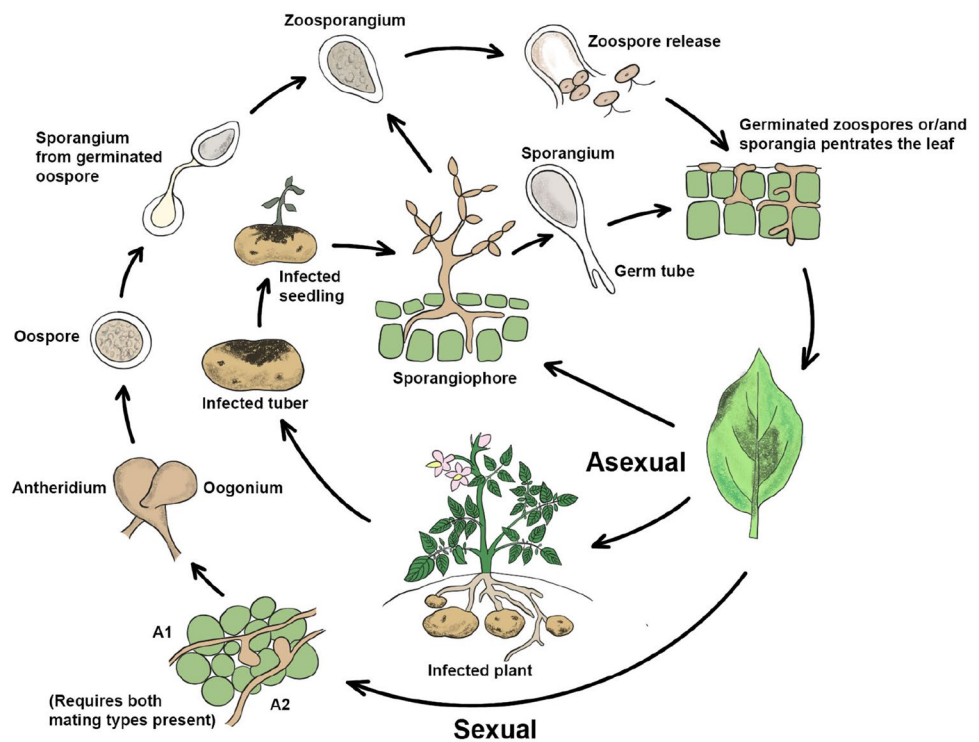
Species-level classification is based on the morphological characterization of reproductive structures including the sporangium (asexual) and oospore (sexual) as well as the production of chlamydospores (Martin et al. 2012). Characteristics that are important for species classification include the diameter of the oogonium and oospore, thickness of the oospore wall, whether or not the oospore fills the oogonium, ornamentation on the oogonial wall, and mode of attachment of the antheridium (Hyde et al. 2014). Identification and classification of *Phytophthora* species into morphological groups based on several characteristics was initially based on the key provided by Waterhouse (1963), which was later updated by Stamps et al. (1990).

Molecular based identification and diversity

Phytophthora has been historically placed in the *Pythiales* with *Pythium* and related genera, however recent phylogenetic analysis with the large (LSU) or small (SSU) rDNA sequences or *cox2* gene has indicated a closer relationship with downy mildew and white rusts (*Albugo*.) in the *Peronosporales* (Beakes and Sekimoto 2009; Thines et al. 2009). Additional multigene analyses are vital to clarify the relationship between the *Peronosporales* and *Pythium*. Early efforts focusing on the phylogenetic relationships in *Phytophthora* used nuclear-encoded rDNA, primarily the ITS region (Crawford et al. 1996; Cooke and Duncan 1997; Förster et al. 2000). The first comprehensive study was based on the phylogenetic study of the ITS region (Cooke et al. 2000). The study by Kroon et al. (2004) was based on analysis using two nuclear (*tef1*, *tub2*) and two mitochondrial (*cox1* and *nad1*) genes. Subsequent phylogenetic analysis was based on sequences of seven nuclear genetic markers (60S ribosomal protein L10, *tub2*, enolase, heat shock protein90, large subunit rDNA, *TigA* gene fusion and *tef1*) which divided the species into 10 well-supported clades (Blair et al. 2008). The phylogenetic study by Martin et al. (2014) was based on seven nuclear and four mitochondrial genes (*cox2*, *nad9*, *rps10* and *secY*). More recently, an extensive study of the genus by Yang et al. (2017) was based on sequences of seven nuclear genetic markers as in Blair et al. (2008).

The number of described species in *Phytophthora* was approximately 55 in 1999, but since then there has been a significant increase in the number of species nearly doubling the number of described species to 105 (Brasier 2007), and over 128 species (Hyde et al. 2014). Additional species have since been described, for example, *P. coccis* (Weir et al. 2015), *P. crassamura* (Scanu et al. 2015), *P. attenuata*, *P.*

Fig. 38 Disease cycle of *Phytophthora infestans* (redrawn from Bengtsson 2013)



xheterohybrida, *P. xincrassata* (Jung et al. 2017) bringing the total to over 150 species (Jung et al. 2019). The phylogenetic tree constructed is presented in Fig. 39 and the accepted species are given in Table 24.

Recommended genetic markers (genus level)—LSU, SSU and *cox2*

Recommended genetic markers (species level)—LSU, *tub2* and *cox2*

Accepted number of species—There are 317 epithets listed in Index Fungorum (2020), however only 162 species have DNA sequence data (Table 24).

References—Waterhouse (1963), Stamps et al. (1990) (morphology); Crawford et al. (1996), Cooke and Duncan (1997), Cooke et al. (2000), Förster et al. (2000), Brasier (2007), Blair et al. (2008) (morphology and phylogeny); Hyde et al. (2014) (phylogeny and accepted species) (Fig. 40).

99. *Pythium* Pringsh., Jb. wiss. Bot. 1: 304 (1858)

Background

Pythium is the largest and most comprehensively studied genus in *Pythiaceae sensu lato*, order *Peronosporales sensu lato*, class *Peronosporomycetes*, phylum Oomycota, and kingdom Straminipila (Beakes et al. 2014). Pringsheim (1858) described the genus. However, the initial classification of *Pythium* has changed many times based on several studies using morphological characteristics (Uzuhashi et al. 2010). *Pythium* comprises of more than 230 extant species (Hyde et al. 2014), however, identification of species has always been problematic due to limited morphological characters,

difficulty in isolating some taxa and lack of molecular data for certain species (Lévesque and de Cock 2004).

Classification—Oomycota, Pythiales, Pythiaceae

Type species—*Pythium monospermum* Pringsh. (Pringsheim 1858)

Distribution—worldwide

Disease symptoms—generally cause rot of fruit, roots and stem including pre- or post-emergence damping-off of seeds and seedlings.

Pythium causes crown and root rot in mature plants, where plants suddenly wilt during warm and sunny weather and when plants have their first heavy fruit load. Often, upper leaves of infected plants wilt in the day and recover overnight. However, plants eventually die (Craft and Nelson 1996; Postma et al. 2000). The first symptoms of *Pythium* root infections include stunting. In the root system, initial symptoms are brown to dark-brown lesions on root tips and feeder roots. As the disease progresses, symptoms are soft, brown, stubby roots and lack of feeder roots. In larger roots, the outer root tissue or cortex peels away, leaving the string-like vascular bundles underneath (Postma et al. 2000; Moorman et al. 2002; Al-Mahmooli et al. 2015). *Pythium* rot also occurs in the crown at the stem base. In cucumber, diseased crowns turn orange-brown, often with a soft rot at the base, while in strawberry seedling roots have dark brown, water-soaked rot and rotten crowns (Columbia and English 1988; Ishiguro et al. 2014). Several species of *Pythium* cause blight of turfgrass, which initially appears as “greasy” water-soaked areas, but later turn brown and grey (Vencelli and Powell 2008).

Fig. 39 Maximum likelihood of *Phytophthora* based on the concatenated seven nuclear genetic markers (60S Ribosomal protein L10 (60S), beta-tubulin (*tub*), elongation factor 1 alpha (*tefl*), enolase (*Enl*), heat shock protein 90 (*hsp90*), 28S ribosomal DNA (28S), and *tigA* gene fusion protein (*TigA*)). ML bootstrap support values over 60% are indicated and BYPP ≥ 0.90 are shown respectively near the nodes. The tree was rooted with *Phytophthiumvexans* and *Pythium undulatum* as the our group. Likelihood of the best scoring ML tree was -114471.902046 . Estimated base frequencies were as follows: A = 0.216570, C = 0.275568, G = 0.312230, T = 0.195632; substitution rates AC = 0.414835, AG = 1.176570, AT = 0.600142, CG = 0.970565, CT = 5.227735, GT = 1.000000

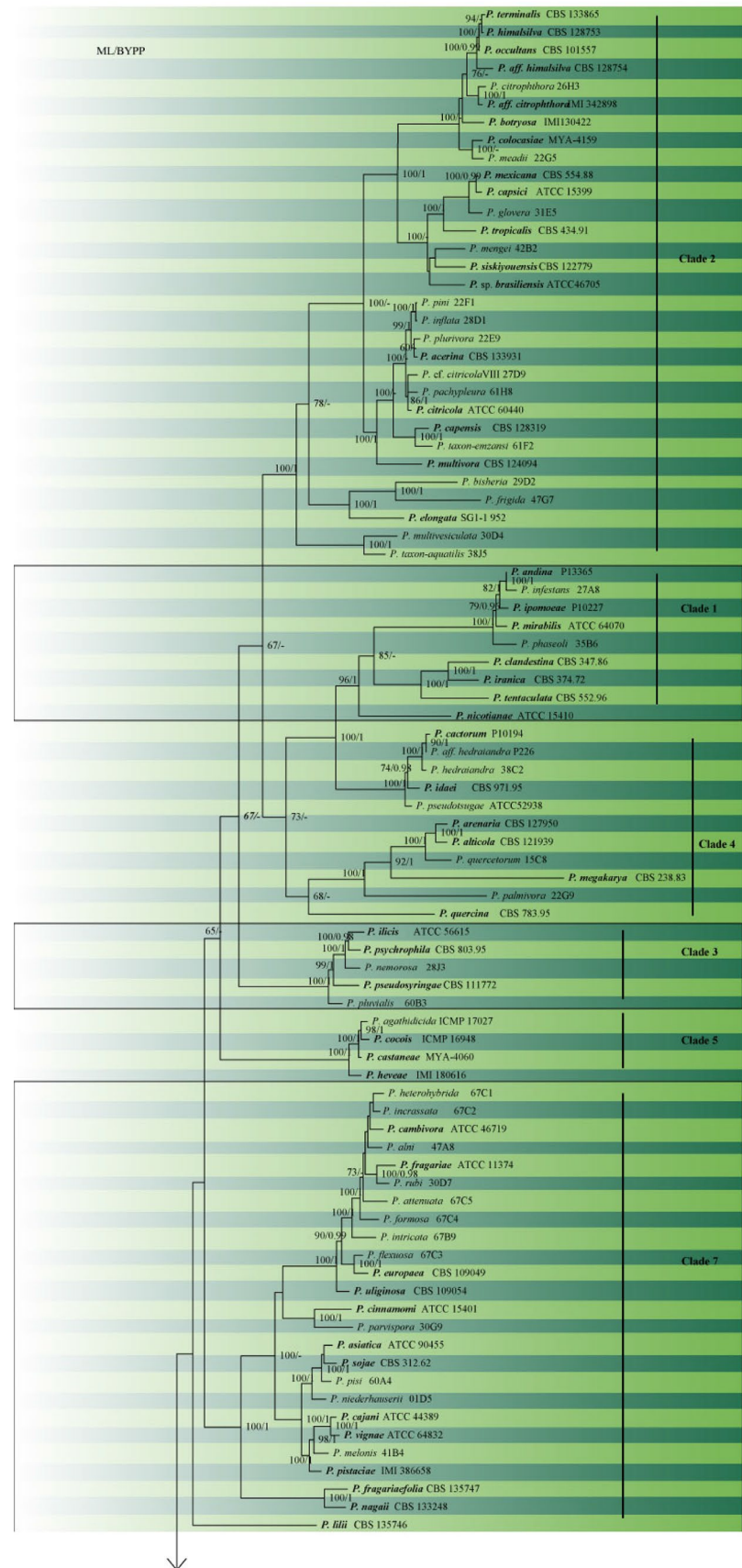


Fig. 39 (continued)

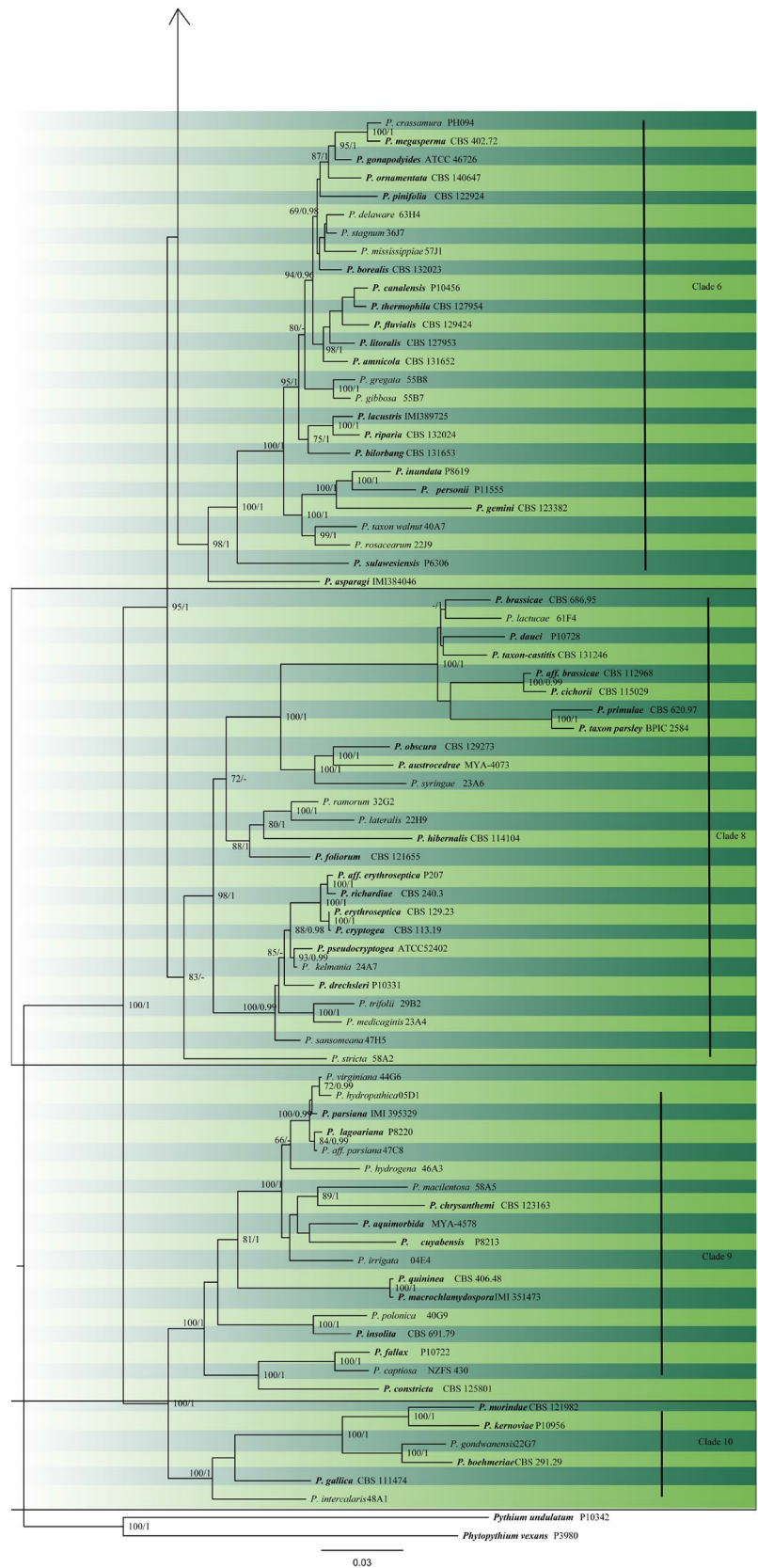


Table 23 DNA barcodes available for *Mucor*

Species	Isolate	ITS	LSU
<i>Mucor abundans</i>	CBS 388.35	JN206111	NG_063979
	CBS 521.66	JN206110	JN206457
<i>M. aligarensis</i>	CBS 993.70*		JN206461
<i>M. ambiguus</i>	CBS 126943	MH864344	MH875788
<i>M. amphibiorum</i>	CBS 763.74	NR_103615	NG_057877
<i>M. ardhaengiktus</i>	CBS 210.80*	NR_152960	JN206504
<i>M. atramentarius</i>	CBS 202.28*	MH854979	JN206418
<i>M. amethystinus</i>	CBS 846.73*	JN206014	
	CBS 526.68	JN206015	JN206426
<i>M. azygosporus</i>	CBS 292.63*	NR_103639	NG_057928
<i>M. bacilliformis</i>	CBS 251.53*	NR_145285	NG_057916
<i>M. bainieri</i>	CBS 293.63*	NR_103628	JN206424
<i>M. caatinguensis</i>	URM 7322		NG_060334
<i>M. circinelloides</i>	B5-2	KT876701	
	CBS 108.16	JN205954	
<i>M. ctenidius</i>	CBS 293.66	MH858796	JN206417
<i>M. durus</i>	CBS 156.51*	NR_145295	NG_057918
<i>M. ellipsoideus</i>	ATCC MYA-4767*	NR_111683	NG_042602
<i>M. endophyticus</i>	CBS 385.95*	NR_111661	NG_057970
<i>M. exponens</i>	CBS 141.20	MH854686	JN206441
<i>M. falcatus</i>	CBS 251.35*	NR_103647	NG_057931
<i>M. flavus</i>	CBS 230.35*	JN206061	JN206464
	CBS 893.73		JN206465
<i>M. fragilis</i>	EML-PUKI06-1	KY047147	
<i>M. fuscus</i>	CBS 132.22	JF723619	
	CBS 230.29	JN206204	
<i>M. fusiformis</i>	CBS 336.68*	NR_111660	NG_057915
<i>M. gigasporus</i>	CBS 566.91*	NR_103646	NG_057926
<i>M. genevensis</i>	CBS 114.08*	HM623318	
	CBS 404.71	JN206042	
<i>M. guiliermondii</i>	CBS 174.27*	NR_103636	NG_057923
<i>M. heterogamus</i>	CBS 338.74	JN206169	JN206488
	CBS 405.58	JN206167	
<i>M. hiemalis</i>	CBS 242.35	JN206134	
	CBS 115.18	JN206127	
<i>M. inaequisporus</i>	CBS 255.36	JN206177	NG_057929
<i>M. indicus</i>	CBS 226.29*	NR_077173	NG_057878
<i>M. irregularis</i>	CBS 977.68	JX976259	
	EML-PUKI12-1	KY047151	
<i>M. japonicus</i>	CBS 154.69	JN206158	JN206446
<i>M. koreanus</i>	<i>EML-QT1*</i>	KT936259	
	<i>EML-QT2</i>	KT936260	
<i>M. lanceolatus</i>	CBS 638.74	JN206205	JN206443
<i>M. laxorrhizus</i>	CBS 143.85*	NR_103642	NG_057914
<i>M. luteus</i>	CBS 243.35	JX976254	
<i>M. megalocarpus</i>	CBS 215.27*	NR_145286	NG_057925
<i>M. merdophylus</i>	URM-7908	MK775467	MK775466
<i>M. minutus</i>	CBS 586.67*	JN206048	JN206463
<i>M. moelleri</i>	CBS 444.65*	MH858663	NG_057875
<i>M. mousanensis</i>	CBS 999.70*	NR_103629	NG_057912

Table 23 (continued)

Species	Isolate	ITS	LSU
<i>M. mucedo</i> [#]	CBS 542.66*	JN206086	JN206480
	CBS 987.68	JN206089	JN206480
<i>M. multiplex</i>	CBS 110662*	NR_111662	NG_057924
<i>M. nidicola</i>	EML-SBD1	KY047148	
	EML-SBD2	KY047149	
<i>M. odoratus</i>	CBS 130.41*	NR_145287	NG_057927
<i>M. parvisseptatus</i>	CBS 417.77	JN206108	JN206453
<i>M. piriformis</i> [#]	CBS 169.25*	NR_103630	NG_057874
<i>M. plasmaticus</i>	CBS 275.49		JN206483
<i>M. plumbeus</i>	CBS 634.74	HM999955	HM849677
<i>M. prayagensis</i>	CBS 652.78	JN206189	JN206498
<i>M. pseudolusitanicus</i>	CBS 540.78*	MF495059	
	CBS 543.80	MF495060	
<i>M. pseudocircinelloides</i>	CBS 541.78	JN206013	JN206431
<i>M. saturninus</i>	CBS 974.68*	NR_103635	JN206458
<i>M. stercorarius</i> [#]	CNUFC-UK2-1*	KX839689	
	CNUFC-UK2-2	KX839680	
<i>M. strictus</i>	CBS 100.66*	JN206035	JN206477
<i>M. racemosus</i>	CBS 260.68*	NR_126135	NG_055727
<i>M. ramosissimus</i>	CBS 135.65*	NR_103627	NG_056280
<i>M. silvaticus</i>	CBS 249.35	JN206122	JN206455
<i>M. ucrainicus</i>	CBS 674.88	JN206192	JN206507
<i>M. variisporus</i>	CBS 837.70*	NR_152951	NG_057972
<i>M. variicolumellatus</i>	CBS 236.35*	JN205979	JN206422.1
	SF012536	MF495054.1	
<i>M. velutinosus</i>	UTHSC-04-1961	JF299208	
<i>M. zonatus</i>	CBS 148.69*	NR_103638	NG_057917
<i>M. zychae</i>	CBS 416.67*	NR_103641	NG_057930
<i>Ellisomyces anomalus</i>	CBS 243.57*	NR_145284	NG_067365
	CBS 697.76	JN205993	

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold. Species confirmed with pathogenicity studies are marked with #

Several *Pythium* species are capable of causing fruit rot in numerous crops (Martin and Loper 1999). *Pythium* fruit rot is commonly known as a cottony leak or watery rot and occurs during wet weather or in poorly drained areas of fields (Ho and Abd-Elsalam 2020; Sharma et al. 2020a). Initial symptoms of the fruit rot are brownish, water-soaked lesions that quickly become large, watery, soft and rotten. The rot generally begins on the parts of fruit in contact with the soil. In cucumber, a brown to dark green blister can be seen on fruit before they become watery and rot. Later, white cottony mycelium can be seen on rotten tissues, especially during humid weather. *Pythium* fruit rot is most severe in poorly-drained fields during wet weather. The disease can render fruit unmarketable (Ho 2009; Sharma et al. 2020a).

Pre-emergence damping-off causes seeds and young seedlings to rot before they emerge from the growing medium in greenhouses, while post-emergence damping-off kills newly

emerged seedlings. In the latter, the pathogen causes a water-soaked, soft brown lesion at the stem base, near the soil line, that pinches off the stem causing the seedling to topple over and die (Weiland et al. 2012).

Hosts—*Pythium* has a wide range of hosts including species of Cucurbitaceae and Poaceae, *Ananas comosus*, *Arachis hypogaea*, *Brassica* sp., *Carica papaya*, *Beta vulgaris*, *Daucus carota* subsp. *sativus*, *Dendrobium* sp, *Solanum* sp. and *Zingiber officinale*. Some species are pathogens of algae, fungi, other oomycetes, nematodes, insects, animals and humans (Van der Plaäts-Niterink 1981; Czeuczuga et al. 2005; Kawamura et al. 2005; Hwang et al. 2009; Li et al. 2010; Weiland et al. 2012; Ho 2013; Hyde et al 2014). Several species inhabit different soils in cultivated and uncultivated fields including forest (Uzhashi et al 2010). *Pythium arrhenomanes*, *P. dissotocum*, *P. elongatum*, *P. myriotylum*, and *P. spinosum* are important pathogens of rice seedlings (Hendrix

Table 24 DNA barcodes available for *Phytophthora*

Species	Strain	60S	tub2	tefl	Enl	HSP90	28S	TigA
<i>Phytophthora ×alni</i>	47A8	KX251595	KX251596	KX251597	KX251598	KX251599	KX251600	KX251601
<i>P. ×heterohybrida</i>	67C1	KX251637	KX251638	KX251639	KX251640	KX251641	KX251642	KX251643
<i>P. ×incrassata</i>	67C2	KX251644	KX251645	KX251646	KX251647	KX251648	KX251649	KX251650
<i>P. ×stagnum</i> [#]	36J7	KX251368	KX251369	KX251370	KX251371	KX251372	KX251373	KX251374
<i>P. acerina</i> [#]	61H1=CBS 133931	KX250712	KX250713	KX250714	KX250715	KX250716	KX250717	KX250718
<i>P. aff. brassicae</i> [#]	CBS 112968	EU079880	EU079881	EU079882	EU079883	EU079884	EU079885	EU079886
<i>P. aff. citrophthora</i> [#]	IMI 342898	EU080384	EU080385	EU080386	EU080387	EU080388	EU080389	EU080390
<i>P. aff. erythroseptica</i>	33A1=P207	KX251979	KX251980	KX251981	KX251982	KX251983	KX251984	KX251985
<i>P. aff. hedraiaandra</i> [#]	33F4=P226	KX250411	KX250412	KX250413	KX250414	KX250415	KX250416	KX250417
<i>P. aff. himalsilva</i>	61G4=CBS 128754	KX250621	KX250622	KX250623	KX250624	KX250625	KX250626	KX250627
<i>P. aff. parsiana</i> [#]	47C8	KX252397	KX252398	KX252399	KX252400	KX252401	KX252402	N/A
<i>P. agathidicida</i> [#]	67D5=ICMP 17027	KX251076	KX251077	KX251078	KX251079	KX251080	KX251081	KX251082
<i>P. alticola</i>	47G5=CBS 121939	KX251006	KX251007	KX251008	KX251009	KX251010	KX251011	KX251012
<i>P. amnicola</i>	61G6=CBS 131652	KX251167	KX251168	KX251169	KX251170	KX251171	KX251172	KX251173
<i>P. andina</i> [#]	P13365	EU080182	EU080183	EU080184	EU080185	EU080186	EU080187	EU080188
<i>P. aquimorbida</i>	40A6=MYA-4578	KX252238	KX252239	KX252240	KX252241	KX252242	KX252243	KX252244
<i>P. arenaria</i>	55C2=CBS 127950	KX251013	KX251014	KX251015	KX251016	KX251017	KX251018	KX251019
<i>P. asiatica</i>	45G1=ATCC 90455	KX251651	KX251652	KX251653	KX251654	KX251655	KX251656	KX251657
<i>P. asparagi</i> [#]	33D7= IMI384046	KX251466	KX251467	KX251468	KX251469	KX251470	KX251471	KX251472
<i>P. attenuata</i>	67C5	KX251609	KX251610	KX251611	KX251612	KX251613	KX251614	KX251615
<i>P. austrocedrae</i>	41B5=MYA-4073	KX252161	KX252162	KX252163	KX252164	KX252165	KX252166	KX252167
<i>P. bilorbang</i> [#]	61G8=CBS 131653	KX251181	KX251182	N/A	KX251183	KX251184	KX251185	KX251186
<i>P. bisheria</i>	29D2	KX250873	KX250874	KX250875	KX250876	KX250877	KX250878	KX250879
<i>P. boehmeriae</i> [#]	45F9=CBS 291.29	EU080161	EU080162	EU080163	EU080164	EU080165	EU080166	EU080167
<i>P. borealis</i>	60B2=CBS 132023	KX251187	KX251188	KX251189	KX251190	KX251191	KX251192	KX251193
<i>P. botryosa</i> [#]	IMI130422=P6945	EU079934	EU079935	EU079936	EU079937	EU079938	EU079939	EU079940
<i>P. brassicae</i> [#]	29D8=CBS 686.95	KX251993	KX251994	KX251995	KX251996	KX251997	KX251998	KX251999
<i>P. cactorum</i> [#]	22E6=P10194	KX250369	KX250370	KX250371	KX250372	KX250373	KX250374	KX250375
<i>P. cajani</i> [#]	45F6=ATCC 44389	KX251679	KX251680	KX251681	KX251682	KX251683	KX251684	KX251685
<i>P. cambivora</i> [#]	22F6=ATCC 46719	KX251494	KX251495	KX251496	KX251497	KX251498	KX251499	KX251500
<i>P. capensis</i>	62C1=CBS 128319	KX250726	KX250727	KX250728	KX250729	KX250730	KX250731	KX250732
<i>P. capsici</i> [#]	22F4=ATCC 15399	KX250635	KX250636	KX250637	KX250638	KX250639	KX250640	KX250641
<i>P. captiosa</i> [#]	46H8=NZFS 430	KX252554	KX252555	KX252556	KX252557	KX252558	KX252559	KX252560
<i>P. castaneae</i>	22H6=MYA-4060	KX251083	KX251084	KX251085	KX251086	KX251087	KX251088	KX251089
<i>P. chrysanthemi</i> [#]	61F1=CBS 123163	KX252266	KX252267	KX252268	KX252269	KX252270	KX252271	KX252272
<i>P. cichorii</i>	62A8=CBS 115029	KX252007	KX252008	KX252009	KX252010	KX252011	KX252012	KX252013
<i>P. cinnamomi</i> [#]	23B2=ATCC 15401	KX251804	KX251805	KX251806	KX251807	KX251808	KX251809	KX251810
<i>P. citricola</i> [#]	33H8=ATCC 60440	KX250747	KX250748	KX250749	KX250750	KX250751	KX250752	KX250753
<i>P. citrophthora</i> [#]	26H3	KX250551	KX250552	KX250553	KX250554	KX250555	KX250556	KX250557
<i>P. clandestina</i>	32G1=CBS 347.86	EU079866	EU079867	EU079868	EU079869	EU079870	EU079871	EU079872
<i>P. cocois</i>	67D6=ICMP 16948	KX251104	KX251105	KX251106	KX251107	KX251108	KX251109	KX251110
<i>P. colcasiae</i> [#]	22F8=MYA-4159	KX250558	KX250559	KX250560	KX250561	KX250562	KX250563	KX250564
<i>P. constricta</i>	55C3=CBS 125801	KX252561	KX252562	KX252563	KX252564	KX252565	KX252566	KX252567
<i>P. crassamura</i>	66C9=PH094	KX251194	KX251195	KX251196	KX251197	KX251198	KX251199	KX251200
<i>P. cryptogea</i> [#]	61H9=CBS 113.19	KX251867	KX251868	KX251869	KX251870	KX251871	KX251872	KX251873
<i>P. dauci</i>	32E6=P10728	KX252028	KX252029	KX252030	KX252031	KX252032	KX252033	KX252034
<i>P. drechsleri</i> [#]	P10331	EU079506	EU079507	EU079508	EU079509	EU079510	EU079511	EU079512
<i>P. elongata</i>	33J3=SG1-1 952	KX250880	KX250881	KX250882	KX250883	KX250884	KX250885	KX250886
<i>P. erythroseptica</i>	61J2=CBS 129.23	KX251895	KX251896	KX251897	KX251898	KX251899	KX251900	KX251901
<i>P. europaea</i> [#]	62A2=CBS 109049	KX251522	KX251523	KX251524	KX251525	KX251526	KX251527	KX251528

Table 24 (continued)

Species	Strain	60S	tub2	tefl	Enl	HSP90	28S	TigA
<i>P. fallax</i> [#]	46J2=P10722	KX252568	KX252569	KX252570	KX252571	KX252572	KX252573	KX252574
<i>P. flexuosa</i>	67C3	KX251616	KX251617	KX251618	KX251619	KX251620	KX251621	KX251622
<i>P. fluvialis</i>	55B6=CBS 129424	KX251208	KX251209	KX251210	KX251211	KX251212	KX251213	KX251214
<i>P. foliorum</i> [#]	49J8=CBS 121655	KX252112	KX252113	KX252114	KX252115	KX252116	KX252117	KX252118
<i>P. formosa</i>	67C4	KX251623	KX251624	KX251625	KX251626	KX251627	KX251628	KX251629
<i>P. fragariae</i> [#]	22G6=ATCC 11374	KX251529	KX251530	KX251531	KX251532	KX251533	KX251534	KX251535
<i>P. fragariaefolia</i>	61H4=CBS 135747	KX251853	KX251854	KX251855	KX251856	KX251857	KX251858	KX251859
<i>P. frigida</i> [#]	47G7	KX250908	KX250909	KX250910	KX250911	KX250912	KX250913	KX250914
<i>P. gallica</i>	50A1=CBS 111474	KX252589	KX252590	KX252591	KX252592	KX252593	KX252594	KX252595
<i>P. gemini</i>	46H1=CBS 123382	KX251125	KX251126	KX251127	KX251128	KX251129	KX251130	KX251131
<i>P. gibbosa</i>	55B7	KX251215	KX251216	KX251217	KX251218	KX251219	KX251220	KX251221
<i>P. glovera</i>	31E5	KX250642	KX250643	KX250644	KX250645	KX250646	KX250647	KX250648
<i>P. gonapodyides</i> [#]	21J5=ATCC 46726	KX251229	KX251230	KX251231	KX251232	KX251233	KX251234	KX251235
<i>P. gondwanensis</i>	22G7	KX252603	KX252604	KX252605	KX252606	KX252607	KX252608	KX252609
<i>P. gregata</i> [#]	55B8	KX251243	KX251244	KX251245	KX251246	KX251247	KX251248	KX251249
<i>P. hedraiandra</i> [#]	38C2	KX250390	KX250391	KX250392	KX250393	KX250394	KX250395	KX250396
<i>P. heveae</i> [#]	22J1=IMI 180616	KX251111	KX251112	KX251113	KX251114	KX251115	KX251116	KX251117
<i>P. hibernalis</i> [#]	32F7=CBS 114104	KX252126	KX252127	KX252128	KX252129	KX252130	KX252131	KX252132
<i>P. himalsilva</i>	61G3=CBS 128753	KX250579	KX250580	KX250581	KX250582	KX250583	KX250584	KX250585
<i>P. hydrogena</i>	46A3	KX252280	KX252281	KX252282	KX252283	KX252284	KX252285	KX252286
<i>P. hydrophatica</i> [#]	05D1	KX252294	KX252295	KX252296	KX252297	KX252298	KX252299	KX252300
<i>P. idaei</i>	34D4=CBS 971.95	EU080129	EU080130	EU080131	EU080132	EU080133	EU080134	EU080135
<i>P. ilicis</i> [#]	23A7=ATCC 56615	KX250936	KX250937	KX250938	KX250939	KX250940	KX250941	KX250942
<i>P. infestans</i> [#]	27A8	KX250474	KX250475	KX250476	KX250477	KX250478	KX250479	KX250480
<i>P. inflata</i> [#]	28D1	KX250761	KX250762	KX250763	KX250764	KX250765	KX250766	KX250767
<i>P. insolita</i> [#]	38E1=CBS 691.79	EU080175	EU080176	EU080177	EU080178	EU080179	EU080180	EU080181
<i>P. intercalaris</i>	48A1	KX252617	KX252618	KX252619	KX252620	KX252621	KX252622	KX252623
<i>P. intricata</i>	67B9	KX251630	KX251631	KX251632	KX251633	KX251634	KX251635	KX251636
<i>P. inundata</i> [#]	P8619	EU080202	EU080203	EU080204	EU080205	EU080206	EU080207	EU080208
<i>P. ipomoeae</i> [#]	31B6=P10227	EU080844	EU080845	EU080846	EU080847	EU080848	EU080849	EU080850
<i>P. iranica</i> [#]	61J4=CBS 374.72	KX250439	KX250440	KX250441	KX250442	KX250443	KX250444	KX250445
<i>P. irrigata</i>	04E4	KX252308	KX252309	KX252310	KX252311	KX252312	KX252313	KX252314
<i>P. kernoviae</i>	46C8=P10956	EU080041	EU080042	EU080043	EU080044	EU080045	EU080046	KX252631
<i>P. lactucae</i>	61F4	KX252042	KX252043	KX252044	KX252045	KX252046	KX252047	KX252048
<i>P. lacustris</i> [#]	IMI389725=P10337	EU080530	EU080531	EU080532	EU080533	EU080534	EU080535	EU080536
<i>P. lateralis</i> [#]	22H9	KX252133	KX252134	KX252135	KX252136	KX252137	KX252138	KX252139
<i>P. lilii</i>	CBS 135746	AB856779	AB856782	AB856788	AB856791	AB856794	AB856797	AB856800
<i>P. litoralis</i>	55B9=CBS 127953	KX251278	KX251279	KX251280	KX251281	KX251282	KX251283	KX251284
<i>P. macilentosa</i>	58A5	KX252329	KX252330	KX252331	KX252332	KX252333	KX252334	KX252335
<i>P. macrochlamydospora</i> [#]	G231E9=IMI 351473	EU080658	EU080659	EU080660	N/A	EU080661	EU080662	EU080663
<i>P. meadii</i> [#]	22G5	KX250586	KX250587	KX250588	KX250589	KX250590	KX250591	KX250592
<i>P. medicaginis</i> [#]	23A4	KX251902	KX251903	KX251904	KX251905	KX251906	KX251907	KX251908
<i>P. megakarya</i> [#]	61J5=CBS 238.83	KX251034	KX251035	KX251036	KX251037	KX251038	KX251039	KX251040
<i>P. megasperma</i> [#]	62C7=CBS 402.72	KX251285	KX251286	KX251287	KX251288	KX251289	KX251290	N/A
<i>P. melonis</i> [#]	41B4	KX251700	KX251701	KX251702	KX251703	KX251704	KX251705	KX251706
<i>P. mengei</i>	42B2	KX250656	KX250657	KX250658	KX250659	KX250660	KX250661	KX250662
<i>P. mexicana</i>	45G4=CBS 554.88	KX250670	KX250671	KX250672	KX250673	KX250674	KX250675	KX250676
<i>P. mirabilis</i>	30C2=ATCC 64070	KX250488	KX250489	KX250490	KX250491	KX250492	KX250493	KX250494
<i>P. mississippiae</i>	57J1	KX251291	KX251292	KX251293	KX251294	KX251295	KX251296	KX251297
<i>P. morindae</i>	62B5=CBS 121982	KX252633	KX252634	KX252635	KX252636	KX252637	KX252638	KX252639

Table 24 (continued)

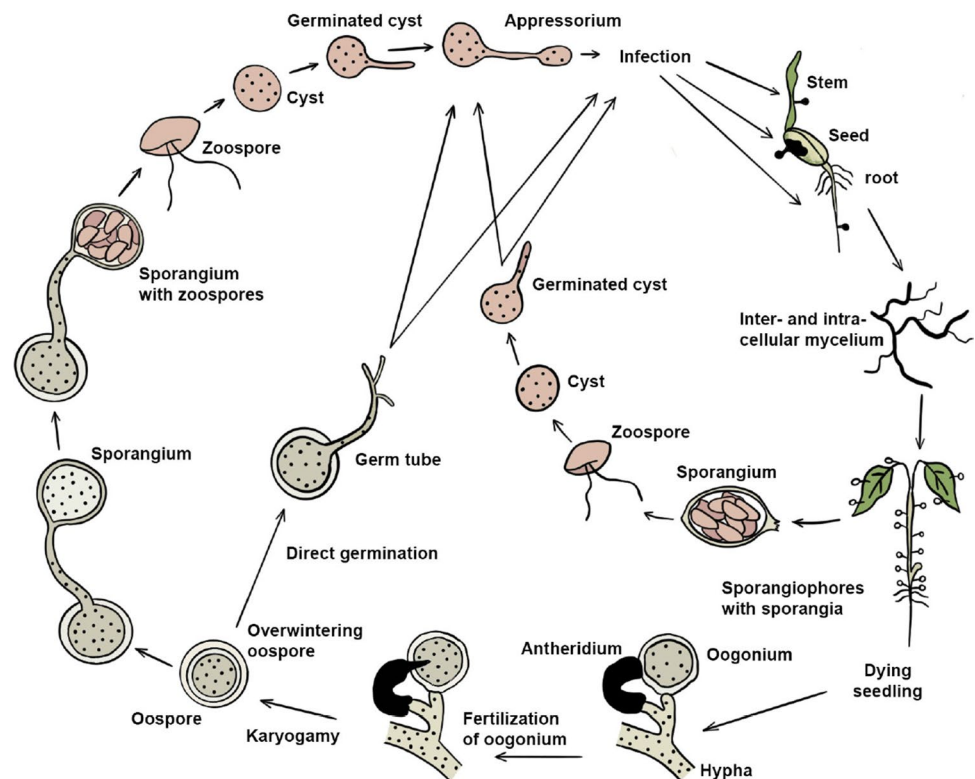
Species	Strain	60S	tub2	tefl	Enl	HSP90	28S	TigA
<i>P. multivesiculata</i> [#]	30D4	KX250922	KX250923	KX250924	KX250925	KX250926	KX250927	KX250928
<i>P. multivora</i> [#]	55C5=CBS 124094	KX250775	KX250776	KX250777	KX250778	KX250779	KX250780	KX250781
<i>P. nagaii</i>	61H5=CBS 133248	KX251860	KX251861	KX251862	KX251863	KX251864	KX251865	KX251866
<i>P. nemorosa</i>	28J3	KX250957	KX250958	KX250959	KX250960	KX250961	KX250962	KX250963
<i>P. nicotianae</i> [#]	22F9=ATCC 15410	KX250509	KX250510	KX250511	KX250512	KX250513	KX250514	KX250515
<i>P. niederhauserii</i> [#]	01D5	KX251714	KX251715	KX251716	KX251717	KX251718	KX251719	KX251720
<i>P. obscura</i>	60E9=CBS 129273	KX252175	KX252176	KX252177	KX252178	KX252179	KX252180	KX252181
<i>P. occultans</i> [#]	65B9=CBS 101557	KX250600	KX250601	KX250602	KX250603	KX250604	KX250605	KX250606
<i>P. ornamentata</i>	66D2=CBS 140647	KX251319	KX251320	KX251321	KX251322	KX251323	KX251324	KX251325
<i>P. pachypleura</i> [#]	61H8	KX250796	KX250797	KX250798	KX250799	KX250800	KX250801	KX250802
<i>P. palmivora</i> [#]	22G9	KX251055	KX251056	KX251057	KX251058	KX251059	KX251060	KX251061
<i>P. parsiana</i> [#]	47C3=IMI 395329	KX252357	KX252358	KX252359	KX252360	KX252361	KX252362	KX252363
<i>P. parvispora</i> [#]	30G9	KX251818	KX251819	KX251820	KX251821	KX251822	KX251823	KX251824
<i>P. phaseoli</i>	35B6	KX250502	KX250503	KX250504	KX250505	KX250506	KX250507	KX250508
<i>P. pini</i> [#]	22F1	KX250803	KX250804	KX250805	KX250806	KX250807	KX250808	KX250809
<i>P. pinifolia</i>	47H1=CBS 122924	KX251333	KX251334	KX251335	KX251336	KX251337	KX251338	KX251339
<i>P. pisi</i>	60A4	KX251735	KX251736	KX251737	KX251738	KX251739	KX251740	KX251741
<i>P. pistaciae</i> [#]	33D6=IMI 386658	KX251748	KX251749	KX251750	KX251751	KX251752	KX251753	KX251754
<i>P. plurivora</i> [#]	22E9	KX250817	KX250818	KX250819	KX250820	KX250821	KX250822	KX250823
<i>P. pluvialis</i> [#]	60B3	KX250971	KX250972	KX250973	KX250974	KX250975	KX250976	KX250977
<i>P. polonica</i>	40G9	KX252532	KX252533	KX252534	KX252535	KX252536	KX252537	KX252538
<i>P. primulae</i> [#]	29E9=CBS 620.97	KX252063	KX252064	KX252065	KX252066	KX252067	KX252068	KX252069
<i>P. pseudocryptogea</i> [#]	ATCC52402	EU080626	EU080627	EU080628	EU080629	EU080630	EU080631	N/A
<i>P. pseudosyringae</i> [#]	30A8=CBS 111772	KX250978	KX250979	KX250980	KX250981	KX250982	KX250983	KX250984
<i>P. pseudotsugae</i>	ATCC52938	EU080426	EU080427	EU080428	EU080429	EU080430	EU080431	EU080432
<i>P. psychrophila</i>	29J5=CBS 803.95	KX250992	KX250993	KX250994	KX250995	KX250996	KX250997	KX250998
<i>P. quercetorum</i>	15C8	KX251069	KX251070	KX251071	KX251072	KX251073	KX251074	KX251075
<i>P. quercina</i> [#]	30A4=CBS 783.95	KX252647	KX252648	KX252649	KX252650	KX252651	KX252652	KX252653
<i>P. quininea</i>	45F2=CBS 406.48	EU080107	EU080108	EU080109	N/A	KX252522	EU080110	KX252523
<i>P. ramorum</i> [#]	32G2	KX252147	KX252148	KX252149	KX252150	KX252151	KX252152	KX252153
<i>P. richardiae</i>	45F5=CBS 240.3	KX251923	KX251924	KX251925	KX251926	KX251927	KX251928	KX251929
<i>P. riparia</i>	60B1=CBS 132024	KX251347	KX251348	KX251349	KX251350	KX251351	KX251352	KX251353
<i>P. rosacearum</i>	22J9	KX251431	KX251432	KX251433	KX251434	KX251435	KX251436	KX251437
<i>P. rubi</i>	30D7	KX251550	KX251551	KX251552	KX251553	KX251554	KX251555	KX251556
<i>P. sansomeana</i> [#]	47H5	KX251944	KX251945	KX251946	KX251947	KX251948	KX251949	KX251950
<i>P. siskiyouensis</i> [#]	41B7=CBS 122779	KX250677	KX250678	KX250679	KX250680	KX250681	KX250682	KX250683
<i>P. sojae</i> [#]	22D8=CBS 312.62	KX251762	KX251763	KX251764	KX251765	KX251766	KX251767	KX251768
<i>P. sp. brasiliensis</i>	ATCC46705=P0630	EU080419	EU080420	EU080421	EU080422	EU080423	EU080424	EU080425
<i>P. sp. canalensis</i>	P10456	EU079569	EU079570	EU079571	EU079572	EU079573	EU079574	N/A
<i>P. sp. citricola VIII</i>	27D9	KX250838	KX250839	KX250840	KX250841	KX250842	KX250843	KX250844
<i>P. sp. cuyabensis</i>	P8213	EU080664	EU080665	EU080666	EU080667	EU080668	EU080669	EU080331
<i>P. sp. delaware</i>	63H4	KX251396	KX251397	KX251398	KX251399	KX251400	KX251401	KX251402
<i>P. sp. kelmania</i>	24A7	KX251986	KX251987	KX251988	KX251989	KX251990	KX251991	KX251992
<i>P. sp. lagoariana</i>	60B4=P8220	EU080358	KX252502	EU080359	EU080360	EU080361	EU080362	EU080363
<i>P. sp. personii</i>	P11555	EU080312	EU080313	EU080314	EU080315	EU080316	EU080317	EU080318
<i>P. sp. sulawesiensis</i>	P6306	EU080345	N/A	EU080346	EU080347	EU080348	EU080349	EU080350
<i>P. stricta</i>	58A2	KX252217	KX252218	KX252219	KX252220	KX252221	KX252222	KX252223
<i>P. syringae</i> [#]	23A6	KX252203	KX252204	KX252205	KX252206	KX252207	KX252208	KX252209
<i>P. taxon parsley</i>	61G1=BPIC 2584	KX252105	KX252106	KX252107	KX252108	KX252109	KX252110	KX252111
<i>P. taxon walnut</i>	40A7	KX251452	KX251453	KX251454	KX251455	KX251456	KX251457	KX251458

Table 24 (continued)

Species	Strain	60S	tub2	tef1	Enl	HSP90	28S	TigA
<i>P. taxon-aquatilis</i>	38J5	KX250929	KX250930	KX250931	KX250932	KX250933	KX250934	KX250935
<i>P. taxon-castitis</i>	61E7=CBS 131246	KX252098	KX252099	KX252100	KX252101	KX252102	KX252103	KX252104
<i>P. taxon-emzansi</i>	61F2	KX250859	KX250860	KX250861	KX250862	KX250863	KX250864	KX250865
<i>P. tentaculata</i> [#]	29F2=CBS 552.96	EU079955	EU079956	EU079957	EU079958	EU079959	EU079960	EU079961
<i>P. terminalis</i>	65B8=CBS 133865	KX250607	KX250608	KX250609	KX250610	KX250611	KX250612	KX250613
<i>P. thermophila</i>	55C1=CBS 127954	KX251354	KX251355	KX251356	KX251357	KX251358	KX251359	KX251360
<i>P. trifolii</i>	29B2	KX251951	KX251952	KX251953	KX251954	KX251955	KX251956	KX251957
<i>P. tropicalis</i> [#]	35C8=CBS 434.91	KX250698	KX250699	KX250700	KX250701	KX250702	KX250703	KX250704
<i>P. uliginosa</i>	62A3=CBS 109054	EU080011	EU080012	EU080013	KX251571	KX251572	EU080015	KX251573
<i>P. vignae</i> [#]	45G9=ATCC 64832	KX251783	KX251784	KX251785	KX251786	KX251787	KX251788	KX251789
<i>P. virginiana</i>	44G6	KX252371	KX252372	KX252373	KX252374	KX252375	KX252376	KX252377

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains and voucher strains are in bold. Species confirmed with pathogenicity studies are marked with [#]. (VdPN) are strains used by Van der Plaäts-Niterink (1981) for descriptions

Fig. 40 Disease cycle of a *Pythium* species (redrawn from van West et al. 2003)



and Campbell 1973; Hsieh 1978; Ventura et al. 1981; Chun and Schneider 1998; Eberle et al. 2007; Kreye et al. 2009; Oliva et al. 2010; Banaay et al. 2012; Van Buyten and Höfte 2013). *Pythium insidiosum* causes pythiosis in mammals including humans (van der Plaäts-Niterink 1981; de Cock et al. 1987). Some species target below-ground plant parts and some species can cause fruit rot, however, some *Pythium* species can also benefit plants as endophytes by acting as biocontrol agents (Benhamou et al. 1997) and by stimulating plant growth (Martin and Loper 1999; Mazzola et al. 2002).

Pathogen biology, disease cycle and epidemiology

Pythium species grow and colonize a plant by producing hyphae which extract nutrients from the host. Once the hyphae from opposite mating types meet, they produce thick-walled oospores which serve as overwintering structures. Upon germination, an oospore may produce more hyphae, or develop a zoosporangium, which produces motile zoospores that swim to and infect plants. Zoosporangia can also germinate and directly infect plants (Ho 2009; van West et al. 2003).

Morphological based identification and diversity

Pythium has hyaline hyphae which are coenocytic without cross septa (van der Plaäts-Niterink 1981). Filamentous and globose sporangia are present, and zoospores develop in a vesicle, which is formed at the tip of a discharge tube from a sporangium. After fertilization with paragynous or hypogynous antheridia, oospores are formed in smooth or ornamented oogonia. The oospore can fill the whole organism or can have space between the walls of the oogonia and oospore. The process of zoospore formation within a vesicle is a characteristic feature of the genus, which distinguishes it from morphologically similar genera such as *Phytophthora* and *Halophytophthora*. However, the formation of zoospores is similar to *Lagenidium*, which features endobiotic and holocarpic features not observed in *Pythium* (Dick 2001). Species delimitation based on morphological characteristics such as shape and size of sporangia and oogonia is difficult as these characteristics are often shared among different species.

Molecular based identification and diversity

Lévesque and de Cock (2004) separated the genus into 11 clades (A–K) using phylogenies of ITS and 28S. Clade K, which includes *P. vexans* was transferred to a new genus *Phytopythium* with *Phytopythium sindhum* as type species (Bala et al. 2010), while the remaining clades can be divided into two groups: species with filamentous sporangia (clades A–D) and species with globose sporangia (clades E–J). Identification of *Pythium* isolates to species level is recommended based on *cox1* and ITS gene regions. The use of ITS region alone cannot accurately identify all *Pythium* species. Several species are indistinguishable based on both ITS and *cox1* sequences. Lévesque and de Cock (2004) provided the first extensive study of *Pythium*, accepting 116 species. Additional species have recently been described for example *P. alternatum* (Rahman et al. 2015), *P. biforme*, *P. brachiatum*, *P. junctum*, *P. utonaiense* (Uzuhashi et al. 2015), *P. cedri* (Chen et al. 2017), *P. heteroogonium*, *P. longipapillum*, *P. oryzicollum* (Salmaninezhad and Mostowfzadeh-Ghalemarsa 2019). Currently, there are more than 130 accepted species in the genus (Arafa et al. 2020). The phylogenetic tree constructed is presented in Fig. 41 and the information of species are given in Table 25.

Recommended genetic markers (generic level within *Pythium sensu lato*)—18S (small subunit, SSU) and 28S (large subunit, LSU) nuclear rRNA genes

Recommended genetic markers (sub-generic, inter- and intra-specific level)—The internal transcribed spacers (ITS including ITS1, 5.8S rRNA, and ITS2), cytochrome c oxidase subunit 2 (*cox2*)

Accepted number of species—There are 330 epithets listed in Index Fungorum (2020), however only 157 species have DNA sequence data (Table 25).

References—van der Plaäts-Niterink (1981), Dick (2001) (morphology), Lévesque and de Cock (2004), Hyde et al. (2014), Arafa et al. (2020) (phylogeny and accepted species numbers)

100. *Rhizopus* Ehrenb., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 10: 198 (1821)

Background

Rhizopus is classified in the subphylum Mucoromycotina, class Mucoromycetes, order Mucorales and family Rhizopodaceae (Wijayawardene et al. 2018, 2020). The genus is one of the most diverse and constitutes an important genus within the order Mucorales. *Rhizopus* species are common post-harvest pathogens of fruits, vegetables, crops and stored foods, while some *Rhizopus* species are human pathogens. *Rhizopus arrhizus* and *Rhizopus microsporus* can cause mucromycosis in immunocompromised humans (Yildirim et al. 2010; Benedict and Brandt 2016). Morphology-based (size of sporangia and sporangiophores, and rhizoids) and physiology-based (growth temperature) identification and classification grouped the genus in three groups: *R. microsporus*, *R. stolonifer*, and *R. arrhizus* (syn: *R. oryzae*) (Schipper 1984). Schipper (1984) and Schipper and Stalpers (1984), provided the first significant monographs of *Rhizopus*. Fundamental morphological-based identification was provided which is still widely used in current taxonomic classification for *Rhizopus* (Schipper 1984; Schipper and Stalpers 1984; Hartanti et al. 2015). The inclusion of DNA-based phylogenetic tools has resulted in significant changes in the taxonomic classification (Vebliza et al. 2018). With the implementation of molecular-based identification, Abe et al. (2006, 2010), Zheng et al. (2007b), and Liu et al. (2007) provided significant contributions in the classification of *Rhizopus*. Briefly, in current taxonomy *Rhizopus arrhizus* is a synonym of *R. oryzae*, *R. reflexus* to *R. lyococcus* and *Amylomyces rouxii* is a synonym of *Rhizopus arrhizus* (Liu et al. 2007; Hyde et al. 2014; Vebliza et al. 2018) (Fig. 42).

Phylogenomic approaches have the potential to provide a clear understanding of the inter-relationships of species (Gryganskyi et al. 2018). In recent revisions, data from whole-genome sequencing have been used (Gryganskyi et al. 2018). Phylogenetic analysis based on a dataset of 192 orthologous protein-coding genes extracted from whole-genome sequencing of representative species provided a robust phylogeny and tree topology for *Rhizopus*. The phylogenetic analysis resulted in similar tree topology obtained from studies which utilize ITS and *pyrG* genes or 76 orthologous proteins from the genomes (Liu et al. 2007; Chibucos et al. 2016). In brief, *R. microsporus* is suggested to be a monophyletic sister clade to other *Rhizopus* clades, *R. stolonifer* was found to be sister to *R. arrhizus* and *R. delemar* and these four species are monophyletic (Gryganskyi et al. 2010, 2018).

A comparative analysis of the mating-type locus across *Rhizopus* revealed that its structure is flexible even between

Fig. 41 Maximum likelihood of *Pythium* species based on the concatenated SSU, ITS, LSU, *cox2* and *tub2* regions. The maximum parsimonious dataset consisted of 528 constant, 71 parsimony-informative and 556 parsimony-uninformative characters. The parsimony analysis of the data matrix resulted in the maximum of ten equally most parsimonious trees with a length of 1637 steps (CI = 0.200, RI = 0.737, RC = 0.147, HI = 0.800). ML and MP bootstrap support values over 60% and BYPP ≥ 0.90 are indicated. Type strains are in bold and the 11 clades (A–K) are indicated. Scale bar indicates number of substitutions per site. The tree was rooted with *Lagenidium giganteum* (CBS 580.84) and *Lagenidium* sp. (DAOM 242348 and CBS 127283). Likelihood of the best scoring ML tree was – 28453.969593. Estimated base frequencies were as follows: A = 0.264872, C = 0.163069, G = 0.213432, T = 0.358627; substitution rates AC = 1.219282, AG = 3.062456, AT = 3.113530, CG = 0.855790, CT = 4.379562, GT = 1.000000

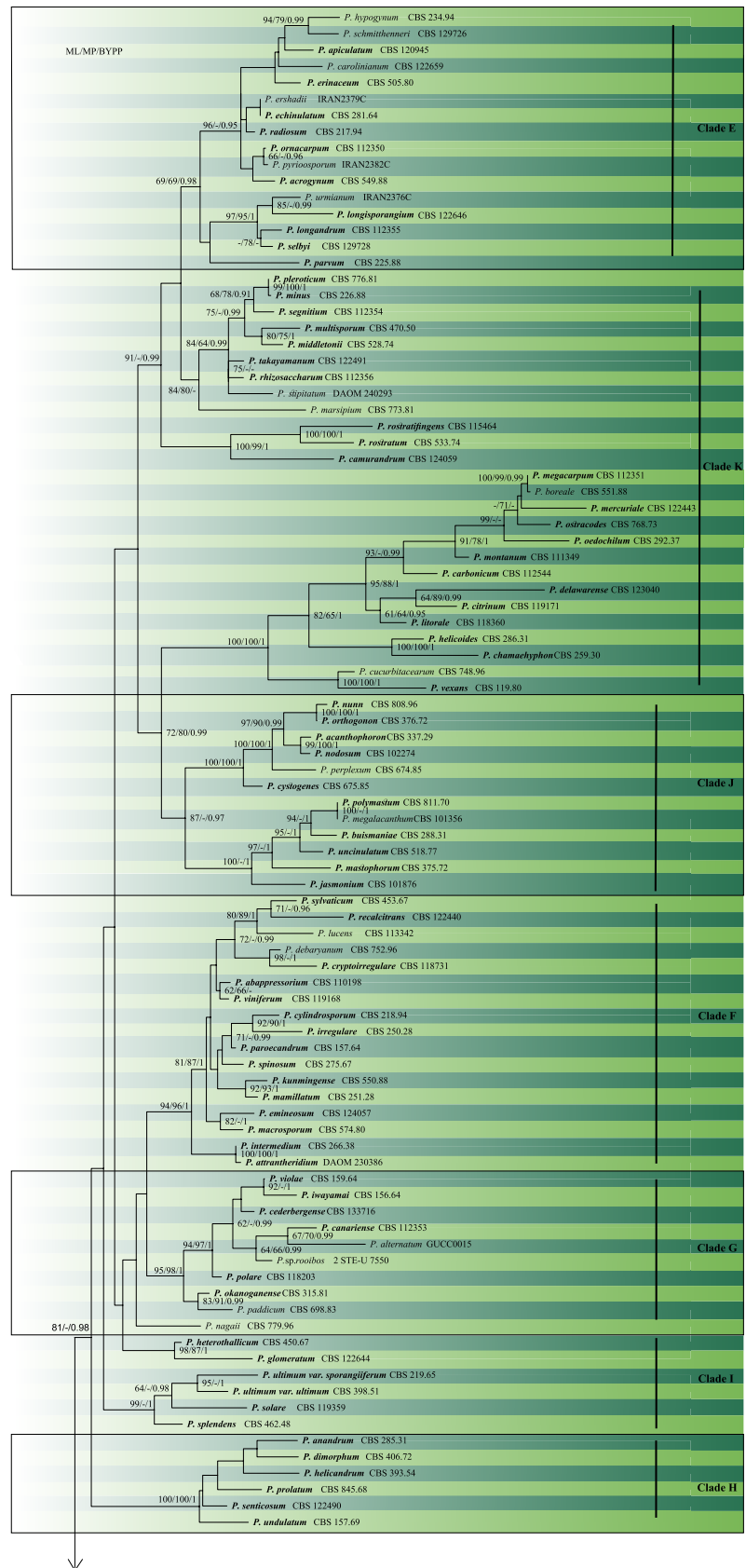


Fig. 41 (continued)

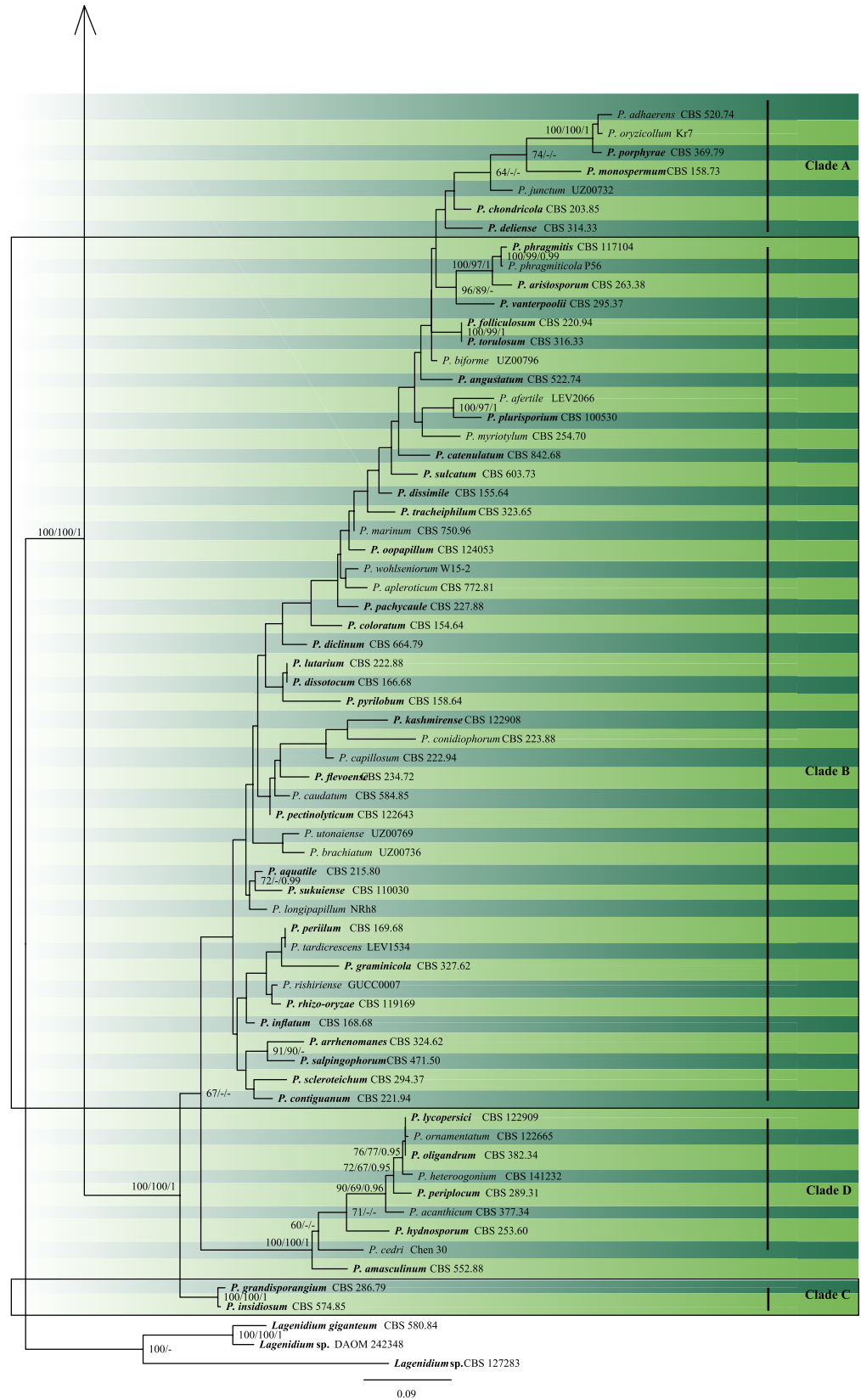


Table 25 DNA barcodes available for *Pythium*

Species	Isolate	Host	SSU	ITS	LSU	<i>cox2</i>	<i>tub2</i>
<i>Pythium abappres-sorium</i> [#]	CBS 110198	<i>Triticum aestivum</i>	HQ643408	HQ643408	HQ643408	KJ595409	KJ595533
<i>P. acanthicum</i> [#]	CBS 377.34	<i>Solanum tuberosum</i>	AY598617	AY598617	AY598617	KJ595380	KJ595504
<i>P. acanthophoron</i> [#]	CBS 337.29	<i>Ananas sativus</i>	AY598711	AY598711	AY598711	KJ595376	KJ595500
<i>P. acrogynum</i>	CBS 549.88	Soil (<i>Spinacia oleracea</i>)	N/A	AY598638	AY598638	AB362324	KJ595458
<i>P. adhaerens</i>	CBS 520.74	Soil	AY598619	AY598619	AY598619	KJ595386	KJ595510
<i>P. afertile</i>	LEV2066	Turf grass	N/A	HQ643416	HQ643416	KJ595440	KJ595563
<i>P. alternatum</i>	GUCC0015	Soil	N/A	AB998876	N/A	-	N/A
<i>P. amasculinum</i>	CBS 552.88	Soil (vegetable garden)	AY598671	AY598671	AY598671	KJ595390	KJ595514
<i>P. anandrum</i> [#]	CBS 285.31	<i>Rheum rhaponticum</i>	AY598650	AY598650	AY598650	AB362328	KJ595450
<i>P. angustatum</i> [#]	CBS 522.74 (VdPN)	Soil	AY598623	AY598623	AY598623	KJ595387	KJ595511
<i>P. aphanidermatum</i> [#]	CBS 118.80	Unknown	AY598622	AY598622	AY598622	KJ595344	KJ595472
<i>P. apiculatum</i>	CBS 120945	Soil (<i>Vitis</i> sp.)	HQ643443	HQ643443	HQ643443	KJ595422	KJ595547
<i>P. aploreticum</i>	CBS 772.81	<i>Nymphoides peltata</i>	AY598631	AY598631	AY598631	KJ595400	KJ595524
<i>P. aquatile</i> [#]	CBS 215.80	Soil	AY598632	AY598632	AY598632	KJ595355	KJ595481
<i>P. aristosporum</i>	CBS 263.38	<i>Triticum aestivum</i>	AY598627	AY598627	AY598627	AB507410	DQ071297
<i>P. arrhenomanes</i> [#]	CBS 324.62 (VdPN)	<i>Zea mays</i>	AKXY02050628	AY598628	AY598628	AKXY02053172	KJ595451
<i>P. attrantheridium</i> [#]	DAOM 230386	<i>Prunus serotina</i>	HQ643476	HQ643476	HQ643476	AB512889	AB512822
<i>P. biforme</i>	UZ00796	Aquatic	N/A	KJ995584	KJ995601	N/A	N/A
<i>P. boreale</i>	CBS 551.88	Soil	AY598662	AY598662	AY598662	EF408876	EF408882
<i>P. brachiatum</i>	UZ00736	Aquatic	N/A	KJ995581	KJ995603	N/A	N/A
<i>P. buismaniae</i>	CBS 288.31	<i>Linum usitatissimum</i>	AY598659	AY598659	AY598659	KJ595368	KJ595493
<i>P. camurandrum</i>	CBS 124059	<i>Hordeum vulgare</i>	GQ244426	GQ244426	GQ244426	KJ595433	KJ595558
<i>P. canariense</i>	CBS 112353	Soil	HQ643482	HQ643482	HQ665069	JX397983	JX397969
<i>P. capillosum</i>	CBS 222.94	Soil	AY598635	AY598635	AY598635	KJ595360	KJ595485
<i>P. carbonicum</i> [#]	CBS 112544	Soil (spoil heap)	HQ643373	HQ643373	HQ643373	AB690678	KJ595464
<i>P. carolinianum</i> [#]	CBS 122659	Soil	N/A	HQ643484	HQ665111	KJ595427	KJ595551
<i>P. catenulatum</i> [#]	CBS 842.68 (VdPN)	Turf grass	AY598675	AY598675	AY598675	KJ595404	KJ595528
<i>P. caudatum</i> [#]	CBS 584.85	<i>Xiphinemarivesi</i>	HQ643136	HQ643136	HQ665277	AF290309	KJ595459
<i>P. cederbergense</i> [#]	CBS 133716	<i>Aspalathus linearis</i>	N/A	JQ412768	KJ716864	JQ412805	JQ412781
<i>P. cedri</i> [#]	Chen 30	roots of <i>Cedrus</i>	N/A	KX423751	N/A	N/A	N/A
<i>P. chamaehyphon</i> [#]	CBS 259.30	<i>Carica papaya</i>	AY598666	AY598666	AY598666	AB257280	KJ595448
<i>P. chondricola</i> [#]	CBS 203.85	<i>Chondrus crispus</i>	N/A	AY598620	AY598620	KJ595354	KJ595480
<i>P. citrinum</i>	CBS 119171	Soil (<i>Vitis</i> sp.)	HQ643375	HQ643375	HQ643375	AB690679	KJ595465
<i>P. coloratum</i> [#]	CBS 154.64	Soil (tree nursery)	AY598633	AY598633	AY598633	KJ595346	KJ595474
<i>P. conidiophorum</i> [#]	CBS 223.88	Soil	AY598629	AY598629	AY598629	KJ595361	KJ595486
<i>P. contiguanum</i>	CBS 221.94	Soil (salt marsh)	HQ643514	HQ643514	HQ665162	KJ595358	KJ595483
<i>P. cryptoirregularis</i> [#]	CBS 118731	<i>Euphorbia pulcherrima</i>	HQ643515	HQ643515	HQ643515	GU071763	GU071888
<i>P. cucurbitacearum</i> [#]	CBS 748.96	Unknown	AY598667	AY598667	AY598667	AB690680	KJ595460
<i>P. cylindrosporum</i> [#]	CBS 218.94	Soil	AY598643	AY598643	AY598643	GU071762	GU071877
<i>P. cystogenes</i> [#]	CBS 675.85	<i>Vicia faba</i>	HQ643518	HQ643518	HQ643518	KJ595396	KJ595520
<i>P. debaryanum</i> [#]	CBS 752.96	<i>Tulipa</i> sp.	AY598704	AY598704	AY598704	KJ595399	KJ595523
<i>P. delawarensis</i>	CBS 123040	<i>Glycine max</i>	KF853241	EU339312	KF853240	KJ595430	KJ595555
<i>P. deliense</i> [#]	CBS 314.33	<i>Nicotiana tabacum</i>	AY598674	AY598674	AY598674	KJ595372	KJ595497
<i>P. diclinum</i> [#]	CBS 664.79	<i>Beta vulgaris</i>	N/A	AY598690	HQ665282	KJ595394	KJ595518

Table 25 (continued)

Species	Isolate	Host	SSU	ITS	LSU	cox2	tub2
<i>P. dimorphum</i> [#]	CBS 406.72	<i>Pinus taeda</i>	AY598651	AY598651	AY598651	AB362331	KJ595454
<i>P. dissimile</i>	CBS 155.64	<i>Pinus radiata</i>	AY598681	AY598681	AY598681	KJ595347	KJ595475
<i>P. dissotocum</i> [#]	CBS 166.68 (VdPN)	<i>Triticum aestivum</i>	AY598634	AY598634	AY598634	KJ595351	KJ595479
<i>P. echinulatum</i> [#]	CBS 281.64 (VdPN)	Soil (forest nursery)	AY598639	AY598639	AY598639	AB362327	KJ595449
<i>P. emineosum</i>	CBS 124057	<i>Juniperus communis</i>	N/A	GQ244427	GQ244427	KJ595432	KJ595557
<i>P. erinaceum</i>	CBS 505.80	Soil	N/A	AY598694	HQ665243	AB362326	KJ595456
<i>P. ershadii</i>	IRAN2379C	Soil	N/A	KT894054	N/A	-	N/A
<i>P. flevoense</i>	CBS 234.72	Soil	AY598691	AY598691	AY598691	KJ595363	KJ595488
<i>P. folliculosum</i> [#]	CBS 220.94	Soil	AY598676	AY598676	HQ665160	N/A	N/A
<i>P. glomeratum</i> [#]	CBS 122644	Soil	N/A	HQ643542	HQ665097	KJ595424	KJ595548
<i>P. graminicola</i> [#]	CBS 327.62	<i>Saccharum officinarum</i>	AY598625	AY598625	AY598625	AF196593	KJ595452
<i>P. grandisporangium</i> [#]	CBS 286.79	Decaying leaf (<i>Zostera marina</i>)	AY598692	AY598692	AY598692	KJ595367	KJ595492
<i>P. helicandrum</i>	CBS 393.54	<i>Rumex acetosella</i>	AY598653	AY598653	AY598653	AB362329	KJ595453
<i>P. helicoides</i> [#]	CBS 286.31	<i>Phaseolus vulgaris</i>	AY598665	AY598665	AY598665	DQ071377	AB511994
<i>P. heteroogonium</i>	079-1 - CBS 141232	Soil	N/A	KX228103	N/A	KX228131	KX228117
<i>P. heterothallicum</i> [#]	CBS 450.67	Soil (<i>Sambucus</i>)	AY598654	AY598654	AY598654	AB512919	AB512850
<i>P. hydno sporum</i> [#]	CBS 253.60 (VdPN)	Unknown	AY598672	AY598672	AY598672	KJ595364	KJ595489
<i>P. hypogynum</i> [#]	CBS 234.94	Soil	AY598693	HQ643565	HQ665171	AB362325	KJ595447
<i>P. inflatum</i> [#]	CBS 168.68 (VdPN)	<i>Saccharum officinarum</i>	AY598626	AY598626	AY598626	KJ595352	N/A
<i>P. insidiosum</i> [#]	CBS 574.85	<i>Equus ferus</i>	AF289981	AY598637	AY598637	KJ595391	KJ595515
<i>P. intermedium</i> [#]	CBS 266.38 (VdPN)	<i>Agrostis stolonifera</i>	AY598647	AY598647	AY598647	AB507410	AB512836
<i>P. irregular</i> [#]	CBS 250.28	<i>Phaseolus vulgaris</i>	AY598702	AY598702	AY598702	GU071760	GU071886
<i>P. iwayamai</i> [#]	CBS 156.64 (VdPN)	Soil (<i>Pinus</i> sp.)	AY598648	AY598648	AY598648	JX397979	JX397965
<i>P. jasmonium</i>	CBS 101876	<i>Arabidopsis thaliana</i>	HQ643778	HQ643778	HQ643778	KJ595406	KJ595530
<i>P. junctum</i>	UZ00732	Aquatic	N/A	KJ995576	KJ995605	N/A	N/A
<i>P. kashmirensis</i> [#]	CBS 122908	Soil	HQ643671	HQ643671	HQ643671	KJ595429	KJ595553
<i>P. kunmingense</i> [#]	CBS 550.88	Soil (<i>Vicia faba</i>)	AY598700	AY598700	HQ665259	KJ595389	KJ595513
<i>P. litorale</i> [#]	CBS 118360	Soil (<i>Phragmites australis</i>)	HQ643386	HQ643386	HQ643386	KJ595418	KJ595543
<i>P. longandrum</i> [#]	CBS 112355	Soil	HQ643679	HQ643679	HQ665071	KJ595413	KJ595538
<i>P. longipapillum</i> [#]	NRh8*	Soil	N/A	KX228105	N/A	KX228130	KX228114
<i>P. longisporangium</i> [#]	CBS 122646	Soil (<i>Vitis</i> sp.)	N/A	HQ643680	HQ665099	KJ595426	KJ595550
<i>P. lucens</i> [#]	CBS 113342	<i>Triticum</i>	HQ643681	HQ643681	HQ643681	KJ595415	KJ595540
<i>P. lutarium</i> [#]	CBS 222.88	Soil	HQ643682	HQ643682	HQ665163	KJ595359	KJ595484
<i>P. lycopersici</i> [#]	CBS 122909	Soil (<i>Lycopersicon esculentum</i>)	N/A	HQ643683	HQ665119	KJ595343	KJ595554
<i>P. macrosporum</i> [#]	CBS 574.80	Flower bulb	AY598646	AY598646	AY598646	AB512916	AB512842
<i>P. mamillatum</i> [#]	CBS 251.28 (VdPN)	<i>Beta vulgaris</i>	AY598703	AY598703	HQ665173	AB362325	AB512844
<i>P. marinum</i> [#]	CBS 750.96	Soil	N/A	AY598689	AY598689	KJ595398	KJ595522
<i>P. marsipium</i> [#]	CBS 773.81	<i>Nymphyoides peltata</i>	N/A	AY598699	HQ665297	KJ595401	KJ595525
<i>P. mastophorum</i> [#]	CBS 375.72 (VdPN)	<i>Apium graveolens</i>	AY598661	AY598661	AY598661	KJ595378	KJ595502
<i>P. megacarpum</i>	CBS 112351	Soil (<i>Vitis</i> sp.)	HQ643388	HQ643388	HQ643388	AB690665	KJ595536

Table 25 (continued)

Species	Isolate	Host	SSU	ITS	LSU	cox2	tub2
<i>P. megalacanthum</i> [#]	CBS 101356	<i>Chrysanthemum</i>	N/A	HQ643693	KJ716865	KJ595435	N/A
<i>P. mercurial</i> [#]	CBS 122443	<i>Macadamia integ-rifolia</i>	KF853243	DQ916363	KF853236	AB690666	KJ595466
<i>P. middletonii</i> [#]	CBS 528.74(VdPN)	Soil	N/A	AY598640	AY598640	AB362318	KJ595457
<i>P. minus</i> [#]	CBS 226.88	Soil	HQ643696	HQ643696	HQ665168	AB362320	KJ595446
<i>P. monospermum</i> [#]	CBS 158.73 (VdPN)	Soil	HQ643697	HQ643697	HQ643697	KJ595350	KJ595478
<i>P. montanum</i>	CBS 111349	Soil (<i>Picea abies</i>)	HQ643389	HQ643389	HQ643389	KJ595410	KJ595534
<i>P. multisporum</i>	CBS 470.50	Soil	AY598641	AY598641	AY598641	AB362319	KJ595455
<i>P. nagaii</i> [#]	CBS 779.96	Soil	AY598705	AY598705	AY598705	KJ595402	KJ595526
<i>P. nodosum</i> [#]	CBS 102274	Soil	N/A	HQ643709	HQ665055	KJ595407	KJ595531
<i>P. nunn</i> [#]	CBS 808.96	Soil	AY598709	AY598709	AY598709	AF196609	DQ071325
<i>P. oedoehilum</i> [#]	CBS 292.37	Unknown	AY598664	AY598664	AY598664	AB108011	EF408883
<i>P. okanoganense</i> [#]	CBS 315.81	<i>Triticum aestivum</i>	AY598649	AY598649	AY598649	KJ595373	KJ595498
<i>P. oligandrum</i> [#]	CBS 382.34 (VdPN)	<i>Viola</i> sp.	AY598618	AY598618	AY598618	KJ595381	KJ595505
<i>P. oopapillum</i> [#]	CBS 124053	<i>Cucumis sativus</i>	N/A	FJ655174	FJ655174	KJ595431	KJ595556
<i>P. ornacarpum</i>	CBS 112350	Soil	HQ643721	HQ643721	HQ643721	KJ595411	KJ595535
<i>P. ornamentatum</i>	CBS 122665	Soil	N/A	HQ643722	HQ665117	KJ595428	KJ595552
<i>P. orthogonon</i> [#]	CBS 376.72	<i>Zea mays</i>	AY598710	AY598710	HQ665221	KJ595379	KJ595503
<i>P. oryzicollum</i> [#]	Kr7	Soil	N/A	KX228072	N/A	KX228125	KX228108
<i>P. ostracodes</i> [#]	CBS 768.73 (VdPN)	Soil	AY598663	AY598663	AY598663	AB690668	EF408880
<i>P. pachycaule</i> [#]	CBS 227.88	Soil	AY598687	AY598687	HQ665169	KJ595362	KJ595487
<i>P. paddicum</i> [#]	CBS 698.83	<i>Triticum</i> and <i>Hor-deum</i>	AY598707	AY598707	AY598707	JX397982	JX397968
<i>P. paroecandrum</i> [#]	CBS 157.64 (VdPN)	Soil	AY598644	AY598644	AY598644	DQ071391	DQ071332
<i>P. parvum</i>	CBS 225.88	Soil	AY598697	AY598697	AY598697	AB362322	KJ595445
<i>P. pectinolyticum</i>	CBS 122643	Soil	HQ643739	HQ643739	HQ643739	N/A	KJ595469
<i>P. periulum</i> [#]	CBS 169.68 (VdPN)	Soil	AY598683	AY598683	HQ665141	N/A	KJ595444
<i>P. periplocum</i> [#]	CBS 289.31	<i>Citrullus vulgaris</i>	AY598670	AY598670	AY598670	KJ595369	KJ595494
<i>P. perplexum</i> [#]	CBS 674.85	<i>Vicia faba</i>	AY598658	AY598658	AY598658	KJ595395	KJ595519
<i>P. phragmitis</i> [#]	CBS 117104	Soil (<i>Phragmites australis</i>)	HQ643746	HQ643746	HQ665081	AJ890351	EU152854
<i>P. pleroticum</i>	CBS 776.81	<i>Nymphyoides peltata</i>	AY598642	AY598642	AY598642	AB362321	KJ595461
<i>P. plurisporium</i> [#]	CBS 100530	<i>Agrostis</i>	AY598684	AY598684	AY598684	KJ595405	KJ595529
<i>P. polare</i> [#]	CBS 118203	<i>Sanionia uncinata</i>	KJ716858	AB299390	KJ716859	KJ595417	KJ595542
<i>P. polymastum</i> [#]	CBS 811.70 (VdPN)	<i>Lactuca sativa</i>	AY598660	AY598660	AY598660	KJ595403	KJ595527
<i>P. porphyrae</i> [#]	CBS 369.79 (VdPN)	<i>Porphyraezoensis</i>	AY598673	AY598673	AY598673	KJ595377	KJ595501
<i>P. phragmiticola</i>	P56	Soil	N/A	KC145165	N/A	KC145166	KC145167
<i>P. prolatum</i> [#]	CBS 845.68	<i>Rhododendron</i> sp.	AY598652	AY598652	AY598652	AB362330	KJ595462
<i>P. pyriosporum</i>	IRAN2382C	Soil	N/A	KT894052	N/A	-	N/A
<i>P. pyrilibum</i> [#]	CBS 158.64	<i>Pinus radiata</i>	AY598636	AY598636	AY598636	KJ595349	KJ595477
<i>P. radiosum</i>	CBS 217.94	Soil	N/A	AY598695	HQ665156	KJ595356	N/A
<i>P. recalcitrans</i> [#]	CBS 122440	Soil (<i>Vitis vinifera</i>)	N/A	DQ357833	KJ716861	KJ595423	EF195143
<i>P. rishiriense</i>	GUCC0007	Aquatic	N/A	AB998878	N/A	-	N/A
<i>P. rhizo-oryzae</i> [#]	CBS 119169	Soil	HQ643757	HQ643757	HQ643757	KJ595420	KJ595545

Table 25 (continued)

Species	Isolate	Host	SSU	ITS	LSU	<i>cox2</i>	<i>tub2</i>
<i>P. rhizosaccharum</i>	CBS 112356	Soil (<i>Saccharum officinarum</i>)	N/A	HQ643760	HQ665072	AB362323	KJ595463
<i>P. rostratifingens</i> [#]	CBS 115464	Soil (<i>Malus</i> sp.)	HQ643761	HQ643761	HQ643761	KJ595416	KJ595541
<i>P. rostratum</i> [#]	CBS 533.74	Soil	AY598696	AY598696	AY598696	KJ595388	KJ595512
<i>P. salpingophorum</i> [#]	CBS 471.50 (VdPN)	<i>Lupinus angustifolius</i>	AY598630	AY598630	AY598630	KJ595384	KJ595508
<i>P. schmittthenneri</i> [#]	CBS 129726	<i>Glycine max</i>	N/A	JF836869	KJ716862	JF895530	KJ595470
<i>P. scleroteichum</i> [#]	CBS 294.37	<i>Ipomoea batatas</i>	AY598680	AY598680	AY598680	KJ595370	KJ595495
<i>P. segnitium</i>	CBS 112354	Soil	HQ643772	HQ643772	HQ643772	KJ595412	KJ595537
<i>P. selbyi</i> [#]	CBS 129728	<i>Zea mays</i>	N/A	JF836871	KJ716863	JF895532	KJ595471
<i>P. senticosum</i> [#]	CBS 122490	Soil (forest)	HQ643773	HQ643773	HQ643773	AB362317	KJ595467
<i>P. solare</i>	CBS 119359	<i>Phaseolus vulgaris</i>	N/A	EF688275	KJ716860	KJ595421	KJ595546
<i>P. spinosum</i> [#]	CBS 275.67 (VdPN)	Compost	AY598701	AY598701	AY598701	KJ595366	KJ595491
<i>P. splendens</i> [#]	CBS 462.48 (VdPN)	Unknown	AY598655	AY598655	AY598655	AB512921	AB512852
<i>P. stipitatum</i>	DAOM 240293	Soil	N/A	KJ716866	KJ716866	KJ595437	KJ595560
<i>P. sukuiense</i>	CBS 110030	Soil	N/A	HQ643836	HQ665059	KJ595408	KJ595532
<i>P. sulcatum</i> [#]	CBS 603.73	<i>Daucus carota</i>	AY598682	AY598682	HQ665281	KJ595393	KJ595517
<i>P. sylvaticum</i> [#]	CBS 453.67	Soil	AY598645	AY598645	AY598645	KJ595383	KJ595507
<i>P. takayamanum</i>	CBS 122491	Soil	HQ643854	HQ643854	HQ643854	AB362315	KJ595468
<i>P. tardicrescens</i> [#]	LEV1534	Turfgrass	N/A	HQ643855	HQ643855	KJ595439	KJ595562
<i>P. torulosum</i> [#]	CBS 316.33 (VdPN)	Grass	AY598624	AY598624	AY598624	KJ595374	KJ595499
<i>P. tracheiphilum</i> [#]	CBS 323.65	<i>Lactuca sativa</i>	N/A	AY598677	HQ665207	KJ595375	N/A
<i>P. ultimum</i> var. <i>sporangiferum</i> [#]	CBS 219.65	<i>Chenopodium album</i>	AKYB02045405	AY598656	AY598656	KJ595357	KJ595482
<i>P. ultimum</i> var. <i>ultimum</i> [#]	CBS 398.51	<i>Lepidium sativum</i>	AY598657	AY598657	AY598657	KJ595382	KJ595506
<i>P. uncinulatum</i> [#]	CBS 518.77	<i>Lactuca sativa</i>	AY598712	AY598712	AY598712	KJ595385	KJ595509
<i>P. undulatum</i> [#]	CBS 157.69 (VdPN)	Soil (<i>Pinus</i> sp.)	AY598708	AY598708	AY598708	KJ595348	KJ595476
<i>P. urmianum</i>	IRAN2376C	Soil	N/A	KT894049	N/A	-	N/A
<i>P. utonaiense</i>	UZ00769	Aquatic	N/A	KJ995587	KJ995600	N/A	N/A
<i>P. vanterpoolii</i> [#]	CBS 295.37	<i>Triticum aestivum</i>	AY598685	AY598685	AY598685	KJ595371	KJ595496
<i>P. vexans</i> [#]	CBS 119.80 (VdPN)	Soil	HQ643400	HQ643400	HQ643400	GU133518	EF426556
<i>P. viniferum</i> [#]	CBS 119168	Soil (<i>Vitis</i> sp.)	HQ643956	HQ643956	HQ643956	KJ595419	KJ595544
<i>P. violae</i> [#]	CBS 159.64 (VdPN)	Soil	AY598706	AY598706	AY598706	JX397980	JX397966
<i>P. wohlseniorum</i>	W15-2	Aquatic	N/A	MH277978	MH289800	MH289798	MH289799
<i>Pythium</i> sp. <i>rooibos</i> 2	STE-U 7550	<i>Aspalathus linearis</i>	N/A	JQ412777	N/A	JQ412813	JQ412789

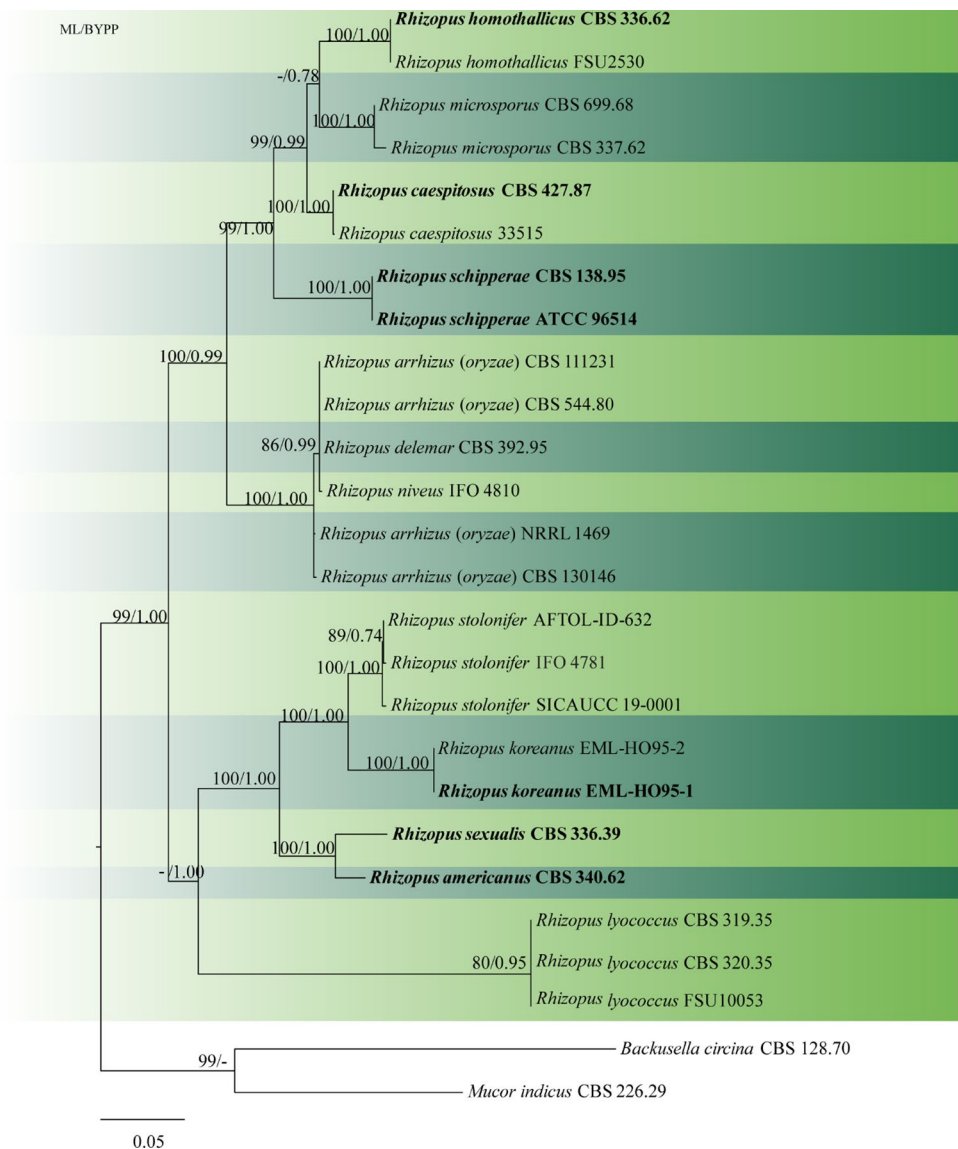
Ex-type/ex-epitype/ex-neotype/ex-lectotype strains and voucher strains are in bold. Species confirmed with pathogenicity studies are marked with [#]. (VdPN) are strains used by Van der Plaäts-Niterink (1981) for descriptions

different species in the same genus, but shows similarities between *Rhizopus* and other mucoralean taxa. Variation of the genome size was also noted to be approximately three-fold within a species which are induced by changes in transposable element copy numbers and genome duplications (Gryganskyi et al. 2018). Bruni et al. (2019) successfully adapted the CRISPR-Cas 9 technique for inducing *pyrF* gene-specific

mutations in two strains of *R. delemar*, the causative agent of mucoromycosis. This new tool is suggested to be useful in investigating the pathogenesis mechanisms of *R. delemar* and also generating specific mutants of Mucorales fungi.

Classification—Mucoromycota, Mucoromycotina, Mucoromycetes, Mucorales, Rhizopodaceae

Fig. 42 Phylogenetic tree generated by maximum likelihood analysis of combined ITS- LSU-SSU sequence data of *Rhizopus*, *Bauskella* and *Mucor* species. Twenty-six taxa containing 2600 characters including gaps were used in the phylogenetic analysis. The tree was rooted using *Bauskella circina* (CBS 128.70) and *Mucor indicus* (CBS 226.29). The best scoring RAxML tree with a final likelihood value of -11138.113172 is presented. The matrix contained 761 distinct alignment patterns, with 41.20% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.293528, C = 0.180262, G = 0.236482, T = 0.289728; substitution rates AC = 0.787730, AG = 2.127667, AT = 1.579251, CG = 0.715792, CT = 3.683423, GT = 1.000000; gamma distribution shape parameter $\alpha = 0.181944$. ML bootstrap support values greater than 70% are shown near the nodes. The type species are in bold. Scale bar indicates the number of substitutions per site



Type species—*Rhizopus stolonifera* (Ehrenb.) Vuill. 1902

Distribution—worldwide

Disease symptoms—*Rhizopus* blight, *Rhizopus* head rot and *Rhizopus* soft rot

Rhizopus blight: *Rhizopus* blight can affect flowers, leaves, and stems. When infected, the plant shows symptoms such as soft and mushy brown rot. The rot produces white mycelia with black sporangia and the abundant mycelia projects a ‘bearded’ appearance. Spores of the fungus can be spread by water and air. The mode of infection is similar to bacterial soft rot in which enzymes secreted by the fungus causes cell deterioration of the host tissue. The fungi require high temperatures, high humidity and weakened host tissues or wounds (Hartley 1992).

Rhizopus head rot on sunflowers: *Rhizopus* head rot may be caused by several *Rhizopus* species such as *Rhizopus arrhizus*, *R. microsporus* and *R. stolonifera* (Markell et al. 2015). Historically, *Rhizopus* head rot was deemed

as a minor disease. However, recent surveys have shown their severity. Initial signs of *Rhizopus* head rot are dark spots of different sizes on different types of wounds on the plant. Soft watery rot appears on the infected fruit which often turns dark brown and extends to the back of the flower head, sepals and peduncles as the disease progresses. The infected sunflower receptacle disintegrates and becomes soft and pulpy. Infection by *Rhizopus* causes the head to shrivel and dry. Morphological characteristics are mycelial strands bearing sporangiophore and sporangia which are seen as the disease advances (Markell et al. 2015; Zhou et al. 2018). These whiskers are tufts of hyphae containing numerous sporangia and generally appear around lenticels or breaks in the periderm. Sometimes hyphae may not be visible on the outside of the root but can be viewed by pulling apart the infected tissue, giving it a stringy appearance (Clark et al. 2013).

Table 26 DNA barcodes available for *Rhizopus*

Species name	Isolate no	SSU	ITS	LSU
<i>Rhizopus americanus</i>	CBS 340.62*	NG_062623	HM999967	NG_057873
<i>R. arrhizus</i> [#]	CBS 111231		JN206338	
	CBS 544.80		JN206337	
	NRRL 1469		DQ641279	
<i>R. caespitosus</i>	CBS 427.87*	NG_062622	NR_137056	NG_057871
	33515		AF115730	DQ466604
<i>R. delemar</i>	CBS 392.95		MH862535	MH874170
<i>R. homothallicus</i>	CBS336.62*	NG_062624	HM999968	NG_057870
	FSU2530	KJ408537	KJ408567	KJ408554
<i>R. koreanus</i>	EML-HO95-1*	KU058194	KU058202	KU058196
	EML-HO95-2	KU058195	KU058203	KU058197
<i>R. lycococcus</i>	strain FSU10053	KJ408545		KJ408562
	CBS 319.35		AB100449	
	CBS 320.35		JN206373	JN206534
<i>R. microsporus</i> [#]	CBS 699.68*		HM999970	
	CBS 337.62	AB250177	JN206362	MH869765
<i>R. niveus</i> [#]	IFO 4810		DQ641284	
<i>R. oryzae</i> [#]	CBS 112.07*	NG_062621	NR_103595	NG_056282
	CBS 130146		MH865585	MH877020
<i>R. schipperae</i>	CBS 138.95		NR077174	HM849672
	ATCC 96514*	NG_064824	DQ641323	NG_059417
<i>R. sexualis</i> [#]	CBS 336.39*	NG_063011	AB113017	MH867536
<i>R. stolonifer</i> [#]	CBS 389.95		DQ641318	
	SICAUCC 19-0001	MN148534	MN267051	MN148530

Ex-type/ex-epitype/ex-neotype/ex-lectotype strains are in bold and marked with an asterisk (*). Voucher strains are also in bold. Species confirmed with pathogenicity studies are marked with [#]

Rhizopus soft rot: Common causative agents of Rhizopus soft rot are *Rhizopus stolonifer* and *Rhizopus oryzae*. The disease is considered as one of the most common and destructive postharvest diseases in many plants such as sweet potato (*Ipomoea batatas*), potato (*Solanum tuberosum*) and tomato (*Solanum lycopersicum*). The most frequent mode of infection is wounds and injuries present on the plants. Studies have also shown that the type of wounding and storage time have a significant impact on the susceptibility of infection by *Rhizopus* species (Scruggs and Quesada-Ocampo 2016). Earliest symptoms of infections are soft water-soaked lesions. The disease spreads across the wounded area and progresses to the extremities of the substrate. Hyphae soon develop on the rotten tissues and produce grey sporangio-phores which subsequently bear sporangia (Khokhar et al. 2019). Whiskers are characteristic features of Rhizopus soft rot and have been reported in the case of soft rot on sweet potatoes (Clark et al. 2013; Scruggs and Quesada-Ocampo 2016) (Table 26).

Hosts—Wide range of hosts including species of *Allium*, *Ananas*, *Brassica*, *Cucumis*, *Cucurbita*, *Fragaria*, *Lycopersicon*, *Phaseolus*, *Pisum* and *Solanum* (Farr and Rossman 2020)

Pathogen biology, disease cycle and epidemiology

The pathogen reproduces asexually. Spores of *Rhizopus* species are commonly found in the air and can survive easily on crop debris, fruits, vegetables, and even on tools and equipment. Factors such as the *Rhizopus* species, type of fruit, stage of maturity of the plant and fruit or the storage will have a slight difference in the disease cycle. *Rhizopus stolonifer*, as well as the other species causing post-harvest diseases such as Rhizopus soft rot, require wound injuries, cracks or any mechanical damage for entry (Hartley 1992; Bautista-Baños et al. 2014; Scruggs and Quesada-Ocampo 2016). Infection and colonization are highly dependent on the enzymes produced by the fungi. To establish within the host, *Rhizopus* species produce numerous enzymes, including amylase, pectinase, and cellulase that can damage cell walls and permit host colonization (Ogundero 1988; Tang et al. 2012). This results in the softening of the host tissue; one of the symptoms of the disease (Nelson 2009; Kwon et al. 2012; Bautista-Baños et al. 2014; Feliziani and Romanazzi 2016). During initial stages of infection, Rhizopus rot appears as water-soaked areas and in the case of *Rhizopus stolonifer*, the rot also exudes clear leachate. In the case of Rhizopus soft rot caused by *R. oryzae* in banana,

the symptoms and disease cycle are similar to *R. stolonifer* (Kwon et al. 2012). In Okinawan sweet potatoes, the disease causes a soft and moist appearance and a stringy flesh during the initial stages and as the disease progresses, the tissue of the sweet potato turns brownish and eventually black (Nelson 2009). In the case of *R. stolonifer*, the fungal mycelia quickly spread across the infection site. The sporangia formed are normally black and the whole plant is covered by fungal mycelia (Bautista-Baños et al. 2014). The enzymes exuded from the pathogen generally liquefy the internal tissues, for an example in sweet potato parenchyma of the root becomes liquefied, leaving the periderm and outer fibres of the root intact (Scruggs and Quesada-Ocampo 2016). The disease becomes more severe in warm, humid environments (Zoffoli and Latorre 2011). Avoidance of *Rhizopus* species is difficult due to their ubiquitous nature; therefore, sanitation and storing produce under unfavourable disease conditions is the key to control this pathogen.

Morphology- based identification and diversity

Rhizopus is normally distinguished by rhizoids, stolons and single or branched sporangiophores (Vebliza et al. 2018). Identification of species takes into account the growth temperature, size of sporangiophore and sporangium and the branching of rhizoids (Abe et al. 2007). The white mycelia consist of coenocytic hyphae which bear the sporangiophore with normally black sporangia. These taxa are fast-growing and form rhizoids at the base of sporangiophores. The sporangium contains a columella and spores (Bullerman 2003). During the sexual stage, there is the formation of zygospores and chlamydo spores can also be seen during the growth of the fungi (Bullerman 2003; Abe et al. 2007).

Molecular identification and diversity

Traditionally, *Rhizopus* species were classified using morphological characters such as the shape and size of the structures (chlamydo spores, rhizoids, sporangiophores and columellae) and physiological features such as optimal growth conditions. Current classification and taxonomic grouping follow that of Schipper (Schipper 1984). Schipper classified *Rhizopus* into three groups namely *R. microsporus*, *R. stolonifer* and *R. arrhizus* based on the physiological factors and morphology (Abe et al. 2010; Gryganskyi et al. 2018). Later, studies such as Abe et al. (2006), Liu et al. (2007), Zheng et al. (2007a, b), Abe et al. (2010) implemented molecular phylogeny using DNA sequence data in the classification of these fungi. With novel approaches used, the classification proposed by Schipper was found to agree with some recent studies while others divided the genus into ten species and seven varieties or eight species. Zheng et al. (2007b) used zygospore formation, and molecular systematic

morphological characters, mating compatibility, physiology and molecular systematic to accept the division of the genus in ten species and seven varieties. Abe et al. (2010) also used the rDNA ITS gene region together with actin-1 and *tef1*, to reorganize the proposed taxonomy into eight species instead of ten species. One important data provided by this study was the problematic rDNA ITS region of *R. americanus*. It was discovered that *R. sexualis* var. *americanus* has three rDNA ITS gene regions which are distinct from each other. However, Liu et al. (2007) were not able to obtain all three rDNA ITS gene region instead they were able to amplify only one ITS region which was similar to that of *Rhizopus oryzae*. So, this led to the conclusion that *R. americanus* was phylogenetically different from *R. sexualis*.

Genetic markers (species and genus level)—ITS and *rpb1*
Genetic markers (higher-level phylogeny)—SSU, LSU and *act*

Accepted number of species—There are 152 species epithets in Index Fungorum (2020), however only 12 species have DNA sequence data (Table 25).

References—Bullerman (2003), Abe et al. (2007) (morphology); Abe et al. (2010), Gryganskyi et al. (2018), Vebliza et al. (2018) (morphology and phylogeny)

Discussion

This is the fourth in the *One Stop Shop* series focusing on providing a stable platform for the taxonomy of plant pathogenic fungi and fungus-like organisms. These series aim to provide updated backbone trees and information regarding plant pathogens in one place for ease of access. Databases play an important role in aggregating the scattered data into an easily accessible form and many of the pathogenic genera were annotated in the UNITE database (Nilsson et al. 2014). However, this database mainly focused on ITS region rather than the protein-coding gene regions. There are very few databases dedicated to identify the plant pathogens and related fungi-like organisms. We have been trying to provide a stable and updated taxonomy for 97 genera and three families since 2014, which are listed in Table 1. All this information is available in <http://www.onestopshopfungi.org>.

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Affiliations

Ruvishika S. Jayawardena^{1,2,7} · Kevin D. Hyde^{1,2,3,18} · Yi Jyun Chen^{2,7} · Viktor Papp⁴ · Balázs Palla⁴ · Dávid Papp^{5,6} · Chitrabhanu S. Bhunjun^{2,7} · Vedprakash G. Hurdeal^{2,7} · Chanokned Senwannan^{2,8} · Ishara S. Manawasinghe^{2,9,18} · Dulanjalee L. Harischandra^{2,7,9} · Ajay Kumar Gautam¹⁰ · Shubhi Avasthi¹¹ · Boontiya Chuankid^{2,7} · Ishani D. Goonasekara^{2,7} · Sinang Hongsanan¹² · XiangYu Zeng^{2,7,19} · Kapila K. Liyanage^{2,17,20} · NingGuo Liu² · Anuruddha Karunarathna^{2,8} · Kalani K. Hapuarachchi² · Thatsanee Luangharn^{2,3} · Olivier Raspé^{2,7} · Rashika Brahmanage^{2,7,9} · Mingkwan Doilom^{3,16,17} · Hyang B. Lee¹³ · Liu Mei⁹ · Rajesh Jeewon¹⁴ · Naruemon Huanraluek² · Napalai Chaiwan^{2,7} · Marc Stadler¹⁵ · Yong Wang¹

¹ Department of Plant Pathology, Agriculture College, Guizhou University, Guiyang 550025, Guizhou, China

² Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai, Thailand

³ Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, People's Republic of China

⁴ Department of Botany, Szent István University, Villányi út 29-43, Budapest 1118, Hungary

⁵ Plant Pathology and Plant-Microbe Biology Section, Cornell University, Geneva, NY 6 14456, USA

⁶ Department of Pomology, Szent István University, Villányi út 29-43, Budapest 1118, Hungary

⁷ School of Science, Mae Fah Luang University, Chiang Rai 57100, Thailand

⁸ Department of Entomology and Plant Pathology, Faculty of Agriculture, Chiang Mai University, No. 9 of Shuanghuayuanzhonglu, Chiang Mai 50200, Thailand

⁹ Institute of Plant and Environment Protection, Beijing Academy of Agriculture and Forestry Sciences, Haidian District Haidian District, Beijing 100097, People's Republic of China

¹⁰ School of Agriculture, Abhilashi University, Mandi, Himachal Pradesh 175028, India

¹¹ School of Studies in Botany, Jiwaji University, Gwalior 474011, India

¹² Guangdong Provincial Key Laboratory for Plant Epigenetics, College of Life Sciences and Oceanography, Shenzhen University, Shenzhen 518055, PR China

¹³ Environmental Microbiology Lab, Dept. of Agricultural Biological Chemistry, College of Agriculture and Life Sciences, Chonnam National University, Gwangju 61186, Korea

¹⁴ Department of Health Sciences, Faculty of Science, University of Mauritius, Reduit, Mauritius

¹⁵ Department of Microbial Drugs, Helmholtz Centre for Infection Research, Inhoffenstraße 7, 38124 Braunschweig, Germany

¹⁶ Honghe Innovation Center for Mountain Futures, Kunming Institute of Botany, Honghe County, Yunnan 654400, People's Republic of China

¹⁷ World Agroforestry Centre, East and Central Asia, Kunming 650201, Yunnan, People's Republic of China

¹⁸ Institute of Plant Health, Zhongkai University of Agriculture and Engineering, Guangzhou 510225, China

¹⁹ Faculty of Agriculture, Natural Resources and Environment, Naresuan University, Phitsanulok 65000, Thailand

²⁰ Rubber Research Institute of Sri Lanka, Dartonfield, Agalawatta, Sri Lanka