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One stop shop: backbones trees for important phytopathogenic genera: I (2014)

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Abstract Many fungi are pathogenic on plants and cause significant damage in agriculture and forestry. They are also part of the natural ecosystem and may play a role in regulating plant numbers/density. Morphological identification and analysis of plant pathogenic fungi, while important, is often hampered by the scarcity of discriminatory taxonomic characters and the endophytic or inconspicuous nature of these fungi. Molecular (DNA sequence) data for plant pathogenic fungi have emerged as key information for diagnostic and classification studies, although hampered in part by non-standard laboratory practices and analytical methods. To facilitate current and future research, this study provides phylogenetic synopses for 25 groups of plant pathogenic fungi in the Ascomycota, Basidiomycota, Mucormycotina (Fungi), and Oomycota, using recent molecular data, up-to-date names, and the latest taxonomic insights. Lineage-specific laboratory protocols together with advice on their application, as well as general observations, are also provided. We hope to maintain updated backbone trees of these fungal lineages over time and to publish them jointly as new data emerge. Researchers of plant pathogenic fungi not covered by the present study are invited to join this future effort. *Bipolaris, Botryosphaeriaceae,*

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Botryosphaeria, Botrytis, Choanephora, Colletotrichum, Curvularia, Diaporthe, Diplodia, Dothiorella, Fusarium, Gilbertella, Lasiodiplodia, Mucor, Neofusicoccum, Pestalotiopsis, Phyllosticta, Phytophthora, Puccinia, Pyrenophora, Pythium, Rhizopus, Stagonosporopsis, Ustilago and Verticillium are dealt with in this paper.

Keywords Ascomycota · Basidiomycota · Endophytes · Mucormycotina · Molecular identification · Oomycota · Plant pathogens · Protozoa

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Introduction

Fungi form a large and heterogeneous eukaryotic kingdom with an estimated 1.5 million extant species. While all fungi are heterotrophic, a wide range of nutritional strategies is known in the kingdom. Most of the ca. 100,000 described species of fungi are associated with plants through interactions including symbiosis, endophytism, saprotrophy and parasitism (Stajich et al. 2009; Delaye et al. 2013; Persoh 2013; Hyde et al. 2013b). As plant parasites, fungi can cause significant economic loss with far-reaching social implications and consequences in agriculture, forestry and natural ecosystems (Fisher et al. 2012). They are also part of the natural ecosystem and play an important role in regulation of species (Hantsch et al. 2014).

The study of plant pathogenic fungi–their systematics, biology, and biological control–has a long and rich history (Udayanga et al. 2011; Maharachchikumbura et al. 2011; Manamgoda et al. 2011). The inconspicuous nature of most fungi makes their study difficult. For example, there are typically few discriminatory morphological characters, which often makes precise field- or laboratory-based identification problematic. Morphological characters that vary with the choice of host or environmental conditions form an additional, serious concern. Many species are difficult or impossible to keep alive in culture, which excludes them from physiological and often molecular tests that are available. The formation of sexual fruiting bodies is rarely observed in many plant pathogenic fungi, which has hampered their integration in the fungal tree of life, resulting in the proliferation of polyphyletic asexual genera. The biology of most plant pathogenic fungi remains poorly understood.

The last 25 years have witnessed the emergence of molecular data (DNA sequences) as a source of high fidelity information that has revolutionised mycology (Nilsson et al. 2014). DNA sequences offer a means by which to examine and compare fungi, independent of morphological plasticity, cultivability, and host-pathogen interactions. Since integration of molecular data in the study of plant pathogenic fungi in the early 1990s, there has been a much deeper understanding of the ecology, distribution, and systematics of plant pathogenic fungi (Bridge et al. 2005; Wingfield et al. 2012; Udayanga et al. 2013; Manamgoda et al. 2013). The use of molecular data in diagnostics and systematic studies is not without pitfalls and shortcomings that researchers must consider (Kang et al. 2010; Ko et al. 2011; Hyde et al. 2013a). Synonyms, homonyms, asexual-sexual relationships, ambiguous and misidentified specimens are rife in the plant pathology literature and public databases of DNA sequences, which posses an enormous challenge for the unwary. Equally challenging is the large number of unidentified and seemingly unidentifiable fungi and fungal sequences isolated from plants (Kõljalg et al. 2013; Unterseher et al. 2013). Certain plant pathogenic fungi require specialized extraction and PCR primers/protocols in order to amplify their DNA. Furthermore, the same genetic markers that give unparalleled phylogenetic resolution in some fungi may give none whatsoever in others. Many plant pathology studies focus on single species of fungi, and recent revisions or synopses at the generic or higher levels are lacking for the majority of plant pathogenic fungi.

The present study seeks to facilitate present and future studies of plant pathogenic fungi by providing phylogenetic backbone trees for as many groups of fungi as our expertise allowed. Our ambition is to synthesize all recent molecular data, recommendations on correct names, type material, geo/ecological observations, literature, and lineage-specific laboratory advice into a comprehensive, uniform molecular treatise for some of the largest and most widely encountered lineages of plant pathogenic fungi.

Material and methods

The phylogenetic analyses were performed based on up to date ex-type, ex-epitype or otherwise authentic sequence data available in GenBank as a concerted effort of the multiple contributors listed in authors section. By authentic sequence data we refer to those sequences used for names that are considered by the current working groups with the support of reliable publications in each genus as representative for each species. Sequences for the genes and genetic markers recommended for each genus were selected based on the current publications and have commonly been used for each of the genera (Table 1). The single gene sequence alignments were initially aligned with Clustal X and improved in MAFFTv. 7.017 (Katoh et al. 2002). Individual alignments were then concatenated and used to construct the backbone trees of each pathogenic genus listed. The phylogenetic analyses were performed for maximum parsimony in PAUP v. 4.0b10 (Swofford 2002), maximum likelihood in RAxML 7.4.2 Black Box or RAxMl GUI (Stamatakis 2006; Stamatakis et al. 2008), PhyML 3.0 (Guindon et al. 2010) or Bayesian inference in MrBayes v. 3.1.2 (Huelsenbeck and Ronquist 2001) as specified in the legend of each phylogenetic tree. The trees used to represent each genus were analyzed by multiple contributors based on the selection of genes in given publications under each description.

Backbone tree for important phytopathogens

Condensed synopses are provided for 25 important plant pathogenic group or genera. Each synopsis includes notes on background, species identifications and numbers, molecular phylogeny, recommended genetic markers, tables of species

Table 1 Gene regions and primers

Genus	Gene regions	Primers		Reference
		Forward	Reverse	
Bipolaris	ITS	ITS5	ITS4	White et al. 1990
	GPDH	GPD1	GPD2	Berbee et al. 1999
Botryosphaeriaceae	ITS	ITS5	ITS4	White et al. (1990)
	LSU	LROR	LR5	Vilgalys and Hester (1990)
	SSU	NS1	NS4	White et al. (1990)
	TEF	728F	986R	Carbone and Kohn (1999)
	β- tubulin	BT2A	BT2B	Glass and Donaldson (1995)
Botryosphaeria	ITS	ITS5	ITS4	White et al. (1990)
	LSU	LROR	LR5	Vilgalys and Hester (1990)
	SSU	NS1	NS4	White et al. (1990)
	TEF	728F	986R	Carbone and Kohn (1999)
	β- tubulin	BT2A	BT2B	Glass and Donaldson (1995)
Botrytis	RPB2	RPB2for+	RPB2rev+	Staats et al. (2005)
	HSP60	HSP60for+	HSP60rev+	Staats et al. (2005)
	GPDH	G3PDHfor+	G3PDHrev+	Staats et al. (2005)
	NEP1	NEP1(−207)for, NEP1for	NEP1revA, NEP1revB, NEP1(+1124)rev	Staats et al. (2007a, b)
	NEP2	NEP2(−200)for, NEP2forD, NEP2forE, NEP2forF	NEP2(+1124)rev, NEP2revD, NEP2revE	Staats et al. (2007a, b)
Choanephora	ITS	V9G	LR3	de Hoog and Gerrits Van den Ende (1998)
Colletotrichum	ITS	ITS1-F	ITS4	Gardes and Bruns (1993)
	GPDH	GDF	GDR	Templeton et al. 1992
	CHS-1	CHS-79F	CHS-345R	Carbone and Kohn (1999)
	HIS3	CYLH3F	CYLH3R	Crous et al. 2004
	ACT	ACT-512F	ACT783R	Carbone and Kohn (1999)
	β- tubulin	T1	T2	O'Donnell and Cigelnik 1997
	ApMat	AM-F	AM-R	Silva et al. (2012)
Curvularia	ITS	ITS5	ITS4	White et al. 1990
	GPDH	GPD1	GPD2	Berbee et al. 1999
Diaporthe	ITS	ITS5	ITS4	White et al. (1990)
	TEF	728F	986R	Carbone and Kohn (1999)
	β- tubulin	BT2A	BT2B	Glass and Donaldson (1995)
	CAL	228F	737R	Carbone and Kohn (1999)
	HIS	CYLH3F	CYLH3R	Crous et al. 2004
Diplodia	ITS	ITS5	ITS4	White et al. (1990)

Table 1 (continued)

Genus	Gene regions	Primers		Reference
		Forward	Reverse	
	TEF	728F	986R	Carbone and Kohn (1999)
	β- tubulin	BT2A	BT2B	Glass and Donaldson (1995)
Dothiorella	ITS	ITS5	ITS4	White et al. (1990)
	TEF	728F	986R	Carbone and Kohn (1999)
Fusarium	RPB1	5F2 and 7cF	7cR and 11aR	Reeb et al. 2004
	RPB2	Fa and F5	G2R and F7	O'Donnell et al. 2010
Gilbertella	ITS	V9G:	LR3	de Hoog and Gerrits Van den Ende 1998
Lasiodiplodia	ITS	ITS5	ITS4	White et al. (1990)
	TEF	728F	986R	Carbone and Kohn (1999)
	β- tubulin	BT2A	BT2B	Glass and Donaldson (1995)
Mucor	LSU	NL1	1492R	O'Donnel (1993)
				Vilgalys and Hester 1990
Neofusicoccum	ITS	ITS5	ITS4	White et al. (1990)
	LSU	LROR	LR5	Vilgalys and Hester (1990)
	SSU	NS1	NS4	White et al. (1990)
	TEF	728F	986R	Carbone and Kohn (1999)
	β- tubulin	BT2A	BT2B	Glass and Donaldson (1995)
Pestalotiopsis	ITS	ITS5	ITS4	White et al. 1990
	TEF	526F	1567R	Rehner 2001
	β-tubulin	BT2A	BT2B	Glass and Donaldson 1995; O'Donnell and Cigelnik 1997
Phyllosticta	ITS	ITS1	ITS4	White et al. 1990
	ACT	ACT512F	ACT783R	Carbone and Kohn 1999
	TEF	EF1–728F	EF1–786R	Carbone and Kohn 1999
	GPDH	GDF1	Gpd2–LM	Myllys et al. 2002; Guerber et al. 2003
Phytophthora	LSU	LROR-O (LSUFint)	LR6-O (LSURint)	Blair et al. (2008)
	β-tubulin	Btub_F1	Btub_R1A	Blair et al. (2008)
	cox2	FM35	Phy10b	Martin et al. (2014)
	nad9	Nad9-F	Nad9-R	Blair et al. (2008)
	rps10	Prv9-F	Prv9-R	Blair et al. (2008)
Puccinia	LSU	Rust 2INV	LR6	Aime (2006), Vilgalys and Hester (1990)
	SSU	NS1	Rust 18SR	White et al. (1990), Aime (2006)
	ITS	ITS5-u	ITS4	Pfunder et al. (2001); White et al. (1990)

Table 1 (continued)

Genus	Gene regions	Primers		Reference
		Forward	Reverse	
Pyrenophora	ITS	ITS5	ITS4	White et al. 1990
	LSU	LROR	LR5	Vilgalys and Hester (1990)
	GPDH	GDF	GDR	Templeton et al. 1992
Pythium	5.8S, ITS2, LSU	Oom-up5.8S01	Un-lo28S1220	Man in 't Veld et al. (2002), Bala et al. (2010a)
	SSU, ITS1, 5.8S	NS1	Oom-lo5.8S47	White et al. (1990), Man in 't Veld et al. (2002)
	cox2	COX2F, FM35, FM82	COX2R, FM78_Pyt, FM52, FM83, Oom-cox1-lev-lo	Hudspeth et al. (2000), Martin (2000), Martin and Tooley (2003b), Robideau et al. (2011), Eggertson (2012)
	β-tubulin	BtubF1A, Oom-Btub-up-415	Oom-Btub-lo-1401, BT-R2 (5′- CTTGATGTTG TTNGGRATCCACTC-3′)	Bilodeau et al. (2007), Blair et al. (2008), this study
Rhizopus	ITS	V9G	LR3	de Hoog and Gerrits Van den Ende 1998
Stagonosporopsis	ITS	V9G/ITS1	ITS4	V9G, de Hoog and Gerrits Van den Ende 1998
	SSU	NS1	NS4	White et al. 1990
	LSU	LROR	LR7	Rehner and Samuels 1994; Vilgalys and Hester 1990
	CAL	CAL-228F	CAL-737R /CAL2Rd	Carbone and Kohn (1999), Quaedvlieg et al. (2011)
	ACT	ACT-512F	ACT-783R	Carbone and Kohn (1999)
	β-tubulin	BT2Fd	BT4R	Woudenberg et al. (2009)
Ustilago	ITS	ITS1F	ITS4	Gardes and Bruns (1993), White et al. (1990)
	LSU	LROR	LR7	Vilgalys and Hester (1990)
Verticillium	ITS	ITS1-F	ITS4	Gardes and Bruns (1993), White et al. (1990)
	TEF	VEFf	VEFr	Inderbitzin et al. (2011b)
	ACT	VActF	VActR	Inderbitzin et al. (2011b)
	GPDH	VGPDf2	VGPDr	Inderbitzin et al. (2011b)
	TS	VTs3f	VTs3r	Inderbitzin et al. (2011b)

and the latest phylogenetic trees. We have not been able to include all important phytopathogenic genera (e.g. *Alternaria*, powdery mildews), but intend to update or add these in future publications. Interested parties should contact the corresponding author.

Bipolaris

Background

The genus *Bipolaris* belongs to the family *Pleosporaceae* of the *Pleosporales* in Dothideomycetes (Ascomycota). *Bipolaris* was introduced by Shoemaker (1959) and typified with *B. maydis*. *Bipolaris* species are pathogens, saprobes or endophytes mostly associated with grasses including cultivated cereals. Some species are important plant pathogens. The Bengal famine in 1943 was caused by *B. oryzae* and caused 90 % of crop losses in India as well as the loss of 1.5 million human lives (Scheffer 1997). In the 1970s, around 19 million metric tons of wheat were destroyed in the USA due to southern corn leaf blight caused by *B. maydis*. *Bipolaris sorokiniana* causes southern leaf blotch, seedling blight and crown rot. *Bipolaris sorokiniana* was confirmed as the most economically important foliar pathogen in warm areas by the conference "Wheat for the national warm areas" held in Brazil in 1990. *Bipolaris* species have also been recorded from other plant families such as *Alliaceae*, *Anacardiaceae*, *Araceae*, *Euphorbiaceae*, *Fabaceae*, *Malvaceae*, *Rutaceae* and *Zingiberaceae* (Manamgoda et al. 2011).

Species identification and numbers

Bipolaris species were formerly described in *Helminthosporium*, however, species associated with grasses were morphologically distinct from *H. velutinum*, the type species (Luttrell 1963; Ellis 1971; Alcorn 1988). In several taxonomic refinements, these graminicolous *Helminthosporium* species were segregated into four genera; *Bipolaris*, *Curvularia*, *Drechslera* and *Exserohilum* (Sivanesan 1987). Later Subramanian and Jain (1966) placed all *Bipolaris* species in *Drechslera*, but this transfer was not accepted by later authors (Sivanesan 1987; Alcorn 1988). After molecular data became available, *Drechslera* was shown to be a phylogenetically different genus from *Bipolaris* (Berbee et al. 1999). The sexual state of *Bipolaris* is *Cochliobolus* (Drechsler 1934). *Cochliobolus* is the older name but conservation of the name *Bipolaris* over *Cochliobolus* has been proposed to avoid numerous name changes and *Bipolaris* is the most common name among plant pathologists (Manamgoda et al. 2012a; Rossman et al. 2013).

Morphology-based classification of *Bipolaris* species is challenging as the asexual state has overlapping conidia and conidiophore dimensions (Sivanesan 1987). A few *Bipolaris* species are known to be host-specific, while most of the other species are generalists (Manamgoda et al. 2011). However, some of the host-specific species are known only from limited collections. Therefore, the information on host-specificity may change with further collections. Interspecific compatibility can be observed between some taxa. For example, successful hybridization leading to ascospore production has been reported between *B. zeicola* and *B. victoriae* (Nelson 1960a, b) as well as between *B. maydis* and *B. oryzae* (Alcorn 1988). However, the latter species are definitively distinct phylogenetic species and also they are commonly recorded pathogens, causing different symptoms on their respective hosts. Identification of *Bipolaris* species using morphological and biological species concepts is not always correct and it is essential to use molecular tools in identifying species. Lack of DNA sequences from type material/ex-type cultures (or other authentic material) in public sequence databases is a problematic issue regarding the molecular identification of the *Bipolaris* species (Nilsson et al. 2014). Currently there are 118 *Bipolaris* names listed in Index Fungorum (2014), but nine of them do not belong to this genus based on phylogenetic evidence.

Molecular phylogeny

The first phylogenetic analysis for *Bipolaris* with its sister genus *Curvularia* was carried out by Berbee et al. (1999) and Goh et al. (1998) using a combined ITS and GPDH analysis. These studies showed that *Bipolaris* species cluster in two clades. Combined ITS, GPDH, EF and LSU phylogenetic analysis for *Bipolaris* and *Curvularia* by Manamgoda et al. (2012a) showed that *Bipolaris* and *Curvularia* cluster into two major clades. Nine *Bipolaris* species clustered with the generic type, *Curvularia lunata* Boedijn, while other species of *Bipolaris* clustered with the generic type, *Bipolaris maydis*. Accordingly, the nine *Bipolaris* species were moved to *Curvularia,* and *Bipolaris* was maintained as a distinct genus based on the generic type and those species that clustered with it. In this section we provide a backbone tree (Table 2, Fig. 1) for *Bipolaris* using combined ITS and GPDH sequence data.

Recommended genetic markers

GPDH is the best single genetic marker for the genus *Bipolaris* (Manamgoda et al. 2012a). Combined ITS, EF and GPDH can resolve almost all species of *Bipolaris* currently known from sequence data (Manamgoda et al. 2012a).

Table 2 *Bipolaris*. Details of the isolates used in the phylogenetic tree

Species	Isolate	Host	GenBank accession number		
			ITS	GPDH	TEF
Bipolaris chloridis	**CBS 242.77***	*Chloris gayana*	JN192372	JN600961	
B. cynodontis	**ICMP 6128***	*Cynodon dactylon*	JX256412	JX276427	JX266581
B. drechsleri	**CBS 136207**	*Microstegium vimineum*	KF500530	KF500533	
B. drechsleri	CBS 136208	*Microstegium vimineum*	KF500532	KF500535	
B. eleusines	**8749C***	*Eleusine indica*	AF081451	AF081405	
B. luttrellii	**14643-1***	*Dactyloctenium aegyptium*	AF071350	AF081402	
B. maydis	**C5***	*Zea mays*	AF071325	AF081380	
B. melinidis	**BRIP 12898**	*Melinis minutiflora*	JN601035	JN600972	
B. microlenae	**CBS 280.91**	*Microlaena stipoides*	JN601032	JN600974	JN601017
B. oryzae	**MFLUCC 100694***	*Oryza sativa*	JX256413	JX276428	JX266582
B. oryzae	MFLUCC 100716	*O. sativa*	JX256415	JX276429	JX266584
B. peregianensis	**BRIP 12970**	*Cynodon dactylon*	JN601034	JN600977	JN601022
B. sorghicola	**MAFF511378***	*Sorghum sudanense*	AF071332	AF081387	
B. sorokiniana	**ICMP 6233a**	*Lolium perenne*	JX256418		
B. urochloae	**DAOM 171970***	*Urochloa panicoides*	AF071334	AF081389	
B. victoriae	**CBS 174.57***	*Avena sativa*	JN601027		JN601005
Curvularia lunata	**CBS 730.96**	Unknown	JX256429	JX276441	JX266596

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

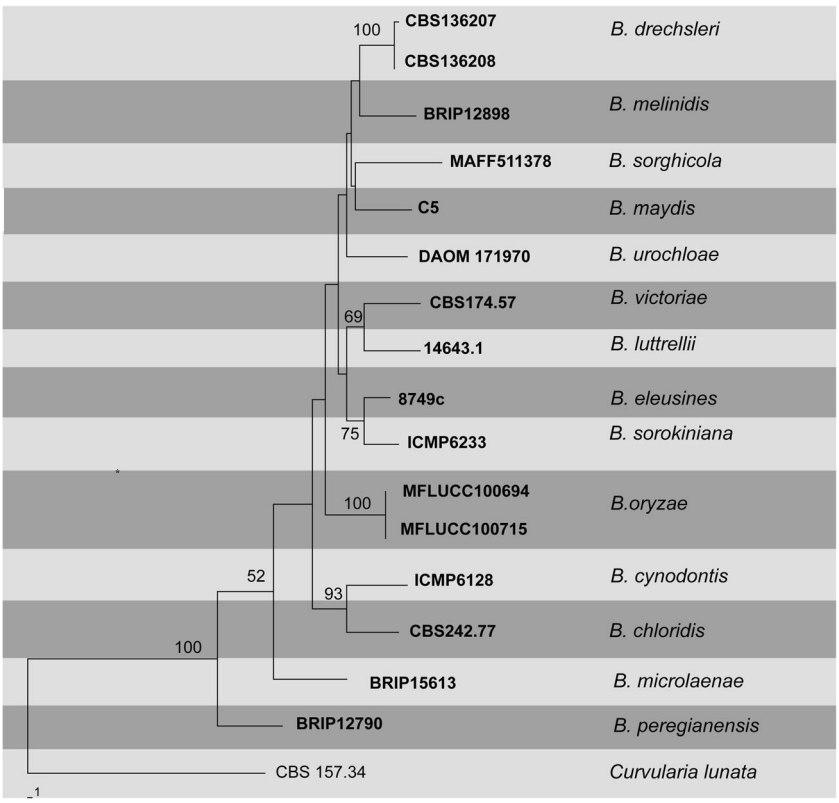


Fig. 1 Phylogram generated from parsimony analysis based on combined ITS and GPDH sequenced data of *Bipolaris*. Bootstrap support values greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*. The tree is rooted with *Curvularia lunata*

Botryosphaeriaceae

The family *Botryosphaeriaceae* is classified in the order *Botryosphaeriales* of the Dothideomycetes (Ascomycota). Members of the fungal family *Botryosphaeriaceae* were described in the 1820's as species of *Sphaeria* (Fr.) (Crous et al. 2006; Schoch et al. 2006). There have subsequently been various treatments of the family. von Arx and Müller (1954) included 15 genera, but later reduced it to 14 genera (von Arx and Müller 1975). Barr (1987) included only nine genera, which are mostly different from those of von Arx and Müller (1954). Hawksworth et al. (1995) listed five genera. Lumbsch and Huhndorf (2010) included 11 genera, while Hyde et al. (2011) and Wijayawardene et al. (2012) listed 16 genera. Liu et al. (2012) included 17 genera in the family based on molecular data and examination of generic types. Species of *Botryosphaeriaceae* range in habit from saprobic to parasitic or endophytic (Smith et al. 1996; Denman et al. 2000; Phillips et al. 2006; Slippers and Wingfield 2007; Huang et al. 2008; Pérez et al. 2010; Ghimire et al. 2011; González and Tello 2011). Members are cosmopolitan in distribution and occur on a wide range of monocotyledonous, dicotyledonous and gymnosperm hosts; on woody branches, herbaceous leaves, stems and culms of grasses; and on twigs and in the thalli of lichens (Barr 1987; Denman et al. 2000; Mohali et al. 2007; Lazzizera et al. 2008; Marincowitz et al. 2008).

Species identification and numbers

Currently, more than 2,000 species names are linked to *Botryosphaeriaceae*, including sexual and asexual states of *Diplodia, Botryosphaeria, Fusicoccum, Dothiorella, Lasiodiplodia* and *Sphaeropsis*. Identification to genus and species is presently undergoing major revision and it is likely that many older names will not be used in modern treatments. Identification of species in *Botryosphaeria*, *Diplodia*, *Dothiorella*, *Lasiodiplodia* and *Neofusicoccum* are dealt separately under this family entry.

Molecular phylogeny

Recent advances in DNA-based molecular techniques have begun to provide efficient tools to characterize the presence and identity of species of the *Botryosphaeriaceae* (Slippers and Wingfield 2007). Studies applying these tools are revealing significantly greater diversity on some hosts than was previously realized. Recent studies on the taxonomy of *Botryosphaeria* have employed molecular methods to reveal phylogenetic relationships among species (Jacobs and Rehner 1998) and to resolve species complexes (Denman et al. 2003; Alves et al. 2004; Phillips et al. 2005). Two major clades corresponding to species with *Diplodia* and *Fusicoccum* asexual morphs were revealed based on ITS phylogenies (Jacobs and Rehner 1998; Denman et al. 2003). Later studies, including additional species and a larger suite of genetic markers, supported this grouping (Zhou and Stanosz 2001; Alves et al. 2004; Slippers et al. 2004d). *Lasiodiplodia* has been treated as a distinct genus from *Diplodia* by many authors due to its distinct phylogeny (usually ITS or EF-1α) and morphology (striated or smooth conidia and presence or absence of pseudoparaphyses). Pavlic et al. (2004) employed morphological and phylogenetic data to separate *Lasiodiplodia* from *Diplodia*. The value of the intron-dominated sequences of the ITS, β-tubulin and TEF markers (on which most previous studies were based) to infer phylogenetic relationships across the diversity of the genus is, however, unclear. The more conserved mtSSU data have, for example, suggested that *B. dothidea* and *B. corticis* (Demaree and Wilcox) are unrelated to *Fusicoccum* (Zhou and Stanosz 2001) even though they are typically assigned to this genus.

Most taxonomic studies on *Botryosphaeriaceae* using molecular data have employed ITS rDNA phylogenies, but this single marker can underestimate the species diversity among closely related or cryptic species. Multiple gene sequence concordance phylogenies have therefore been applied to identify cryptic or previously overlooked species of *Botryosphaeriaceae* (Slippers et al. 2004a, b, c; Burgess et al. 2005; Phillips et al. 2005). As the elongation fctor 1-alpha (TEF) gene is consistently more variable than the ITS rDNA region in these fungi, most commonly data from TEF have been combined with ITS sequence data. Unfortunately no single genetic region is sufficient to distinguish all species, because not all single nucleotide polymorphisms (SNPs) represent restriction sites, especially between some closely related species.

The *Botryosphaeriaceae* has been separated into numerous distinct genera (Crous et al. 2006; Liu et al. 2012). A natural classification is needed for a more stable and accurate taxonomic framework and this will strongly influence the understanding of the ecology of the *Botryosphaeriaceae*. In this part we provide a tree to the genera of *Botryosphaeriaceae* (Table 3, Fig. 2) and deal with the important genera *Botryosphaeria*, *Diplodia*, *Dothiorella*, *Lasiodiplodia* and *Neofusicoccum* in the following parts.

Recommended genetic markers

- LSU, SSU, β-tubulin and ITS–generic level
- TEF–species level

LSU has been shown to be suitable for distinguishing many ascomycetes at the generic level due to its relatively conserved nature (Crous et al. 2006; Schoch et al. 2006; Hibbett et al. 2007). The study of Liu et al. (2012) suggested that the combined TEF and β- tubulin gene

Table 3 *Botryosphaeriaceae*. Details of the isolates used in the phylogenetic tree

Species	Isolate	ITS	β- tubulin	TEF	SSU	LSU
Barriopsis fusca	**CBS 174.26***	EU673330	EU673109	EU673296	EU673182	DQ377857
B. iraniana	**IRAN1448C***	KF766150	KF766127	FJ919652	KF766231	KF766318
Botryobambusa fusicoccum	**MFLUCC 11-0143***	JX646792	–	JX646857	JX646826	JX646809
Botryosphaeria agaves	**MFLUCC 11-0125***	JX646791	JX646841	JX646856	JX646825	JX646808
B. corticis	**CBS 119047***	DQ299245	EU673107	EU017539	EU673175	EU673244
B. dothidea	**CMW 8000***	AY236949	AY236927	AY236898	EU673173	AY928047
B. fusispora	**MFLUCC 10-0098***	JX646789	JX646839	JX646854	JX646823	JX646806
Cophinforma eucalypti	**MFLUCC 11-0425***	JX646800	JX646848	JX646865	JX646833	JX646817
Diplodia corticola	**CBS 112549***	AY259100	DQ458853	AY573227	EU673206	AY928051
D. cupressi	**CBS 168.87***	DQ458893	DQ458861	DQ458878	EU673209	EU673263
D. mutila	**CBS 112553***	AY259093	DQ458850	AY573219	EU673213	AY928049
Dothiorella iberica	**CBS 115041***	AY573202	EU673096	AY573222	EU673155	AY928053
D. sarmentorum	**IMI 63581b***	AY573212	EU673102	AY573235	EU673158	AY928052
D. thailandica	**MFLUCC11-0438***	JX646796	JX646844	JX646861	JX646829	JX646813
Endomelanconiopsis endophytica	**CBS 120397***	KF766164	KF766131	EU683637	KF766249	EU683629
E. microspora	**CBS 353.97***	KF766165	–	EU683636	KF766250	KF766330
Lasiodiplodia crassispora	**CBS 118741***	DQ103550	EU673133	EU673303	EU673190	DQ377901
L. gonubiensis	**CBS 115812***	DQ458892	DQ458860	DQ458877	EU673193	DQ377902
L. parva	**CBS 494.78***	EF622084	EU673114	EF622064	EU673201	EU673258
L. pseudotheobromae	**CBS 116459***	EF622077	EU673111	EF622057	EU673199	EU673256
L. theobromae	**CBS 164.96***	AY640255	EU673110	AY640258	EU673196	EU673253
Macrophomina phaseolina	**CBS 227.33***	KF766195	–	KF766422	KF766281	KF766364
Neodeightonia palmicola	**MFLUCC 10-0822***	HQ199221	–	–	HQ199223	HQ199222
N. phoenicum	**CBS 122528***	EU673340	EU673116	EU673309	EU673205	EU673261
N. subglobosa	**MFLUCC11-0163***	JX646794	JX646842	JX646859	–	JX646811
Neofusicoccum luteum	**CBS 110299***	AY259091	DQ458848	AY573217	EU673148	AY928043
N. mangiferae	**CBS 118532***	AY615186	AY615173	DQ093220	EU673154	DQ377921
N. parvum	**CMW 9081***	AY236943	AY236917	AY236888	EU673151	AY928045
Neoscytalidium dimidiatum	IP127881	AF258603	FM211167	EU144063	AF258603	DQ377925
N. hyalinum	**CBS145.78***	KF531816	KF531796	KF531795	KF531815	DQ377922
N. novaehollandiae	**WAC 12691***	EF585543	–	EF585574	–	EF585548
Phaeobotryon mamane	**CPC 12440***	EU673332	EU673121	EU673298	EU673184	EU673248
Pseudofusicoccum adansoniae	**WAC 12689***	EF585534	–	EF585567	–	EF585554
P. ardesiacum	**CMW 26159***	KF766221	–	EU144075	KF766307	KF766387
P. kimberleyense	**CMW 26156***	KF766222	–	EU144072	KF766308	KF766388
P. stromaticum	**CMW13434***	KF766223	EU673094	KF766437	KF766309	KF766389
Spencermartinsia viticola	**CBS 117009***	AY905554	EU673104	AY905559	EU673165	DQ377873
Sphaeropsis citrigena	**ICMP 16812***	EU673328	EU673140	EU673294	EU673180	EU673246
S. eucalypticola	**CBS 133993***	JX646802	JX646850	JX646867	JX646835	JX646819
S. porosa	**CBS 110496***	AY343379	EU673130	AY343340	EU673179	DQ377894
S. visci	**CBS 186.97***	EU673325	EU673128	EU673293	EU673178	DQ377868
Tiarosporella graminis var. karoo	CBS 118718	KF531828	KF531808	KF531807	KF531827	DQ377939
T. tritici	**CBS 118719***	KF531830	KF531810	KF531809	KF531829	DQ377941
T. urbis-rosarum	**CMW 36479***	JQ239408	JQ239382	JQ239395	–	JQ239421
Melanops tulasnei	**CBS 116805***	FJ824769	–	KF766423	KF766474	KF766365

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

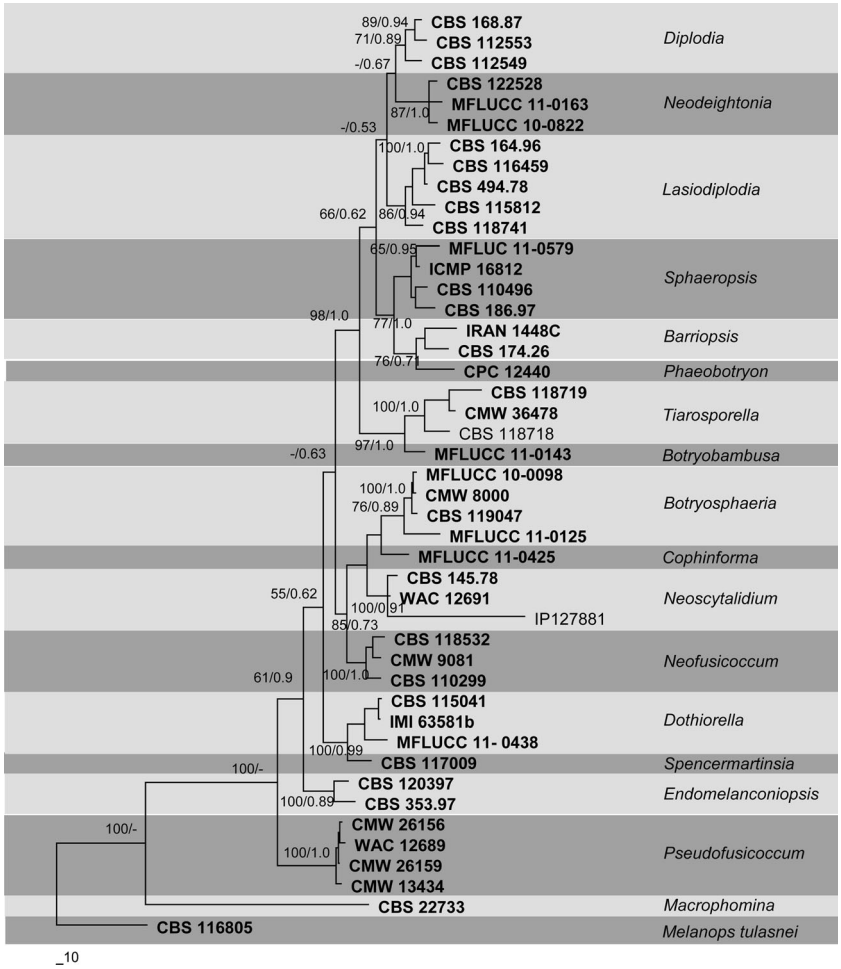


Fig. 2 Phylogram generated from parsimony analysis based on combined SSU, LSU, TEF, β-tubulin and ITS sequence data of *Botryosphaeriaceae*. Parsimony bootstrap support values greater than 50 % and Bayesian posterior probabilities greater than 0.5 are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*. The *scale bar* indicates ten changes. The tree is rooted with *Melanops tulasnei* CBS 116805

analysis is best for delimiting genera of *Botryosphaeriaceae*. It has also been recommended that the RPB2 gene should be considered in similar combined analyses of genus and species levels of *Botryosphaeriaceae* (Pavlic et al. 2009a, b).

Botryosphaeria

Background

The genus *Botryosphaeria* (*Botryosphaeriaceae*) was introduced by Cesati and de Notaris (1863), amended by Saccardo (1877), and is based on the type species *Botryosphaeria dothidea* (Barr 1972; Slippers et al. 2004c). Species in *Botryosphaeria* were described largely on the basis of the morphology of their ascomata and host associations, and this has led to a proliferation of names. von Arx and Müller (1954) examined 183 taxa of *Botryosphaeriales* and reduced them to 11 species, with extensive synonymies under *B. dothidea* and *B. quercuum*, together with nine new combinations. In later studies these synonymies were not always accepted (Shoemaker 1964; Sivanesan 1984; Slippers et al. 2004a). Slippers et al. (2004b) epitypified the type species *Botryosphaeria dothidea* based on morphology and phylogeny (combined ITS, TEF and β-tubulin analysis) and this enabled a better resolution of species. Species of *Botryosphaeria* occur on a wide range of monocotyledonous, dicotyledonous and gymnosperm hosts, on woody branches, herbaceous leaves and grasses (Barr 1987). The life styles may be saprobic, parasitic and endophytic (Smith et al. 1996; Denman et al. 2000), and species can cause die-back and canker diseases of numerous woody hosts (von Arx 1987). Species in the genus *Botryosphaeria* have hyaline to dark ascospores, multiloculate ascomata, and a wide range of asexual morphs that typically lack a mucoid sheath and apical appendage.

Species identification and numbers

More than 18 asexual genera have been associated with *Botryosphaeria*. A phylogenetic study based on part of the 28S ribosomal DNA gene together with morphological characters revealed that *Botryosphaeria* comprises several distinct lineages, each comprising individual genera (Crous et al. 2006). In that study, only *B. dothidea* and *B. corticis* were retained in *Botryosphaeria*, while most species were reduced

to synonymy under *Diplodia* (conidia mostly ovoid, pigmented, thick-walled), or *Fusicoccum* (conidia mostly fusoid, hyaline, thin-walled). Studies have also linked *Botryosphaeria* to species with pigmented, septate ascospores and *Dothiorella* asexual morphs, or *Fusicoccum* asexual morphs with *Dichomera* synanamorphs. More recently *B. agaves* (which has been epitypified), *B. fusispora* (Liu et al. 2012), and *B. schariffi* (Abdollahzadeh et al. 2013) were described in the genus *Botryosphaeria,* while *B. fabicerciana* was illustrated from *Eucalyptus* sp. in southern China (Chen et al. 2011). Phylogenetically, *B. fabicerciana* is closely related to *B. corticis*, *B. dothidea*, *B schariffi* and *B. ramosa*. The present phylogenetic analysis was performed based on up to date holotype or ex-epitype sequence data available in GenBank (Table 4).

Molecular phylogeny

Recent studies on the taxonomy of *Botryosphaeria* have employed molecular methods to reveal phylogenetic relationships among species (Jacobs and Rehner 1998) and to resolve species complexes (Smith and Stanosz 2001; Phillips et al. 2002, 2005; Denman et al. 2003; Alves et al. 2004; Slippers et al. 2004c). Studies including additional species and a larger suite of DNA-based markers supported this grouping (Zhou and Stanosz 2001; Alves et al. 2004; Slippers et al. 2004c). Based on combined ITS and TEF sequence data seven species are currently recognised in *Botryosphaeria* (Phillips et al. 2013). The phylogenetic tree constructed with holotype or ex-epitype sequences is presented in Fig. 3.

Recommended genetic markers

- LSU, SSU and ITS–generic level
- β-tubulin and TEF–species level

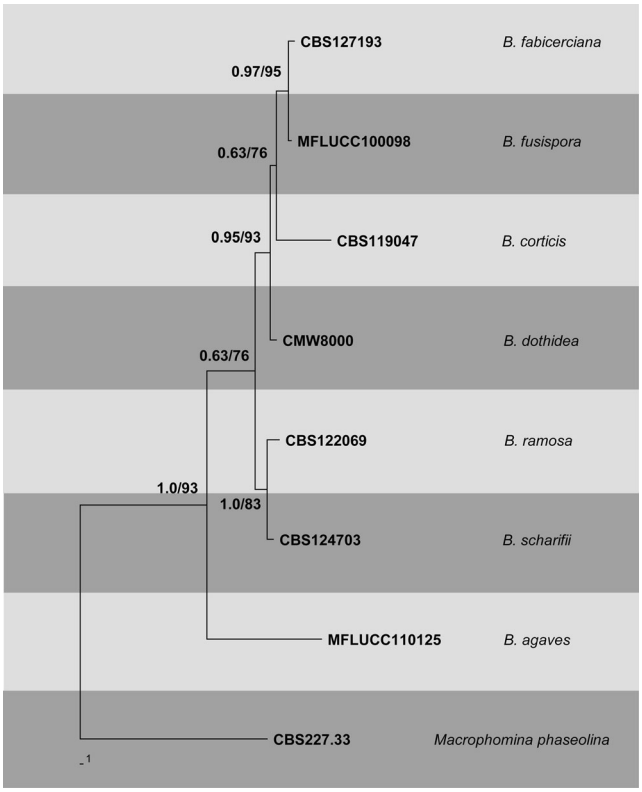


Fig. 3 Phylogram generated from parsimony analysis based on combined ITS, TEF, β- tubulin, LSU and SSU sequenced data of *Botryosphaeria*. Parsimony bootstrap support values greater than 50 % and Bayesian posterior probabilities greater than 0.5 are indicated near the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*. The tree is rooted with *Macrophomina phaseolina* CBS 227.33

Botrytis

Background

Erected by Micheli in 1729, the genus *Botrytis* is one of the first described genera of fungi. Persoon (1801) designated five

Table 4 *Botryosphaeria*. Details of the ex-type and voucher isolates used in the phylogenetic tree

Species	Isolate	GenBank accession numbers				
		SSU	ITS	LSU	TEF	β-tubulin
Botryosphaeria agaves	**CBS 133992***	JX646825	JX646825	JX646808	JX646856	JX646841
B. corticis	**CBS 119047***	EU673175	DQ299245	EU673244	EU017539	EU673107
B. dothidea	**CBS 115476***	EU673173	AY236949	AY928047	AY236898	AY236927
B. fabicerciana	**CBS 127193***	N/A	HQ332197	N/A	HQ332213	N/A
B. fusispora	**MFLUCC 10-0098***	JX646823	JX646789	JX646806	JX646854	JX646839
B. ramose	**CBS 122069***	N/A	EU144055	N/A	EU144070	N/A
B. scharifii	**CBS 124703***	N/A	JQ772020	N/A	JQ772057	N/A
Macrophomina phaseolina	**CBS 227.33***	KF531823	KF531825	DQ377906	KF531804	KF531806

Type strains and voucher stains are bolded

species under the binomial system of Linnaeus, validated the genus, and included one of Micheli's species, *B. cinerea*, so named by Von Haller (1771). The genus name refers to the structure of the macroconidia, which rise and form clusters with the shape of grape bunches: 'botryose'. *Botrytis* is the asexual stage of *Botryotinia*. The *Botrytis* community has in its recent meeting (Italy, 23–28 June 2013) unanimously recommended the exclusive use of the asexual name *Botrytis* over *Botryotinia,* the name of the sexual stage, since *Botrytis* is historically the oldest name and it is commonly used by plant pathologists, breeders and growers. In line with this recommendation, a list of generic names of fungi for protection under the International Code of Nomenclature has included this genus under the name *Botrytis* and not *Botryotinia* (Kirk et al. 2013). We therefore follow this recommendation in this paper and use *Botrytis*. Species of the genus *Botrytis* infect >250 host species, including major greenhouse and field crops such as tomato, grape, strawberry, onion and ornamentals such as rose, lily, and tulip (Staats et al. 2005). Most *Botrytis* species are necrotrophic pathogens that (are able to) kill the host tissue during infection. Interestingly, an endophytic species (*B. deweyae*) has recently been discovered, which under appropriate conditions can cause 'spring sickness' in ornamental *Hemerocallis* (daylily) hybrids (Grant-Downton et al. 2014). *Botrytis cinerea* is the best-studied species in the genus (Williamson et al. 2007) and was recently elected as the second most important plant pathogenic fungal species (Dean et al. 2012).

In the asexual state, *Botrytis* produces different tissues including mycelia, macroconidia, microconidia, and sclerotia. Macroconidia are ellipsoidal to obovoid shape and rise from conidiophore branches into botryose clusters. They are pale brown and range in size from 9–23×8–15 μm. Microconidia are more sphaerical and much smaller than macroconidia (about 1 μm), and function as male spermatia (Groves and Loveland 1953; Faretra et al. 1988; Beever and Parkes 1993; Fukumori et al. 2004). Sclerotia are irregularly hemispherical, convex and normally have a concave surface. They are usually black, with sizes ranging between 1 and 10 mm (Whetzel 1945), and function as survival structures during winter and serve as maternal parent in the production of apothecia.

The sexual state forms fruiting bodies called apothecia: a cup- or open saucer-shaped ascoma at the top of a stalk, that acts as a platform to discharge ascospores from the ascus. *Botrytis* apothecia vary in size depending on the species, between 1 and 25 mm high and 1–6 mm diam. (Hennebert and Groves 1963; Bergquist and Lorbeer 1972). Apothecia are brown and become darker when mature (Hennebert and Groves 1963; Bergquist and Lorbeer 1972; Faretra and Antonacci 1987). Generally multiple apothecia can develop on a single sclerotium. Mature apothecia normally can be observed 2 months after fertilization (Faretra et al. 1988; Hennebert and Groves 1963; Van Der Vlugt-Bergmans et al. 1993). In the genus *Botrytis*, both homothallic and heterothallic reproductive lifestyles have been reported. Homothallic (self-fertile) species can undergo sexual reproduction and form apothecia and generate progeny in the absence of a mating partner, e.g. *B. porri* and *B. globosa* (Buchwald 1953; Elliott 1964). By contrast, heterothallic (self-sterile, self-incompatible) species require isolates with compatible mating types in order to complete the sexual cycle. *B. cinerea* is considered a typical heterothallic fungus (Elliott 1964; Faretra et al. 1988). Mating is controlled by the mating type locus with two alleles, MAT1-1 and MAT1-2 (Faretra et al. 1988), each carrying two distinct, non-homologous genes (Amselem et al. 2011).

Species identification and numbers

Approximately half of the *Botrytis* species are named after the host that they are derived from (listed in Table 5). One hybrid species, *B. allii* which originated from hybridization between *B. byssoidea* and *B. aclada* (Nielsen and Yohalem 2001; Yohalem et al. 2003) could not be placed in the phylogeny (Staats et al. 2005) and was omitted from Table 3. The genus *Botrytis* predominantly comprises narrow host range pathogens that infect a single, or a few (often related) host species. There are two exceptions to this rule: *B. cinerea* can infect more than 200 host species (Jarvis 1977), and *B. pseudocinerea* has been isolated from several unrelated host species (Fournier et al. 2005; Leroch et al. 2013).

The taxonomic classification and nomenclature in *Botrytis* have rarely been comprehensively reviewed. Morphological descriptions of most species have been published in the 19th and first half of the 20th century in separate papers, many of which are not easily accessible. The most recent taxonomic compilation of the genus is in a monograph by Jarvis (1977), which also lists ~25 excluded or doubtful species, and briefly describes the historical debates between mycologists and the confusion in classification of *Botrytis* species. Morphological features were often inadequate to distinguish species and the variability among isolates of the same species further complicated the situation (Jarvis 1977). Recent studies have identified *B. cinerea* and *B. pseudocinerea* as species that are very similar in morphology, yet recognized as distinct taxa that diverged several million years ago (Walker et al. 2011). Even more puzzling, the morphology and narrow host range of *B. fabae* separate this species clearly from *B. cinerea* and *B. pseudocinerea*, but phylogenetic studies revealed it to be a sister species of *B. cinerea* (see below). These examples illustrate the limitations of morphological characters for *Botrytis* species identification.

Molecular phylogeny

Holst-Jensen et al. (1998) were the first to use nuclear ribosomal ITS sequences to infer a phylogeny of the family

Table 5 *Botrytis*. Details of the isolates used in the phylogenetic tree

Species	Isolate	Host	GenBank accession numbers				
			RPB2	HSP60	G3DPDH	NEP1	NEP2
Botrytis aclada	MUCL8415	*Allium* spp.	AJ745664	AJ716050	AJ704992	AM087059	AM087087
B. byssoidea	**MUCL94**	*Allium* spp.	AJ745670	AJ716059	AJ704998	AM087045	AM087079
B. calthae	MUCL1089	*Caltha palustris*	AJ745672	AJ716061	AJ705000	AM087031[a]	AM087088[a]
B. cinerea	**MUCL87**	>200 species	AJ745676	AJ716065	AJ705004	DQ211824[a]	DQ211825[a]
B. caroliniana	**CB15***	*Rubus fruticosus*	JF811590	JF811587	JF811584	JF811593	NA
B. convoluta	MUCL11595	*Iris* spp.	AJ745680	AJ716069	AJ705008	AM087035	AM087062
B. croci	**MUCL436**	*Crocus* spp.	AJ745681	AJ716070	AJ705009	AM087047	AM087065
B. deweyae	**CBS134649***	*Hemerocallis* spp.	HG799518	HG799519	HG799521	HG799527	HG799520
B. elliptica	BE9714	*Lilium* spp.	AJ745684	AJ716073	AJ705012	AM087049	AM087080
B. fabae	**MUCL98**	*Vicia* spp.	AJ745686	AJ716075	AJ705014	DQ211829	DQ211831
B. ficariarum	**MUCL376**	*Ficaria verna*	AJ745688	AJ716077	AJ705016	AM087056	AM087085a
B. fabiopsis	**BC-2***	*Vicia faba*	EU514473	EU514482	EU519211	NA	NA
B. galanthina	MUCL435	*Galanthus* spp.	AJ745689	AJ716079	AJ705018	AM087057	AM087067[a]
B. gladiolorum	MUCL3865	*Gladiolus* spp.	AJ745692	AJ716081	AJ705020	AM087041	AM087072[a]
B. globosa	MUCL444	*Allium ursinum*	AJ745693	AJ716083	AJ705022	AM087044[a]	AM087071
B. hyacinthi	**MUCL442**	*Hyacinthus* spp.	AJ745696	AJ716085	AJ705024	AM087048	AM087066[a]
B. narcissicola	MUCL2120	*Narcissus* spp.	AJ745697	AJ716087	AJ705026	AM087046	AM087078
B. paeoniae	MUCL16084	*Paeonia* spp.	AJ745700	AJ716089	AJ705028	AM087033	AM087064[a]
B. pelargonii	**CBS 497.50**	*Pelargonium* spp.	AJ745662	AJ716046	AJ704990	AM087030	DQ211834[a]
B. polyblastis	**CBS287.38**	*Narcissus* spp.	AJ745702	AJ716091	AJ705030	AM087039	AM087074
B. porri	**MUCL3234**	*Allium* spp.	AJ745704	AJ716093	AJ705032	AM087060	AM087063
B. pseudocinerea	VD110	*Vitis vinifera*	Unpublished	Unpublished	Unpublished	NA	NA
B. ranunculi	CBS178.63	*Ranunculus* spp.	AJ745706	AJ716095	AJ705034	AM087054	AM087086
B. sinoallii	HMAS250008	*Allium* spp.	EU514479	EU514488	EU519217	NA	NA
B. sphaerosperma	MUCL21481	*Allium triquetrum*	AJ745708	AJ716096	AJ705035	AM087042	AM087068
B. squamosa	MUCL1107	*Allium cepa*	AJ745710	AJ716098	AJ705037	AM087052	AM087084
B. tulipae	BT9830	*Tulipa* spp.	AJ745713	AJ716102	AJ705041	AM087037	AM087077
Monilinia fructigena	9201	Stone fruit and pome fruit	AJ745715	AJ716047	AJ705043	NA	NA
Sclerotinia sclerotiorum	484	>400 species	AJ745716	AJ716048	AJ705044	NA	NA

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

[a] sequences obtained from a different isolate than the one listed in the table.

Sclerotiniaceae, including several members of the genus *Botrytis*. The relationships among many *Botrytis* species could not be resolved because of the limited number of informative characters, however the study permitted the conclusion that *Botryotinia* asexual morphs along with *Botrytis* sexual morphs constitute a monophyletic lineage (Holst-Jensen et al. 1998). The phylogeny of the *Sclerotiniaceae* was further refined by Andrew et al. (2012) using three protein-coding genes: calmodulin, glyceraldehyde 3-phosphate dehydrogenase G3PDH and heat shock protein HSP60.

Staats et al. (2005) performed a comprehensive phylogenetic analysis of the genus *Botrytis*, at that time comprising 22 recognized species and one hybrid. Using three protein-coding genes (G3PDH, HSP60 and the DNA-dependent RNA polymerase subunit II gene RPB2), they corroborated the morphological and host plant-based classification of *Botrytis* spp. and divided the genus into two (rather widely separated) clades. Clade I contained species that only infect eudicot plants, while Clade II contained species that can infect either eudicotyledonous or monocotyledonous plants. The use of the same three genes facilitated the discovery of *Botrytis sinoallii*, a new species infecting *Allium* spp., and its distinction from other *Botrytis* spp. infecting the same hosts (Zhang et al. 2010b); *B. fabiopsis*, a new species infecting broad bean, very distant from *B. fabae* (Zhang et al. 2010a); and *B. caroliniana*, a new species infecting blackberry (Li et al. 2012).

Two genes, encoding phytotoxic proteins NEP1 and NEP2, were shown to provide higher resolution in distinguishing species in the genus *Botrytis* because they seem to be the subject of higher evolutionary rates than the housekeeping

genes G3PDH, HSP60 and RPB2 (Staats et al. 2007a). The NEP1 and NEP2 genes were shown to have evolved under positive selection which suggested a role of these proteins in the infection process (Staats et al. 2007a). One might therefore infer that such genes cannot serve as neutral phylogenetic markers. Functional analysis in *B. cinerea* and *B. elliptica* using targeted knockout mutants failed to reveal a role of NEP genes in virulence of these two species (Staats et al. 2007b; Cuesta Arenas et al. 2010), which would lend support to considering these genes as neutral markers and adequate tools in phylogeny.

The studies by Staats et al. (2005) revealed incongruence between the phylogenies of *Botrytis* spp. and their hosts. Species infecting the same host clustered in different (sub) clades, e.g. *B. aclada*, *B. squamosa*, *B. porri*, *B. byssoidea* and *B. sinoallii* all infecting *Allium*. Conversely, closely related species can infect very different hosts, e.g. *B. elliptica* infecting the monocotyledonous host *Lilium* and *B. ficariarum* infecting the dicotyledonous host *Ficaria* (Staats et al. 2005). More recently, similar incongruence has been reported for newly described species, e.g. *B. fabiopsis* infecting *Vicia faba* is very distant from *B. fabae* infecting the same host (Zhang et al. 2010a), and *B. caroliniana* infecting blackberries and strawberries is very distant from *B. cinerea* (Li et al. 2012).

Recently, Khan et al. (2013) combined data from ITS and IGS regions with the G3PHD gene, with the aim of improving molecular identification of *Botrytis* species that cause neck rot disease on onion. ITS and IGS regions were insufficiently informative to distinguish *B. allii* and *B. byssoidea*. The sequences of ITS and IGS for *B. allii* and *B. byssoidea* confirmed that they have a close relationship, but G3PDH sequences of several *B. allii* isolates were clearly distinct, some clustering with *B. aclada* and others clustering with *B. byssoidea* (Khan et al. 2013), as might be expected for a hybrid species.

Sequence analysis of the G3PDH and β-tubulin genes amplified from herbarium specimens of *Botrytis* collected from grey mould-infected apple (deposited in 1932) enabled O'Gorman et al. (2008) to corroborate the existence of *B. mali*, a species that had been published (Ruehle 1931), but by lack of description was considered doubtful.

Figure 4 shows a maximum likelihood tree of *Botrytis* spp., based on concatenated sequences of parts of the three genes G3PDH, HSP60 and RPB2 (amplified using primers defined by Staats et al. (2005). Five species described after publication of the phylogeny by Staats et al. (2005), i.e. *B. caroliniana, B. deweyae, B. fabiopsis, B. pseudocinerea* and *B. sinoallii*, clearly cluster within the genus and are genuine *Botrytis* species. *Botrytis mali* could not be included in the tree due to lack of sequences for the HSP60 and RPB2 genes. Based on G3PDH and ß-tubulin sequences it would cluster with *B. paeoniae* (O'Gorman et al. 2008).

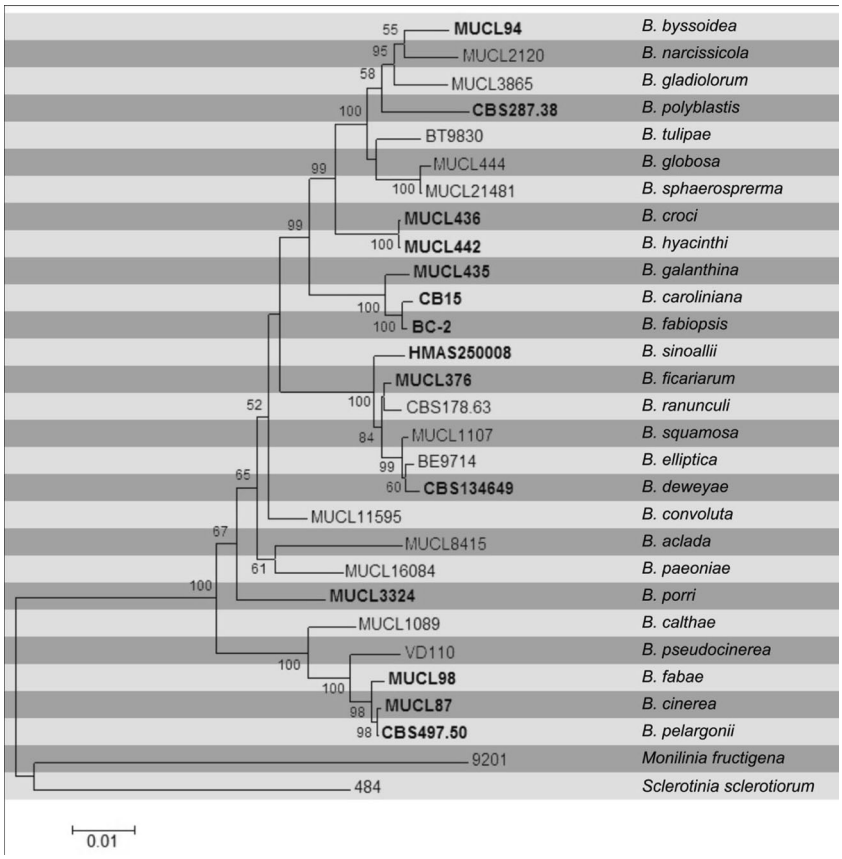


Fig. 4 Phylogram generated from Maximum likelihood analysis based on combined sequences of G3PDH, HSP60 and RPB2 from 28 recognized *Botrytis* species. Bootstrap support values greater than 50 % are indicated above/below the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*. The tree is rooted with *Monilinia fructigena* and *Sclerotinia sclerotiorum*

The *Botrytis cinerea* species complex

The *Botrytis* 'dicot' clade I consists of *B. cinerea*, *B. pelargonii*, *B. fabae, B. pseudocinerea* and *B. calthae*. Molecular data do not fully support a separation between *B. pelargonii* and *B. cinerea* (Staats et al. 2005, 2007a; Plesken et al. 2014), and the existence of *B. pelargonii* as a separate species is therefore doubtful. As mentioned above, *B. cinerea* and *B. pseudocinerea* are morphologically very similar yet phylogenetically more distant from each other than *B. cinerea* and *B. fabae*. All genes tested so far place *B. calthae* as most remote to all other clade I species.

Botrytis cinerea not only has a broad host range, but also shows considerable phenotypic variability in vegetative growth, conidiation and sclerotium formation (Kerssies et al. 1997; Martinez et al. 2003; Schumacher et al. 2013). Numerous studies have documented a similar variability in genotypic characters, such as amplified restriction length polymorphism, detection of transposable elements and microsatellite heterogeneity. Recently, *B. cinerea* strains have been described that produce bikaverin, a reddish pigment. These strains contain an intact bikaverin biosynthesis gene cluster (presumably acquired by horizontal gene transfer from *Fusarium*), which is partially deleted and nonfunctional in most non-bikaverin producing *B. cinerea* strains (Campbell et al. 2012; Schumacher et al. 2013

A subdivision of *B. cinerea* into genetically distinct groups has proved to be difficult. Analysis of the presence or absence of two types of transposable elements, named Boty (Diolez et al. 1995) and Flipper (Levis et al. 1997), was adopted as a tool to divide isolates into four transposon types, Transposa (isolates having both elements), Vacuma (isolates having neither element), Boty and Flipper (Giraud et al. 1997, 1999). This classification led to the discovery of *B. pseudocinerea*, which is usually Vacuma, but the transposon-based classification turned out to be of limited use since *B. cinerea* populations appear to consist of mixtures of different transposon types. Intriguingly, predominance of a certain type appears to be influenced by the host. While on grapes, strawberries and tomatoes, Transposa types are predominant, whereas *B. cinerea* populations from kiwi and apples are dominated by Vacuma types (Esterio et al. 2011; Johnston et al. 2013; Muñoz et al. 2002; Samuel et al. 2012; M. Hahn, unpublished). Reasons for this observation are unknown.

Evidence for genetic differentiation of *B. cinerea* populations with different host preference was obtained with microsatellite markers. In France, isolates from grapes and blackberries were shown to be divergent, indicating limited gene flow between populations on these host plants (Fournier and Giraud 2008). A recent study on grey mould isolates from fungicide-treated strawberry fields revealed the existence of a predominant *B. cinerea* genotype, named group S, that is closely related to but distinct from the common genotype of *B. cinerea* (Leroch et al. 2013). Sequencing of the highly polymorphic *MRR1* gene revealed that group S isolates show more than 4 % divergence from *B. cinerea* strains B05.10 and T4, which have *MRR1* genes with 99.9 % identity. Further sequencing of *HSP60* and *NEP2*, and of two FUNYBASE genes that are suitable for phylogenetic studies (Marthey et al. 2008), partially supported the genetic separation of group S isolates (Johnston et al. 2013; Leroch et al. 2013). Genome sequencing of several *B. cinerea* and group S strains, and the analysis of additional polymorphic genes in isolates collected from various host plants in different countries, revealed at least two subclades that could be separated from the common *B. cinerea* genotype (Plesken and Hahn, unpublished). In fungicide-treated strawberry fields group S isolates dominated, whereas grapes were infected almost exclusively by common *B. cinerea* genotypes. These data, together with those of putative new endophytic *Botrytis* taxa that grouped close to *B. cinerea* (Shipunov et al. 2008), support the idea that *B. cinerea* represents a species complex, comprising genetically and phenotypically distinct groups.

Recommended genetic markers

G3PDH, RPB2 and HSP60—placement within the *Sclerotiniaceae* and the ascomycetes

NEP1 and NEP2—for higher resolution within the genus *Botrytis*,

The NEP1 and NEP2 genes are under positive selection (Staats et al. 2007a) and potentially influence interactions with the host plants. The NEP genes should therefore be used with caution.

Research is ongoing to identify a set of highly polymorphic genes that better resolve the phylogeny of taxa in clade I (Hahn et al., unpublished). It remains to be established whether those gene are equally useful for resolving the clade II species, and whether universal primers can be designed before these genes can be employed to infer a comprehensive phylogeny of the entire genus.

Choanephora

Background

The genus *Choanephora* belongs to family *Choanephoraceae* in the order *Mucorales* (former Zygomycota). The genus was introduced by Currey (1873) for *C. cunninghamii,* to replace the generic name of his newly described species *Cunninghamia infundibulifera*, as *Cunninghamia* already existed as a genus of conifers. Because the specific epithet could not be retained, *Choanephora cunninghamia* remained invalid, based on the same type as *Cunninghamia infundibulifera*. The proper name *Choanephora*

infundibulifera was validly published by Saccardo (1891), so the correct authorship of the species is "(Currey) Sacc." It is also the type species of the genus. *Choanephora* was monographed by Hesseltine (1953), Milko and Beljakova (1970) and Kirk (1984). Currently the genus is classified within the family *Choanephoraceae* which can be distinguished by the presence of a persistent sporangium wall that ruptures at preformed sutures. It is furthermore placed in the subfamily *Choanephoroideae*, which is characterized by the presence of apposed suspensors and smooth zygospores (Hoffmann et al. 2013).

Both species of the genus can grow as saprobes, but they frequently become plant pathogens causing various leaf and fruit rots and blights and are commonly reported from a wide range of plant hosts, including angiosperms (monocotyledons and dicotyledons) and gymnosperms (Farr and Rossman 2014). Their distribution is worldwide, however, disease development is more common in tropical and subtropical regions characterized by high temperatures and humidity. *Choanephora cucurbitarum* is the causal agent of fruit and blossom rot of various cucurbits, e.g. yellow crookneck squash (Kucharek and Simone 1983). This species is also known from crop plants such as green beans (McMillan 1972), garden peas (Oikawa et al. 1986), and okra (El-Sayed and El-Sajed 2013) and is reported as an agent of wet rot of *Mesembryanthemum crystallinum* in hydroponic greenhouse culture in Japan (Kagiwada et al. 2010). It is very common during rainy summers in the southeastern United States and globally in other regions with similar climates. Recently it was isolated also from cultivated *Hyoscyamus muticus* in Japan (Abdel-Motaal et al. 2010) and *Withania* in India (Saroj et al. 2012). *Choanephora* often attacks tissues that have been damaged mechanically by insects or otherwise; plants that are poorly adapted to a hot humid climate are particularly prone to infection by the genus. The general appearance of *Choanephora* rot is similar to that of blights caused by other *Mucorales* representatives. Signs of infections on fruits or leaves include water-soaked, necrotic lesions, which progress rapidly under wet conditions. As the fungus begins to produce spores, affected tissues become dark grey-brown and hairy. This specific appearance results from the tall sporangiophores that produce a cluster of brown, one-spored sporangiola at their tips (Turkensteen 1979).

Species identification and numbers

Although more than ten species (and many varieties) have been described within this genus, only two species (viz. *Choanephora infundibulifera* and *Choanephora cucurbitarum*) were finally recognized in a monograph of the genus (Kirk 1984). These two species can be distinguished by shape and ornamentation of indehiscent sporangiola. *C. cucurbitarum* produces ellipsoid sporangiola, which are usually distinctly longitudinally striate, whereas *C. infundibulifera* forms subglobose to obovoid sporangiola with usually smooth or faint striate ornamentation. The remaining species were synonymized under these taxa (e.g. *C. mandshurica* is currently a synonym of *C. cucurbitarum*) or were moved to other genera (e.g. *C. persicaria* is a synonym of *Gilbertella persicaria*). *Choanephora circinans* with its two varieties (*C. circinans* var. *indica* and *C. circinans* var. *prolifera*) were moved by Kirk (1984) to *Poitrasia*. *Poitrasia* was established for those species belonging to the family *Choanephoraceae* that do not form dehiscent or indehiscent sporangiola (Kirk 1984). Although *Poitrasia* is primarily a soil-borne genus, it has been isolated from *Equisteum arvense* (Rai 1990). Recent molecular studies confirmed the taxonomic position of *Poitrasia* proposed by Kirk (1984).

Molecular phylogeny

All *Choanephora* strains available in CBS culture collection (three strains of *C. infundibulifera* and five strains of *C. cucurbitarum*) have been sequenced for their ITS sequences and included in molecular analysis by Walther et al. (2013). These studies showed that the universal fungal DNA barcoding marker–the ITS region (Schoch et al. 2012)–is sufficient for *Choanephora* species identification (Table 6, Fig. 5). Multigene phylogenetic analysis including representatives of this genus was performed by Hoffmann et al. (2013).

Recommended genetic markers

- The internal transcribed spacer (ITS)–generic and species level
- The large and small subunits (LSU and SSU) of nrDNA–placement within the *Mucorales* order, higher-level phylogeny

Table 6 *Choanephora*. Details of the isolates used in the phylogenetic tree

Species	Isolate	Host	GenBank no
Choanephora infundibilifera	CBS 153.51	–	JN206236
C. infundibilifera	CBS 155.51	–	JN206237
C. infundibilifera	CBS 155.58	–	JN206238
C. cucurbitarum	CBS 445.72	–	JN206234
C. cucurbitarum	CBS 178.76	Dead insect	JN206235
C. cucurbitarum	CBS 674.93	–	JN206233
C. cucurbitarum	CBS 120.25	–	JN206231
C. cucurbitarum	CBS 150.51	–	JN206232
Poitrasia circinans	**CBS 153.58***	**Soil**	**JN206239**
P. circinans	CBS 647.70	Soil	JN206240

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

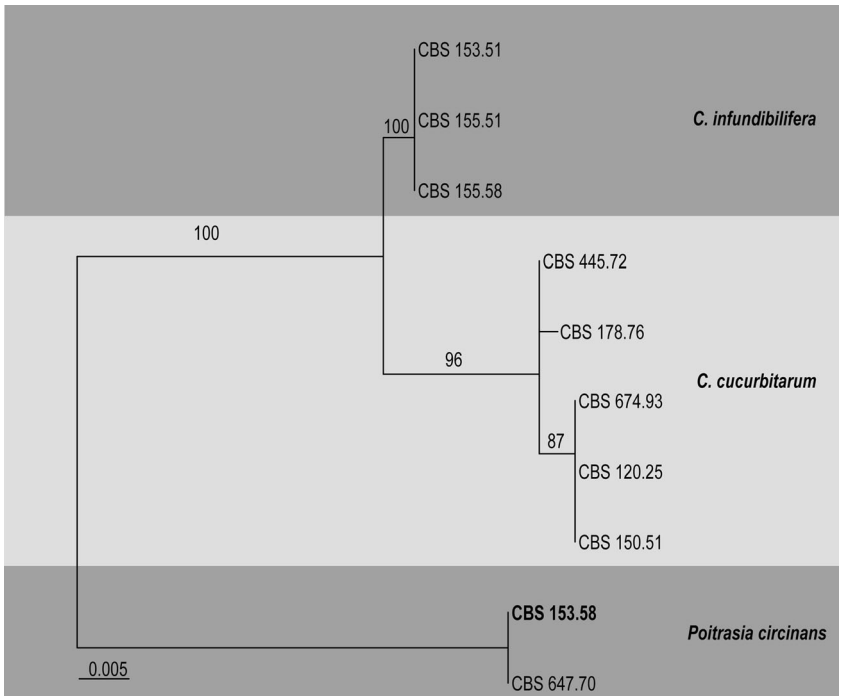


Fig. 5 Phylogram generated from Maximum likelihood analysis based on ITS sequenced data of *Choanephora*. Bootstrap support values greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*

- The partial actin gene (ACT) and the partial translation elongation factor 1-alpha gene (TEF)–higher-level phylogeny

Colletotrichum

Background

The genus *Colletotrichum* was introduced by Corda (1831) and belongs to the family *Glomerellaceae* (*Glomerellales*, Ascomycota). *Colletotrichum* is a coelomycetous phytopathogenic genus with a *Glomerella* sexual state that includes a number of important pathogens causing diseases of crops and fruits worldwide (Cai et al. 2009; Cannon et al. 2012; Doyle et al. 2013). *Colletotrichum* species have furthermore been recorded as endophytes in angiosperms, conifers, ferns, lichens and grasses (Hofstetter et al. 2012; Damm et al. 2012b; Cannon et al. 2012; McKenzie et al. 2009; Petrini et al. 1990; Manamgoda et al. 2013; Tao et al. 2013). This genus was voted the eighth most important group of plant pathogenic fungi in the world, based on perceived scientific and economic importance (Dean et al. 2012). *Colletotrichum* species commonly cause anthracnose resulting in sunken necrotic lesions on leaves, stems, flowers and fruits of numerous hosts, including important crops (Lenne 2002; Waller et al. 2002; Agrios 2005; Cai et al. 2009; Than et al. 2008; Peng et al. 2012; Doyle et al. 2013). It is therefore important to plant health disease practitioners, quarantine personnel and plant breeders to know what species infect which crops (Huang et al. 2013b; Lima et al. 2013; Giaretta et al. 2010; Sangeetha and Rawal 2010; Liu et al. 2009a; Akinbode and Ikotun 2008; Adegbite and Amusa 2008; Peres et al. 2002). Therefore, having a rigid and stable taxonomy for the identification of *Colletotrichum* species is a significant practical concern (Shenoy et al. 2007). Identification of *Colletotrichum* species has been difficult due to the lack of reliable morphological features and confused, ambiguous species boundaries (Hyde et al. 2009a, b; Cai et al. 2009). Difficulties in recognising *Colletotrichum* species has resulted from having a few and variable morphological characters, widespread host ranges and pathogenicity, lost specimens or type specimens in poor condition and incorrectly named sequences in NCBI (Freeman et al. 2000; Du et al. 2005; Thaung 2008; Crouch et al. 2009a, b; Damm et al. 2009; Cai et al. 2009).

Colletotrichum species are extensively studied as model organisms for research in genetics (Cannon et al. 2012). The pathogenicity genes of *C. higginsianum* were discovered by random mutagenesis (Huser et al. 2009). Genomes and transcriptomes of *C. higginsianum* and *C. graminicola* were studied through the use of two different infection strategies by O'Connell et al. (2012). Work on the genetics of pathogenicity in the *C. orbiculare* species aggregate led to transformation of pathogenic strains to endophytic forms (Cannon et al. 2012). Gene manipulation techniques such as *Agrobacterium tumefacien*-mediated transformation or protoplast transformation were established (Tsuji et al. 2003). Peroxisome biogenesis genes, PEX6 and PEX13 were identified and their pathogenesis was functionally analyzed (Fujihara et al. 2010). The importance of the pexophagy factor ATG26 for apressorium formation was discovered by Asakura et al. (2009). Whole genomes of *C. higginsianum* and *C. graminicola* have been

sequenced (O'Connell et al. 2012). Correct species identification is essential in plant pathogenic genera. In order to have effective measures to prevent the unwanted entry of diseases in to a country, the plant pathologists should be able to name the *Colletotrichum* species confidently. Therefore, pathologists need to be able to clarify and identify the species of *Colletotrichum* using the wide genetic variation among the taxa (Cannon et al. 2000).

Species identification and numbers

Colletotrichum species have been traditionally named after their hosts. The history of naming *Colletotrichum* species has been reviewed in several key papers (Cannon et al. 2008, 2012; Hyde et al. 2009a). Cai et al. (2009) outlined the recent polyphasic protocols for species identification: A total of 25 *Colletotrichum* species have been epitypified, one has been neotypified and three have been lectotypified (Cannon et al. 2008; Damm et al. 2009, 2012a, b, 2013; Doyle et al. 2013; Liu et al. 2011a, b, 2013; Su et al. 2011; Weir and Johnston 2010; Weir et al. 2012). Significant changes to the understanding of *Colletotrichum* species took place with incorporation of these polyphasic approaches, especially the use of multimarker phylogenetic analysis, classification and knowledge of species complexes, as well as epitypifications for many species (Cai et al. 2009; Cannon et al. 2012; Damm et al. 2012a, b, 2013; Doyle et al. 2013; Su et al. 2011; Weir et al. 2012). Cannon et al. (2012) studied nearly all presently sequenced species in the genus using a six-gene analysis, and revealed at least nine clades; 119 species previously thought to be well circumscribed proved to be polyphyletic. *Colletotrichum gloeosporioides* (Cannon et al. 2008; Phoulivong et al. 2010a, b; Weir et al. 2012), *C. acutatum* (Marcelino et al. 2008; Shivas and Tan 2009; Damm et al. 2012a), *C. boninense* (Moriwaki et al. 2003; Yang et al. 2009; Damm et al. 2012b), *C. orbiculare* (Damm et al. 2013) form important species complexes within *Colletotrichum* and well-resolved among all the nine clades. Further studies in the *C. gloeosporioides* species complex led to identification of *C. murrayae* (Peng et al. 2012), *C. viniferum* (Peng et al. 2013), *C. citricola* (Huang et al. 2013b), *C. fructivorum* (Doyle et al. 2013), *C. melanocaulon* (Doyle et al. 2013), *C. temperatum* (Doyle et al. 2013), *C. endophyticta* (Manamgoda et al. 2013) and *C. syzygicola* (Udayanga et al. 2013). Tao et al. (2013) introduced seven new species; four species belonging to the graminicola clade, two species belonging to the spaethianum clade and one singleton species. Damm et al. (2013) resolved *C. orbiculare* and introduced four new species. Crouch (2014) introduced a new species complex, *C. caudatum,* with five new species found on warm-season grasses, characterized by the conidial apex reducing into a filiform appendage. The current numbers of species recognised in the genus are listed in Table 7.

Molecular phylogeny

Some species such as *Colletotrichum gloeosporioides* were defined using ITS sequence data, but the outcome was not good partially due to prolific misidentification in GenBank and because ITS does not resolve *Colletotrichum* species well. In *Colletotrichum*, species definitions based on ITS sequence data, the "universal" DNA barcoding marker for fungal species has proved unsatisfactory (Du et al. 2005; Crouch et al. 2009b; García et al. 2009; Cannon et al. 2012; Doyle et al. 2013; Gunjan et al. 2013). Comparison of a phylogenetic tree of *Colletotrichum* species derived from ITS sequence alone and one generated from multi-marker data confirms that ITS resolves major clades well, although it does not reflect their higher-order relationships accurately in all cases (Cannon et al. 2012). Cannon et al. (2012) suggested that a robust sequence-based identification system for *Colletotrichum* species must therefore use an alternative molecular marker or a combination of markers. Damm et al. (2012a) indicated that the most diagnostic markers are β-tubulin and GPDH. β-tubulin performed marginally better than GPDH due to a larger overall number of base pair differences, but even so, some clades differed only by one base pair in the β-tubulin alignment. As single genes that were used are not efficient to differentiate the species, Cai et al. (2009) suggested using multiple markers. Cannon et al. (2012), Weir et al. (2012), and Damm et al. (2012a, b) used several genetic markers: actin (act), chitin synthase (chs1 β-tubulin and ITS which revealed that *Colletotrichum* comprises nine major clades as well as a number of small clusters and singleton species. Many recent studies used multimarker phylogeny including actin (act), chitin synthase (chs1), β-tubulin, calmodulin (cal), glyceraldehydes-3-phosphate dehydogenase (gadph), histamine (HIS3), glutamine synthetase (GS), DNA lyase (*apn2*), intergenic region of *apn2* and *MAT1-2-1* genes (*ApMat*) (Weir et al. 2012; Damm et al. 2012a, b; Cannon et al. 2012; Peng et al. 2012; Doyle et al. 2013; Gunjan et al. 2013) to understand the phylogenetic divergence of *Colletotrichum* species. There is, however, no agreement among mycologists as to which genetic markers should be used (Doyle et al. 2013; Gunjan et al. 2013). Silva et al. (2012) stressed the need to use 'powerful genes' such as *ApMat* and *Apn25L*. The *Apmat* marker provides better resolution as compared to the genetic markers used by Weir et al. (2012), Silva et al. (2012), Doyle et al. (2013) and Gunjan et al. (2013). Up to now it has been a better gene-marker for resolving species within *C. gloeosporioides* species complex (Doyle et al. 2013; Gunjan et al. 2013). Only ITS sequences are available for several species of *Colletotrichum* showing the need of sequencing the other important gene regions and those species

Table 7 *Colletotrichum*. Details of the isolates used in the phylogenetic tree

Species	Isolate	GenBank Accession Number						ApMat
		ITS	GPDH	CHS-1	HIS3	ACT	β-tubulin	
C. acerbum*	**CBS 128530**	JQ948459	JQ948790	JQ949120	JQ949450	JQ949780	JQ950110	–
C. acutatum*	**CBS112996**	JQ005776	JQ948677	JQ005797	JQ005818	JQ005839	JQ005860	–
C. aenigma*	**ICMP 18608**	JX010244	JX010044	JX009774	–	JX009443	JX010389	–
C. aeschynomenes*	**ICMP 17673**	JX010176	JX009930	JX009799	–	JX009483	JX010392	–
C. agaves	CBS 118190	DQ286221	–	–	–	–	–	–
C. alatae*	**ICMP 17919**	JX010190	JX009990	JX009837	–	JX009471	JX010383	KC888932
C. alcorni*	**IMI 176619**	JX076858						
C. alienum*	**ICMP 12071**	JX010251	JX010028	JX009882	–	JX009572	JX010411	KC888927
C. annellatum*	**CBS 129826**	JQ005222	JQ005309	JQ005396	JQ005483	JQ005570	JQ005656	–
C. anthrisci*	**CBS 125334**	GU227845	GU228237	GU228335	GU228041	GU227943	GU228139	–
C. aotearoa*	**ICMP 18537**	JX010205	JX010005	JX009853	–	JX009564	JX010420	KC888930
C. asianum*	**ICMP 18580**	FJ972612	JX010053	JX009867	–	JX009584	JX010406	FR718814
C. australe*	**CBS116478**	JQ948455	JQ948786	JQ949116	JQ949446	JQ949776	JQ950106	–
C. axonopodi	**IMI 279189**	EU554086	–	–	–	–	–	–
C. baltimorense*	**SD11**	JX076866	–	–	–	–	–	–
C. beeveri*	**CBS 128527**	JQ005171	JQ005258	JQ005345	JQ005432	JQ005519	JQ005605	–
C. bletillum*	**CGMCC 3.15117**	JX625178	KC843506	–	–	KC843542	JX625207	–
C. bidentis*	**COAD 1020**	KF178481	KF178506	KF148530	KF178554	KF178578	KF178602	
C. boninense*	**CBS 123755**	JQ005153	JQ005240	JQ005327	JQ005414	JQ005501	JQ005588	–
C. brasiliense*	**CBS 128501**	JQ005235	JQ005322	JQ005409	JQ005496	JQ005583	JQ005669	–
C. brassicola*	**CBS 101059**	JQ005172	JQ005259	JQ005346	JQ005433	JQ005520	JQ005606	–
C. brevisporum*	**BCC 38876**	JQ247623	JQ247599	–	–	JQ247647	JQ247635	–
C. brisbanense*	**CBS292.67**	JQ948291	JQ948621	JQ948952	JQ949282	JQ949612	JQ949942	–
C. carthami*	**SAPA100011**	AB696998	–	–	–	–	AB696992	–
C. caudasporum*	**CGMCC 3.15106**	JX625162	KC843512	–	–	KC843526	JX625190	–
C. caudatum*	**BPI423339**	JX076860	–	–	–	–	–	–
C. cereale	**CBS 129663**	JQ005774	–	JQ005795	JQ005816	JQ005837	JQ005858	–
C.chlorophyti*	**IMI 103806**	GU227894	GU228286	GU228384	GU228090	GU227992	GU228188	–
C. chrysanthemi	**IMI364540**	JQ948273	JQ948603	JQ948934	JQ949264	JQ949594	JQ949924	–
Glomerella cingulata "f.sp. camelliae"	ICMP 10643	JX010224	JX009908	JX009891	–	JX009540	JX010436	–
C. circinans*	**CBS 221.81**	GU227855	GU228247	GU228345	GU228051	GU227953	GU228149	–
C. citri*	**ZJUC41**	KC293581	KC293741	–	–	KC293621	KC293661	–
C. citricola*	**SXC151**	KC293576	KC293736	KC293792	–	KC293616	KC293656	–
C. clidemiae*	**ICMP 18658**	JX010265	JX009989	JX009877	–	JX009537	JX010438	KC888929
C.cliviae*	**CBS 125375**	JX519223	GQ856756	JX519232	–	JX519240	JX519249	–
C.coccodes	**CBS 369.75**	JQ005775	HM171673	JQ005796	JQ005817	JQ005838	JQ005859	–
C. coccodes	ITCC 6079	–	–	–	–	–	–	KC790652
C. colombiense*	**CBS 129818**	JQ005174	JQ005261	JQ005348	JQ005435	JQ005522	JQ005608	–
C. constrictum*	**CBS 128504**	JQ005238	JQ005325	JQ005412	JQ005499	JQ005586	JQ005672	–
C. cordylinicola*	**ICMP 18579**	JX010226	JX009975	JX009864	–	HM470234	JX010440	JQ899274
C. cosmi*	**CBS 853.73**	JQ948274	JQ948604	JQ948935	JQ948604	JQ949595	JQ949925	–
C. costaricense*	**CBS 330.75**	JQ948180	JQ948510	JQ948841	JQ949171	JQ949501	JQ949831	–
C. curcumae*	**IMI 288937**	GU227893	GU228285	GU228383	GU228089	GU227991	GU228187	–
C. cuscutae*	**IMI 304802**	JQ948195	JQ948525	JQ948856	JQ949186	JQ949516	JQ949846	–
C. cymbidiicola*	**IMI 347923**	JQ005166	JQ005253	JQ005340	JQ005427	JQ005514	JQ005600	–
C. dacrycarpi*	**CBS 130241**	JQ005236	JQ005323	JQ005410	JQ005497	JQ005584	JQ005670	–

Table 7 (continued)

Species	Isolate	GenBank Accession Number						ApMat
		ITS	GPDH	CHS-1	HIS3	ACT	β-tubulin	
C. dematium*	**CBS 125.25**	GU227819	GU228211	GU228309	GU228015	GU227917	GU228113	–
C. destructivum	CBS 149.34	AJ301942	–	JQ005785	JQ005806	JQ005827	JQ005848	–
C. dianensei*	**CMM4083**	KC329779	KC517194	–	–	KC517298	KC517254	KJ155461
C.dracaenophilum*	**CBS 118199**	JX519222	–	JX519230	–	JX519238	JX519247	–
C. duyunensis*	**CGMCC 3.15105**	JX625160	KC843515	–	–	KC843530	JX625187	–
C. echinochloae*	**MAFF 511473**	AB439811	–	–	–	–	–	–
C. eleusines*	**MAFF 511155**	JX519218	–	JX519226	–	JX519234	JX519243	–
C. endomagniferae*	**MFLUCC 14-0563**	KC702994	KC702955	KC598113	–	KC702922	KC702922	KJ155453
C. endophytica*	**LC0324**	KC633854	KC832854	–	–	KF306258	–	–
C. endophytum*	**CGMCC 3.15108**	JX625177	KC843521	–	–	KC843533	JX625206	–
C. eremochloae*	**CBS 129661**	JX519220	–	JX519228	–	JX519236	JX519245	–
C. excelsum altitudum*	**CGMCC 3.15130**	HM751815	KC843502	–	–	KC843548	JX625211	–
C. falcatum	**CBS 147945**	JQ005772	–	JQ005793	JQ005814	JQ005835	JQ005856	–
C. fioriniae*	**CBS 128517**	JQ948292	JQ948622	JQ948953	JQ949283	JQ949613	JQ949943	–
C. fructi*	**CBS 346.37**	GU227844	GU228236	GU228334	GU228040	GU227942	GU228138	–
C. fructicola*	**ICMP 18581**	JX010165	JX010033	JX009866	–	FJ907426	JX010405	JQ807838
C. fructivorum*	**Coll1414**	JX145145	–	–	–	–	JX145196	–
C. fuscum	CBS 130.57	JQ005762	–	JQ005783	JQ005804	JQ005825	JQ005846	–
C. gigasporum*	**MUCL 44947**	AM982797	–	–	–	–	FN557442	–
C. gloeosporioides*	**CBS 112999**	JQ005152	JQ005239	JQ005326	JQ005413	JQ005500	JQ005587	JQ807843
C. godetiae*	**CBS 133.44**	JQ948402	JQ948733	JQ949063	JQ949393	JQ949723	JQ950053	–
C. graminicola*	**CBS 130836**	JQ005767	–	JQ005788	JQ005809	JQ005830	JQ005851	–
C. grevilleae*	**CBS 132879**	KC297078	KC297010	KC296987	KC297056	KC296941	KC297102	–
C. guajave*	**IMI 350839**	JQ948270	JQ948600	JQ948931	JQ949261	JQ949591	JQ949921	–
C. guizhouensis*	**CGMCC 3.15112**	JX625158	KC843507	–	–	KC843536	JX625185	–
C. hanaui*	**MAFF 305404**	JX519217	–	JX519225	–	–	JX519242	–
C. hemerocallidis*	**CDLG5**	JQ400005	JQ400012	JQ399998	–	JQ399991	JQ400019	–
C. higginsianum	IMI 349063	JQ005760	–	JQ005781	JQ005802	JQ005823	JQ005844	–
C. hippeastri*	**CBS 125376**	JQ005231	JQ005318	JQ005405	JQ005492	JQ005579	JQ005665	–
C. horii	**ICMP 10492**	GQ329690	GQ329681	JX009752	–	JX009438	JX010450	JQ807840
C. hsienjenchng	MAFF 243051	AB738855	–	AB738846	AB738847	AB738845	–	–
C. incanum*	**ATCC 64682**	KC110789	KC110807	–	KC110798	KC110825	KC110816	–
C. indonesiense*	**CBS 127551**	JQ948288	JQ948618	JQ948949	JQ949279	JQ949609	JQ949939	–
C. jacksonii*	**MAFF 305460**	JX519216	–	JX519224	–	JX519233	JX519241	–
C. jasiminigenum*	**MFU 10-0273**	HM131513	HM131499	–	–	HM131508	HM153770	–
C. johnstonii*	**CBS 128532**	JQ948444	JQ948775	JQ949105	JQ949435	JQ949765	JQ950095	–
C. kahawae*	**ICMP17816**	JX010231	JX010012	JX009813	–	JX009452	JX010444	JQ899282
C. kartsii*	**CORCG6**	HM585409	HM585391	HM582023	–	HM581995	HM585428	–
C. kinghornii*	**CBS 198.35**	JQ948454	JQ948785	JQ949115	JQ949445	JQ949775	JQ950105	–
C. lacticiphilum*	**CBS 112989**	JQ948289	JQ948619	JQ948950	JQ949280	JQ949610	JQ949940	–
C. lilii	CBS 109214	GU227810	GU228202	GU228300	GU228006	GU227908	GU228104	–
C. limetticola*	**CBS 114.14**	JQ948193	JQ948523	JQ948854	JQ949184	JQ949514	JQ949844	–
C. lindemuthianum*	**CBS 144.31**	JQ005779	JX546712	JQ005800	JQ005821	JQ005842	JQ005863	–
C. lineola*	**CBS 125337**	GU227829	GU228221	GU228319	GU228025	GU227927	GU228123	–
C. linicola	CBS 172.51	JQ005765	–	JQ005786	JQ005807	JQ005828	JQ005849	–
C. liriopes*	**CBS 119444**	GU227804	GU228196	GU228294	GU228000	GU227902	GU228098	–
C. lupini	**CBS 109225**	JQ948155	JQ948485	JQ948816	JQ949146	JQ949476	JQ949806	–

Table 7 (continued)

Species	Isolate	GenBank Accession Number						ApMat
		ITS	GPDH	CHS-1	HIS3	ACT	β-tubulin	
C. melanocaulon*	**Coll131**	–	–	–	–	–	–	JX145313
C. malvarum*	**CBS 527.97**	KF178480	KF178504	KF178529	KF178553	KF178577	KF178601	
C. melonis*	**CBS 159.84**	JQ948194	JQ948524	JQ948855	JQ949185	JQ949515	JQ949845	–
C. metake	NBRC 8974	AB738859	–	–	–	–	–	–
C. miscanthi*	**MAFF 510857**	JX519221	–	JX519229	–	JX519237	JX519246	–
C. musae*	**ICMP19119**	JX010146	JX010050	JX009896	–	JX009433	HQ596280	KC888926
C. murrayae*	**GZAAS5.09506**	JQ247633	JQ247609	–	–	JQ247657	JQ247644	–
C. navitas*	**CBS 125086**	JQ005769	–	JQ005790	JQ005811	JQ005832	JQ005853	–
C. nicholsonii*	**MAFF 511115**	JQ005770	–	JQ005791	JQ005812	JQ005833	JQ005854	–
C. nigrum*	**CBS 169.49**	JX546838	JX546742	JX546693	JX546791	JX546646	JX546885	–
C. novae-zelandiae*	**CBS 128505**	JQ005228	JQ005315	JQ005402	JQ005489	JQ005576	JQ005662	–
C. nupharicola*	**ICMP 18187**	JX010187	JX009972	JX009835	–	JX009437	JX010398	JX145319
C. nymphaeae*	**CBS 515.78**	JQ948197	JQ948527	JQ948858	JQ949188	JQ949518	JQ949848	–
C. ochracea*	**CGMCC 3.15104**	JX625156	KC843513	–	–	KC843527	JX625183	–
C. oncidii*	**CBS 129828**	JQ005169	JQ005256	JQ005343	JQ005430	JQ005517	JQ005603	–
C. orbiculare*	**CBS 570.97**	KF178466	KF178490	KF178515	KF178539	KF178563	KF178587	–
C.orchidophilum*	**CBS 632.80**	JQ948151	JQ948481	JQ948812	JQ949142	JQ949472	JQ949802	–
C. parsonsiae*	**CBS 128525**	JQ005233	JQ005320	JQ005407	JQ005494	JQ005581	JQ005667	–
C. paspali*	**MAFF 305403**	JX519219	–	JX519227	–	JX519235	JX519244	–
C. paxtonii*	**IMI 165753**	JQ948285	JQ948615	JQ948946	JQ949276	JQ949606	JQ949936	–
C. petchii*	**CBS 378.94**	JQ005223	JQ005310	JQ005397	JQ005484	JQ005571	JQ005657	–
C.phaseolorum	**CBS 157.36**	GU227896	GU228288	GU228386	GU228092	GU227994	GU228190	–
C. phormii*	**CBS 118194**	JQ948446	JQ948777	JQ949107	JQ949437	JQ949767	JQ950097	–
C. phyllanthi*	**CBS 175.67**	JQ005221	JQ005308	JQ005395	JQ005482	JQ005569	JQ005655	–
C. proteae	**CBS132882**	KC297079	KC297009	KC296986	KC297045	KC296940	KC297101	–
C.pseudoacutatum*	**CBS 436.77**	JQ948480	JQ948811	JQ949141	JQ949471	JQ949801	JQ950131	–
C. psidii	**ICMP 19120**	JX010219	JX009967	JX009901	–	JX009515	JX010443	–
C. pyricola*	**CBS 128531**	JQ948445	JQ948776	JQ949106	JQ949436	JQ949766	JQ950096	–
C. queenslandium*	**ICMP 1778**	JX010276	JX009934	JX009899	–	JX009447	JX010414	KC888928
C. rhexiae*	**Coll 1026**	JX145128	–	–	–	–	JX145179	JX145290
C. rhombiforme*	**CBS 129953**	JQ948457	JQ948788	JQ949118	JQ949448	JQ949778	JQ950108	–
C. rusci*	**CBS 119206**	GU227818	GU228210	GU228308	GU228014	GU227916	GU228112	–
C. salicis*	**CBS 607.94**	JQ948460	JQ948791	JQ949121	JQ949451	JQ949781	JQ950111	–
C. salsolae*	**ICMP 19051**	JX010242	JX009916	JX009863	–	JX009562	JX010403	KC888925
C. sansevieriae	**MAFF 239721**	AB212991	–	–	–	–	–	–
C. scovillei*	**CBS 126529**	JQ948267	JQ948597	JQ948928	JQ949258	JQ949588	JQ949918	–
C. siamense*	**ICMP 18578**	JX010171	JX009924	JX009865	–	FJ907423	JX010404	JQ899289
C. sidae*	**CBS 504.97**	KF178472	KF178497	KF178521	KF178545	KF178569	KF178593	–
C. simmondsii*	**CBS 122122**	JQ948276	JQ948606	JQ948937	JQ949267	JQ949597	JQ949927	–
C. sloanei*	**IMI 364297**	JQ948287	JQ948617	JQ948948	JQ949278	JQ949608	JQ949938	–
C. somersetense*	**JAC 11-11**	JX076862	–	–	–	–	–	–
C. spaethianum*	**CBS 167.49**	GU227847	GU228239	GU228337	GU228043	GU227945	GU228141	–
C. spinaceae	CBS 128.57	GU227847	GU228239	GU228337	GU228043	GU227945	GU228141	–
C. spinosum*	**CBS 515.97**	KF178474	KF178498	KF178523	KF178547	KF178571	KF178595	–
C. sublineola*	**CBS 131301**	JQ005771	–	JQ005792	JQ005813	JQ005834	JQ005855	–
C. syzygicola*	**DNCL021**	KF242094	KF242156	–	–	KF157801	KF254880	–
C. tabacum	CBS 161.53	JQ005763	–	JQ005784	JQ005805	JQ005826	JQ005847	–

Table 7 (continued)

Species	Isolate	GenBank Accession Number						ApMat
		ITS	GPDH	CHS-1	HIS3	ACT	β-tubulin	
C. tamarilloi*	**CBS 129814**	JQ948184	JQ948514	JQ948845	JQ949175	JQ949505	JQ949835	–
C. tanaceti*	**CBS 132693**	–	JX218243	–	–	JX218238	JX218233	–
C. tebeestii*	**CBS 522.97**	KF178473	KF178505	KF178522	KF178546	KF178570	KF178594	–
C. temperatum*	**Coll883**	JX145159	–	–	–	–	JX145211	JX145298
C. thailandicum*	**MFUCC110113**	JN050242	JN050231	–	–	JN050220	JN050248	–
C. theobromicola	**ICMP 18649**	JX010294	JX010006	JX009869	–	JX009444	JX010447	KC790726
C. ti*	**ICMP 4832**	JX010269	JX009952	JX009898	–	JX009520	JX010442	–
C. tofieldiae	CBS 495.85	GU227801	GU228193	GU228291	GU227997	GU227899	GU228095	–
C. torulosum*	**CBS 128544**	JQ005164	JQ005251	JQ005338	JQ005425	JQ005512	JQ005598	–
C.trichellum	CBS 217.64	GU227812	GU228204	GU228302	GU228008	GU227910	GU228106	–
C. trifolii*	**CBS 158.83**	KF178478	KF178502	KF178527	KF178551	KF178575	KF178599	–
C. tropicale*	**ICMP18653**	JX010264	JX010007	JX009870	–	JX009489	JX010407	KC790728
C.tropicicola*	**BCC 38877**	JN050240	JN050229			JN050218	JN050246	–
C. truncatum*	**CBS 151.35**	GU227862	GU228254	GU228352	GU228058	GU227960	GU228156	–
C. verruculosm*	**IMI 45525**	GU227806	GU228198	GU228296	GU228002	GU227904	GU228100	–
C. viniferum*	**GZAAS5.08601**	JN412804	JN412798	–	–	JN412795	JN412813	–
C. viniferum	**GZAAS5.08608**	–	–	–	–	–	–	KJ623242
C. walleri*	**CBS 125472**	JQ948275	JQ948605	JQ948936	JQ949266	JQ949596	JQ949926	–
C. xanthorrhoeae*	**ICMP 17903**	JX010261	JX009927	JX009823	–	JX009478	JX010448	KC790689
C. yunnanense*	**CGMCC AS3.9167**	EF369490	–	JX519231	–	JX519239	JX519248	–
C. zoysia*	**MAFF 238573**	JX076871	–	–	–	–	–	–

Ex-Type (ex-epitype) strains are bolded and marked with an * and authentic stains are bolded

were not included in this analysis. Here we present an analysis using six genetic markers for all the *Colletotrichum* species that are accepted (Fig. 6) and for the *C. acutatum* species complex (Fig. 7). Figure 8 presents the analysis of *C. gloeosporioides* species complex using the *apmat* gene. The whole genomes of several species of *Colletotrichum* have been sequenced, such that it is now possible to carry out whole-genome analysis, and compare this with single gene analysis to establish a gene (or gene combinations) that can really resolve species in the genus.

Recommended genetic markers

- ITS alone will not resolve species in the genus, but it can separate taxa to species complexes. Multigene analysis using the following genes has been recommended for a backbone tree for species of *Colletotrichum*:
- GPDH–Glyceraldehyde-3-phosphate dehydrogenase- resolves to species level, more accurate.
- β-tubulin–Beta-tubulin resolves to species level
- ApMat–Intergenic region of *apn2* and *MAT1-2-1* genes can resolve within the *C. gloeosporioides* complex
- GS–glutamine synthetase–CHS-1. HIS3–Histone3 and ACT–Actin–Placement within the *genus* and also some species-level delineation.

These marker combinations can resolve the phylogenetic positions of most species in the genus. GPDH alone can delineate the majority of species. However, research is ongoing to identify better genetic markers to resolve the phylogenetic position of many species of *Colletotrichum*.

Curvularia

Background

Curvularia is a dematiaceous hyphomycete genus in the family *Pleosporaceae*, *Pleosporales*, Dothideomycetes (Ascomycota) (Boedijn 1933). It is typified by *C. lunata*. *Curvularia* species have been recorded as saprobes and also plant, human and animal pathogens. *Bipolaris* and *Curvularia* species are associated with *Cochliobolus* sexual states (Sivanesan 1987). *Curvularia* species are found as plant pathogens especially associated with the family *Poaceae*. Species such as *C. lunata*, *C. tuberculata* and *C. trifolii* cause leaf spots and leaf blights of some cereal crops such as maize, rice and horticultural crops such as Bermuda grasses and turf grasses (de Luna et al. 2002). The most frequent human and animal pathogens within the genus are *C. aeria, C. geniculata*,

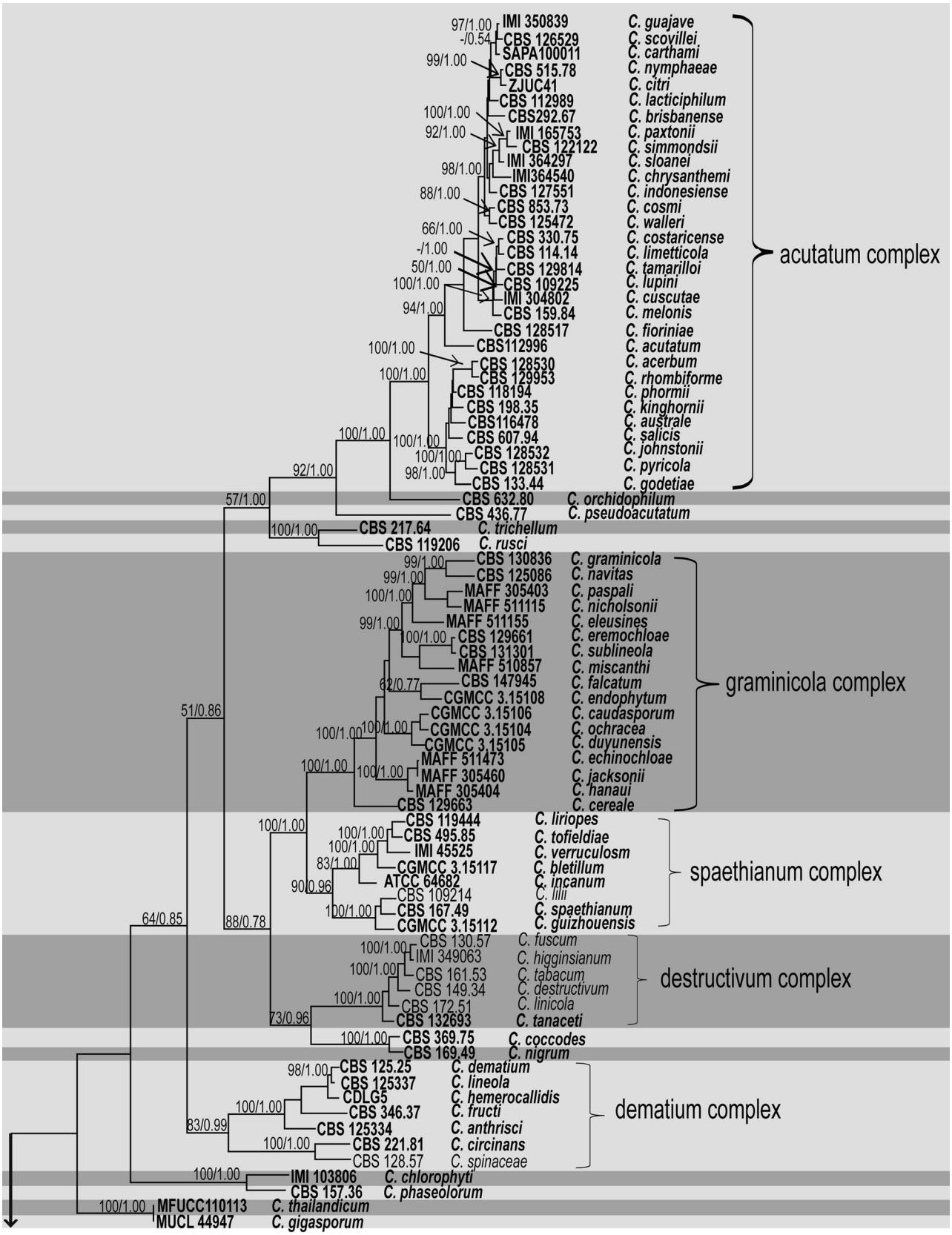


Fig. 6 Phylogram generated from parsimony analysis based on combined ITS, GADPH, CHS-1, ACT, HIS and β- tubulin data of *Colletotrichum*. Parsimony bootstrap support values and Bayesian posterior probabilities greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*. The tree is rooted with *Monilochaetes infuscans* CBS 869.96

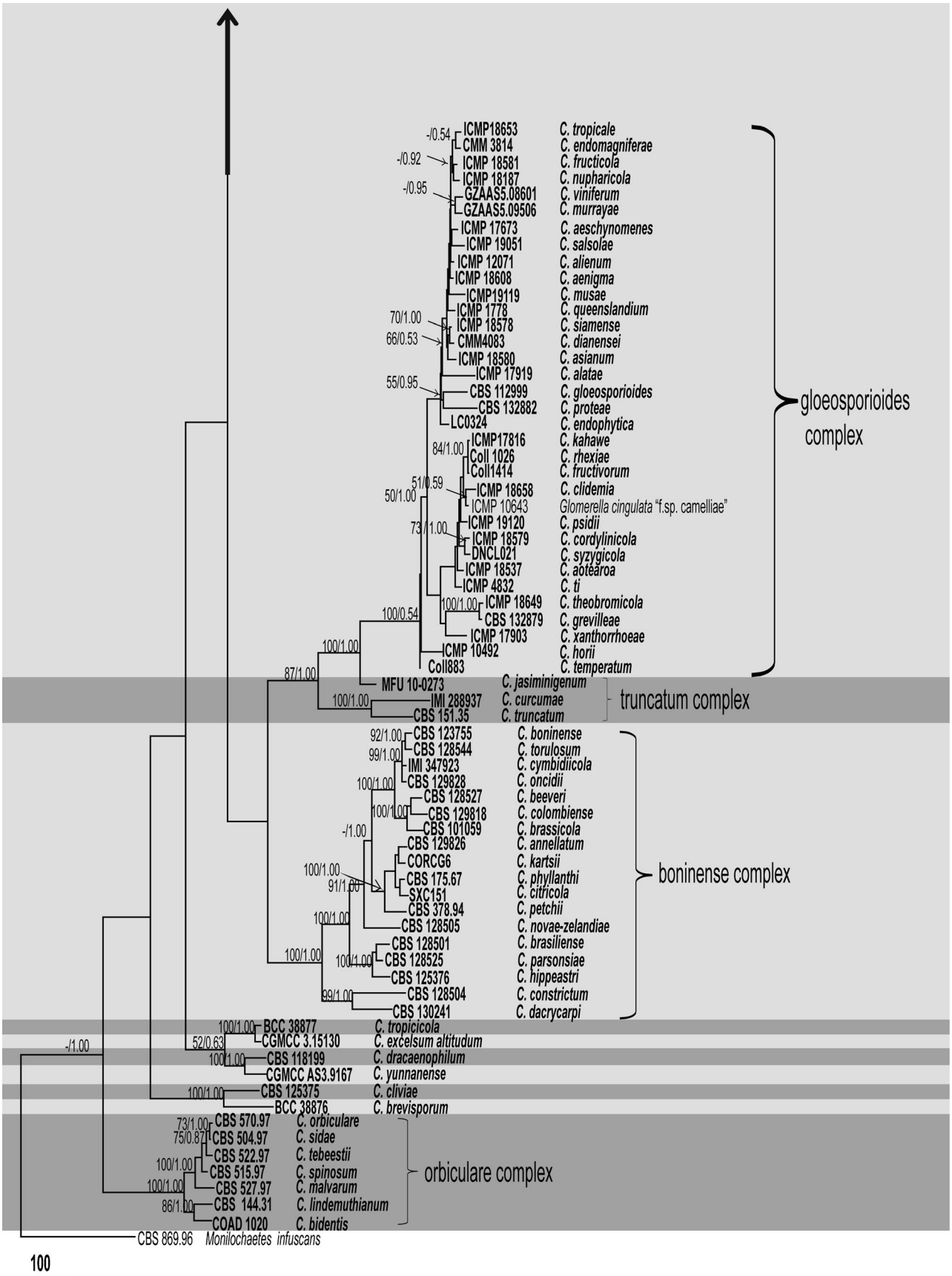


Fig. 6 (continued)

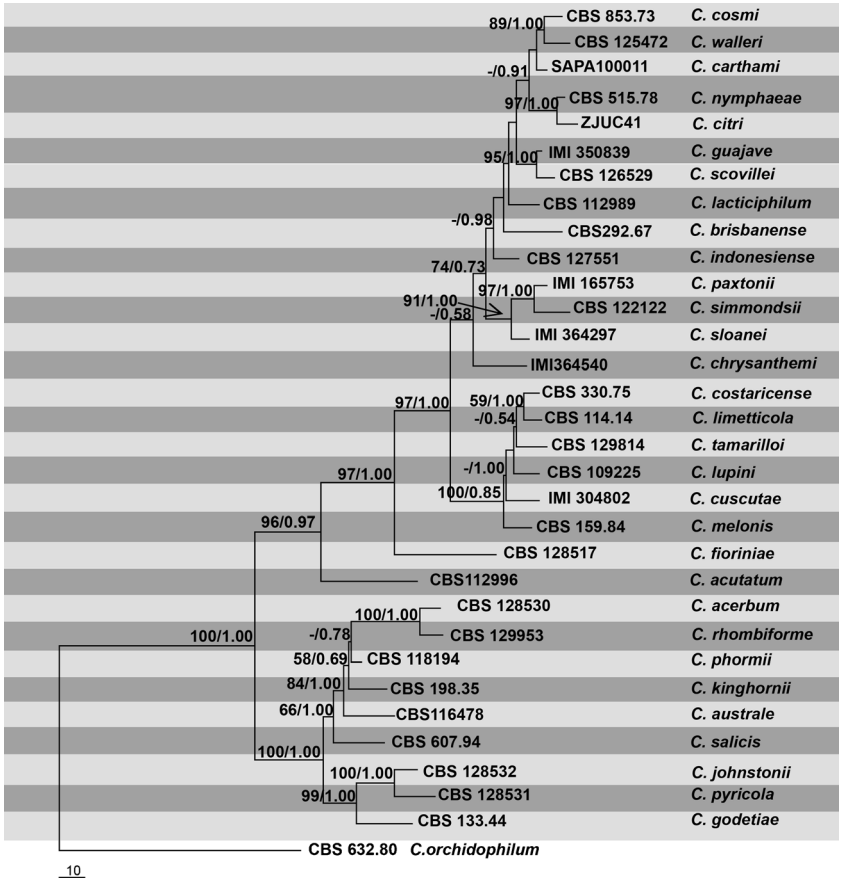


Fig. 7 Phylogram generated from parsimony analysis based on combined ITS, GADPH, CHS-1, ACT, HIS and β- tubulin sequenced data of *Colletotrichum acutatum* complex. Parsimony bootstrap support values and Bayesian posterior probabilities greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*. The tree is rooted with *C. orchidophilum*

C. lunata, *C. inaequalis*, *C. verrucosa* and *C. borreriae*. These species cause keratitis, sinusitis, cutaneous and subcutaneous infections, peritonitis, onychomycosis, endocarditis, endophthalmitis, cerebral phaeohyphomycosis, and allergic bronchopulmonary as well as disseminated disease (da Cunha et al. 2013).

Species identification and numbers

Curvularia is morphologically characterized by its dark mycelium, geniculate conidiophores with sympodial, tretic conidiogenous cells, conidia with smooth to slightly verrucose wall and several false septa (distosepta). Morphological species identification of *Curvularia* species is challenging as many species have morphological similarities and have overlapping conidial dimensions. Most of the clinical isolates and common plant pathogens of *Curvularia* are recorded as *C. lunata,* which was recently epitypified (Manamgoda et al. 2012a). Following phylogenetic assessments, it was revealed that most of the sequences named as *C. lunata* in GenBank are incorrectly identified (Cai et al. 2011; da Cunha et al. 2013). Ellis (1971) and Sivanesan (1987) described 37 species in the genus *Curvularia* and currently there are 122 species epithets in Index Fungorum.

Molecular phylogeny

Phylogenetic recognition is crucial for species identification in *Curvularia*. Former morphological identifications do not correlate with the phylogeny (Manamgoda et al. 2012a, b). Combined ITS and GPDH analysis for *Curvularia* and its sister genus *Bipolaris* by Berbee et al. (1999) revealed that some *Bipolaris* species cluster within the genus *Curvularia*. *Curvularia* was therefore redefined by Manamgoda et al. (2012a) based on a combined phylogenetic analysis of ITS, GPDH, TEF and LSU. Nine *Bipolaris* species clustering within *Curvularia* were transferred and their nomenclature redefined (Manamgoda et al. 2012a). Lack of ex-type cultures and epitypifications form limitations for phylogenetic species recognition. In this paper we present a phylogenetic tree with combined ITS and GPDH sequences obtained from available type material and voucher cultures (Table 8, Fig. 9). This can be used as a backbone in the identification of *Curvularia* species.

Recommended genetic markers

- GPDH is the best single genetic marker for the genus *Bipolaris* (Manamgoda et al. 2012a). It is recommended to use a combination of ITS and GPDH. Another useful gene is TEF.

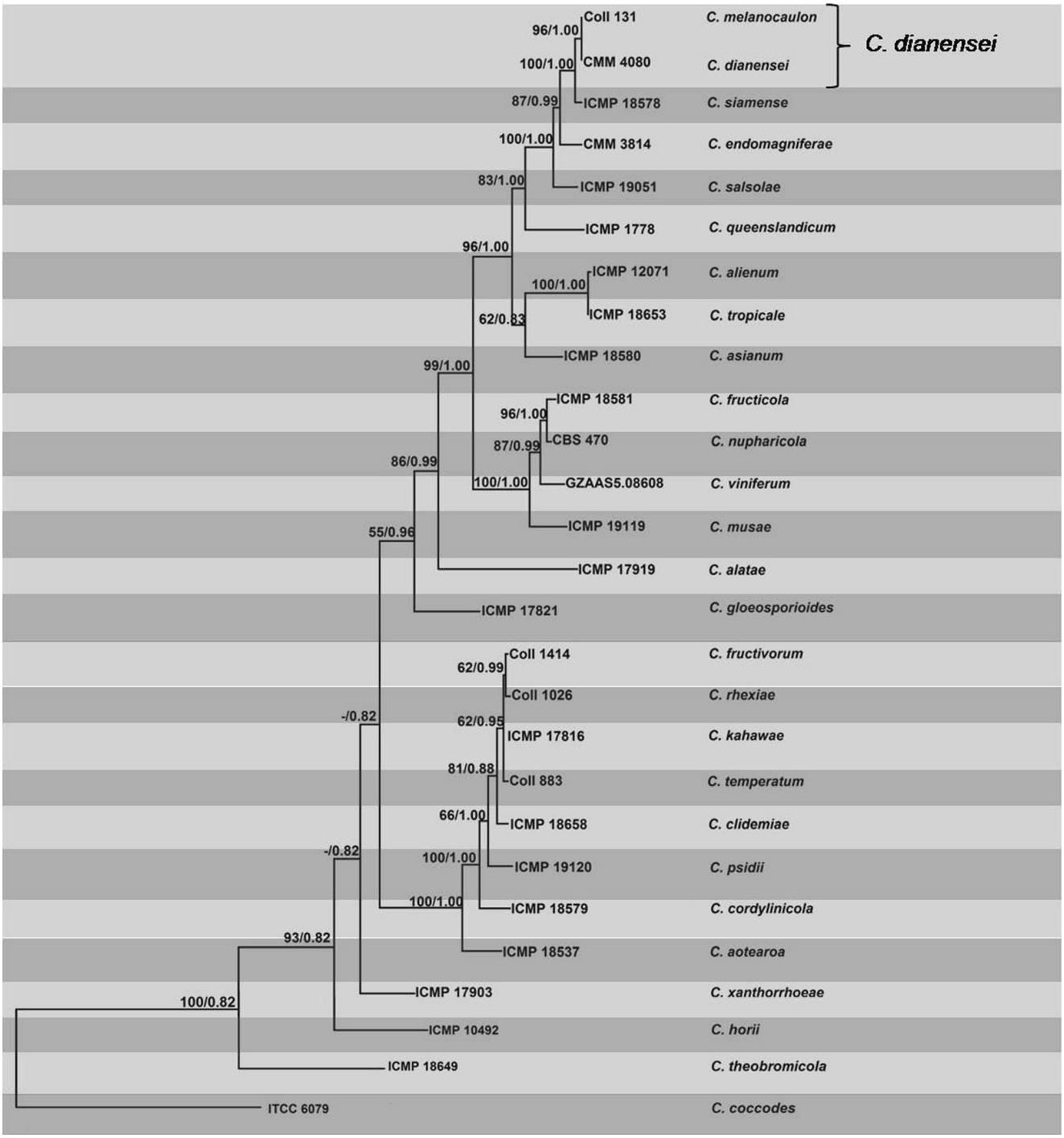


Fig. 8 Phylogram generated from parsimony analysis based on combined ITS, GADPH, CHS-1, ACT, HIS and β- tubulin sequenced data of *Colletotrichum gloeosporioides* complex. Parsimony bootstrap support values and Bayesian posterior probabilities greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*. The tree is rooted with *C. coccodes* ITCC6079

Diaporthe

Background

Diaporthe (=*Phomopsis*) is a cosmopolitan genus of fungi comprised of endophytes, plant pathogens, and saprobes occurring on a wide range of annual and perennial hosts, including economically important crops (Uecker 1988; Farr and Rossman 2014; Udayanga et al. 2011). The genus belongs to class Sordariomycetes, order *Diaporthales* and the family *Diaporthaceae*, typified by the species *Diaporthe eres* Nitschke (Wehmeyer 1933). With the change to one scientific name for fungi (McNeill et al. 2012), *Diaporthe* has priority, being the older generic name compared to *Phomopsis*. Many

Table 8 Details of the isolates used in the phylogenetic tree

Species	Code	Host	Gene bank accession numbers		
			ITS	GPDH	TEF
Curvularia affinis	DAOM 46365		AF071335	AF081390	
C. alcornii	**MFLUCC10703***	*Zea mays*	JX256420	JX276433	JX266589
	MFLUCC10705	*Panicum* sp.	JX256421	JX276434	JX266590
C. australiensis	**CBS 172.57**	*Oryza sativa*	JN601026	JN601036	JN601003
C. clavata	**ICMP 103444**	Lawn	JX256444	JX276455	
C. cymbopogonis	**88109-1**		AF071351	AF081403	
C. ellisii	**CBS 193.62***	Air	JN192375	JN600963	JN601007
C. gladioli	**ICMP 6160**	*Gladiolus* sp.	JX256426	JX276438	JX266595
C. graminicola	**BRIP 23186**		JN192376	JN600964	JN601008
C. gudauskasii	**DAOM165085**		AF071338	AF081393	
C. hawaiiensis	**BRIP 15933**	*Chloris gayana*	JN601028	JN600965	JN601009
	BRIP 10972	*Chloris gayana*	JN192377	JN600968	JN601012
C. heteropogonis	**CBS 284.91***	*Heteropogon contortus*	JN192379	JN600969	JN601013
C. intermedia	**8797-1**		AF071327	AF081383	
C. lunata	**CBS 730.96***	Human lung biopsy	JX256429	JX276441	JX266596
C. ovariicola	**CBS 470.90***	*Eragrostis interrupta*	JN601031	JN600976	JN601020
C. perotidis	**CBS 7846-2**	*Perotis rara*	AF071320	AF081374	
C. ravenelii	**BRIP 13165***	*Sporobolus fertilis*	JN192386	JN600978	JN601024
C. spicifera	**CBS 274.52**	Soil	JN192387	JN600979	JN601023
C. trifolii	**ICMP 6149**	*Setaria glauca*	JX256434	JX276457	JX266600
C. tripogonis	**BRIP 12375***	*Dactyloctenii aeygeptii*	JN192388	JN600980	JX266600
C. tuberculata	**CBS 146.63***	*Zea mays*	JN192374	JN601037	JX266599
C. verrucosa	**MAFF235540**	*Triticum aestivum*	AB444667	AF081388	
Alternaria alternata	**EGS 34.0160***		AF017346	AF081400	

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

species are able to colonise diverse hosts as opportunists; some species are host specific and multiple species can even co-occur on the same host (Mostert et al. 2001; Farr et al. 2002a; Crous and Groenewald 2005). Species of *Diaporthe* cause cankers, diebacks, root rots, fruit rots, leaf spots, blights and wilts on a wide range of plant host including some economically important hosts and have been the subject of considerable phytopathological research. Examples of diseases on major crops include *Diaporthe*/*Phomopsis* complex causing soybean seed decay, pod and stem blight and cankers, sunflower stem canker (*D. helianthi*), dead arm of grapevines (*D. ampelina*) and melanose in *Citrus* (*D. citri*) (Van Niekerk et al. 2005; Santos et al. 2011; Thompson et al. 2011; Udayanga et al. 2014a, b). In addition, several species of *Diaporthe* are known from clinical reports of immunocompromised patients, although these pathogens are only provisionally identified to species level (Garcia-Reyne et al. 2011; Mattei et al. 2013). *Diaporthe* comprises a major component of endophytes in tropical and temperate trees, and several species have been used in secondary metabolite research (Isaka et al. 2001; Li et al. 2010a, b; Kaul et al. 2012).

Species identification and numbers

The Genealogical Concordance Phylogenetic Species Recognition (GCPSR) has been applied in the genus *Diaporthe* to define the species boundaries in recent studies (Udayanga et al. 2012b; Gomes et al. 2013; Tan et al. 2012). Therefore species delimitation is currently based on DNA sequence data and comparison of morphological characters (Santos and Phillips 2009; Santos et al. 2010; Diogo et al. 2010; Udayanga et al. 2014a, b). Although the genus *Diaporthe* has received much attention, few phylogenetic studies have thus far been conducted; hence the taxonomy of some of the species in this genus is still uncertain including many of the common plant pathogens. Index Fungorum lists 892 *Diaporthe* names and 983 *Phomopsis* names whereas MycoBank (2014) lists 919 *Diaporthe* names and 1,040 *Phomopsis* names. However, the names available in the literature are mostly applied based on host association and morphology except fewer species described in last two decades based on DNA sequence data. Ex-type cultures are available for less than 100 species known despite the large number of

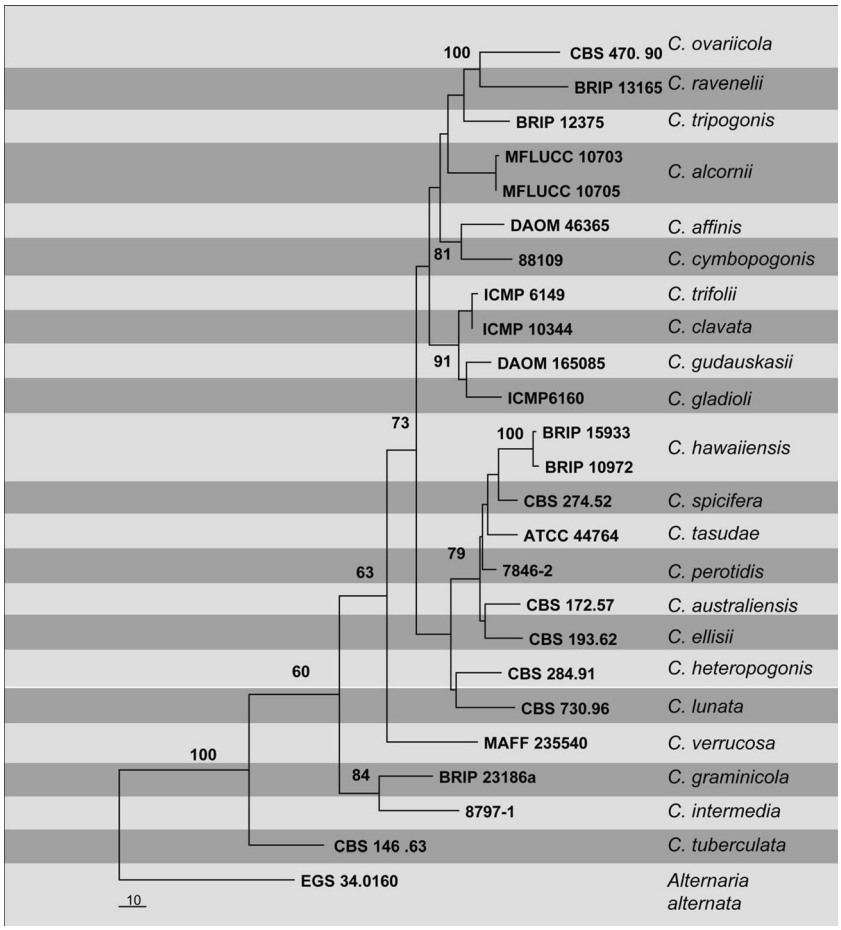


Fig. 9 Phylogram generated from parsimony analysis based on combined ITS and GPDH sequenced data of *Curvularia*. Parsimony bootstrap support values greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*. The *scale bar* indicates ten changes. The tree is rooted with *Alternaria alternata*

species listed in databases and literature. The delimitation of species within the genus *Diaporthe* improved once DNA sequence data were incorporated (Castlebury and Mengistu 2006; Van Rensburg et al. 2006; Santos et al. 2010; Udayanga et al. 2012b, 2014a, b), since this facilitates obtaining detailed insight into complex evolutionary relationships.

Molecular phylogeny

Since the first molecular phylogenetic study in *Diaporthe* (Rehner and Uecker 1994), rDNA ITS, partial sequences of translation elongation factor 1-α (TEF) and mating type genes (MAT 1-1-1/1-2-1) have commonly been used in molecular phylogenetic studies in this genus (Van Niekerk et al. 2005; Van Rensburg et al. 2006; Santos et al. 2010; Udayanga et al. 2011; Sun et al. 2012). Udayanga et al. (2012a) used ITS, TEF, β- tubulin and CAL genes with a selected set of ex-type cultures and additional isolates to infer the phylogeny of the genus. In a parallel study, a multi-marker phylogeny was effectively used to describe novel species in *Diaporthe* based on fresh collections from Thailand (Udayanga et al. 2012b). Gomes et al. (2013) used a Brazilian collection of isolates and existing ex-type cultures for a combined phylogenetic analysis of five genetic markers which included ITS, TEF, β- tubulin, CAL and HIS. They introduced several novel taxa from Brazilian collections from medicinal plants with one epitype for *Diaporthe anarcardi* from Kenya. Udayanga et al. (2014a, b) revisited the *Diaporthe* species associated with *Citrus* worldwide with comprehensive assessment of the genes including ITS, TEF, β- tubulin, CAL and ACT. The study revisited several important phytopathogens including *D. citri, D. cytosporella*, *D. forniculina* and *D. rudis*, with the epitypes designated with modern descriptions. The clarification of *D. foeniculaina* and *D. rudis* revealed the potential extensive host association of some species.

Udayanga et al. (2014a) further emphasized that ITS alone can cause much confusion in defining closely related taxa, which has also been noted by several previous researchers regarding closely related species in *Diaporthe* (Farr et al. 2002a, b; Murali et al. 2006; Santos et al. 2010). The variation of ITS sequences can result in superfluous, multiple terminal branches in combined analyses, even when other gene regions do not support these distinctions

(Udayanga et al. 2014a, b). The TEF gene is informative when it comes to clarifying species limits in *Diaporthe* (Table 9, Fig. 10).

Recommendations

ITS and TEF are recommended for preliminary identification of the species (Castlebury et al. 2001; Castlebury 2005; Santos and Phillips 2009; Santos et al. 2010). ITS, TEF, β- tubulin, CAL, HIS and ACT should be used in combined analysis (selection of 4–5 genes), with recommended primers in relevant publications (Udayanga et al. 2012b, 2014a, b; Gomes et al. 2013).

Diplodia

Background

Species of *Diplodia* (*Botryosphaeriaceae*) are endophytes, pathogens, or saprobes associated with cankers, dieback and fruit rot (Crous et al. 2006; Slippers and Wingfield 2007) in a wide range of hosts of agricultural and forestry importance (Farr and Rossman 2014). Cryptic speciation is common in the genus *Diplodia*, which makes species identification difficult if only based on morphological characters (Phillips et al. 2012, 2013). Denman et al. (2000) suggested that *Lasiodiplodia* could be a synonym of *Diplodia*, however recent studies accepted them as distinct genera (Pavlic et al. 2004; Burgess et al. 2006; Damm et al. 2007; Alves et al. 2008).

The genus *Diplodia* was introduced by Montagne (1834) with concepts altering over the years and has been regarded as including species with dark brown, 1-septate conidia (Phillips et al. 2005). *Diplodia* is defined by having uni or multilocular conidiomata lined with conidiogenous cells that form hyaline, aseptate, thick-walled conidia at their tips (Phillips et al. 2005). *Diplodia mutila* is the type species of *Diplodia* (Montagne 1834; Fries 1849), however, there are no living cultures linked to the holotype. As this has severely hampered studies on taxonomy and phylogeny of *Diplodia*, Alves et al. (2004) provided a detailed description of this species based on one isolate from grapevines in Portugal (CBS 112553).

Species identification and numbers

Diplodia is a large genus and a search in MycoBank (2014) revealed 1,317 names. Species in *Diplodia* were described, often based on host association, which later resulted in a proliferation of species names. According to Slippers et al. (2004d), host is not of primary importance in species differentiation, thus, many of the names in *Diplodia* are likely to be synonyms.

Based on DNA sequence data (single or multimarker) and minor differences in conidial morphology, there are currently about 20 *Diplodia* species (de Wet et al. 2003; Alves et al. 2004, 2006; Gure et al. 2005; Damm et al. 2007; Lazzizera et al. 2008; Pérez et al. 2010; Jami et al. 2012; Phillips et al. 2012, 2013; Linaldeddu et al. 2013; Lynch et al. 2013). The phylogenetic analysis was performed based on up to date holotype or ex-epitype sequence data available in GenBank (Table 10).

Molecular phylogeny

Studies on the taxonomy and phylogeny of *Diplodia* were hampered by a lack of an ex-type culture linked to the generic type, *D. mutila*. A collection of *D. mutila* from *Populus* with an ex-type culture was designated as epitype by Alves et al. (2014). They obtained a large collection of *Diplodia* strains from ash and other woody hosts showing V-shaped cankers and branch dieback. These strains were identified based on morphological characters and DNA sequence data. Since 2003 several new species have been described in *Diplodia* and these species were recognized mainly from DNA sequence data. *Diplodia scrobiculata* was differentiated from *D. sapinea* on the basis of multiple gene genealogies inferred from six protein coding genes and six microsatellite loci (de Wet et al. 2003). *Diplodia africana* (Damm et al. 2007), *D. olivarum* (Lazzizera et al. 2008) and *D. cupressi* (Alves et al. 2006) have been differentiated from *D. mutila* on the basis of formation of distinct clades in phylogenies based on ITS and TEF sequence data and due to their unique conidial morphology (Phillips et al. 2012).

Combined morphological and phylogenetic analyses of DNA sequence data from ITS and TEF (Alves et al. 2014) showed that the *Fraxinus* isolates from Italy, Netherlands, Portugal and Spain belong to three distinct species namely *Diplodia fraxini*, *D. mutila* and *D. subglobosa*. The phylogenetic tree constructed with holotype or ex-epitype sequences is presented in Fig. 11.

Recommended genetic markers

- LSU and SSU–generic level
- ITS, TEF and β-tubulin–species level

ITS, TEF and β-tubulin are the common genetic markers used in identification of *Diplodia* species. Combined ITS and TEF genes provide satisfactory resolution for resolving species.

Dothiorella

Background

Dothiorella (*Botryosphaeriaceae*) was proposed by Saccardo in 1880 (Crous and Palm 1999) with *D. pyrenophora* as the

Table 9 *Diaporthe.* Details of the isolates used in the phylogenetic tree

Species	Isolate	Host	GeneBank accession numbers			
			ITS	β-tubulin	TEF 1-α	CAL
Diaporthe acaciigena	**CBS 129521***	*Acacia retinodes*	KC343005	KC343973	KC343731	KC343247
D. alleghaniensis	**CBS 495.72***	*Betula alleghaniensis*	KC343007	KC343975	KC343733	KC343249
D. alnea	**CBS 146.46***	*Alnus* sp.	KC343008	KC343976	KC343734	KC343250
D. ambigua	**CBS 114015***	*Pyrus communis*	KC343010	KC343978	KC343736	KC343252
D. ampelina	**CBS 114016***	*Vitis vinifera*	AF230751	JX275452	AY745056	AY230751
D. amygdali	**CBS 126679***	*Prunus dulcis*	KC343022	KC343990	AY343748	KC343264
D. anacardii	**CBS 720.97***	*Anacardium ocidentale*	KC343024	KC343992	KC343750	KC343266
D. angelicae	**CBS 111592***	*Heracleum sphondylium*	KC343027	KC343995	KC343753	KC343269
D. aquatica	**IFRDCC 3051***	–	JQ797437	–	–	–
D. arecae	**CBS 161.64***	*Areca catechu*	KC343032	KC344000	KC343758	KC343274
D. arengae	**CBS 114979***	*Arenga engleri*	KC343034	KC344002	KC343760	KC343276
D. aspalathi	**CBS 117169***	*Aspalathus linearis*	KC343036	KC344004	KC343762	KC343278
D. australafricana	**CBS 111886***	*Vitis vinifera*	KC343038	KC344006	KC343764	KC343280
D. beilharziae	**BRIP 54792***	*Indigofera australis*	JX862529	KF170921	JX862535	–
D. bicincta	**CBS 121004***	*Juglans* sp.	KC343134	KC344102	KC343860	KC343376
D. brasiliensis	**CBS 133183***	*Aspidosperma tomentosum*	KC343042	KC344010	KC343768	KC343284
D. caulivora	**CBS 127268***	*Glycine max*	KC343045	KC344013	KC343771	KC343287
D. celastrina	**CBS 139.27***	*Celastrus* sp	KC343047	KC344015	KC343773	KC343289
D. citri	**CBS 135422***	*Citrus* sp.	KC843311	KC843187	KC843071	KC843157
D. citriasiana	**ZJUD 30***	*Citrus sp.*	JQ954645	KC357459	JQ954663	KC357491
D. citrichinensis	**ZJUD 34***	*Citrus sp.*	JQ954648		JQ954666	KC357494
D. crotalariae	**CBS 162.33***	*Crotalaria spectabilis*	KC343056	KC344024	KC343782	KC343298
D. cuppatea	**CBS 117499***	*Aspalathus linearis*	KC343057	KC344025	KC343783	KC343299
D. cynaroidis	**CBS 122676***	*Protea cynaroides*	KC343058	KC344026	KC343784	KC343300
D. cytosporella	**FAU461***	*Citrus limon*	KC843307	KC843221	KC843116	KC843141
D. endophytica	**CBS 133811***	*Schinus terebinthifolius*	KC343065	KC343065	KC343791	KC343307
D. eres	**AR5193***	*Ulmus* Sp.	KJ210529	KJ420799	KJ210550	KJ434999
P. cotoneastri	**CBS 439.82***	*Cotoneaster* sp.	KC343090	KC344058	KC343816	KC343332
D. fraxini-angustifoliae	**BRIP 54781***	*Fraxinus angustifolia*	JX862528	KF170920	JX862534	–
D. foeniculina	**CBS 123208***	*Foeniculum vulgare*	KC343104	KC344072	KC343830	KC343346
D. foeniculina	**CBS 123209***	*Foeniculum vulgare*	KC343105	KC344073	KC343831	KC343347
D. foeniculina	**CBS 187.27 ***	*Camellia sinensis*	KC343107	KC344075	KC343833	KC343349
D. ganjae	**CBS 180.91***	*Cannabis sativa*	KC343112	KC344080	KC343838	KC343354
D. gulyae	**BRIP 54025***	*Helianthus annuus*	JF431299	–	JN645803	–
D. helianthi	**CBS 592.81***	*Helianthus annuus*	KC343115	KC344083	KC343841	KC343357
D. helicis	**AR5211***	*Hedera helix*	KJ210538	KJ420828	KJ210559	KJ435043
D. hickoriae	**CBS 145.26***	*Carya glabra*	KC343118	KC344086	KC343844	KC343360
D. hongkongensis	**CBS 115448***	*Dichroa febrífuga*	KC343119	KC344087	KC343845	KC343361
D. inconspicua	**CBS 133813***	*Maytenus ilicifolia*	KC343123	KC344091	KC343849	KC343365
D. infecunda	**CBS 133812***	*Schinus terebinthifolius*	KC343126	KC344094	KC343852	KC343852
D. kochmanii	**BRIP 54033***	*Helianthus annuus*	JF431295	–	JN645809	–
D. kongii	**BRIP 54031***	*Helianthus annuus*	JF431301	–	JN645797	–
D. longispora	**CBS 194.36***	*Ribes* sp.	KC343135	KC344103	KC343861	KC343377
D. lusitanicae	**CBS 123212***	*Foeniculum vulgare*	KC343136	KC344104	KC343862	KC343378
D. mayteni	**CBS 133185***	*Maytenus ilicifolia*	KC343139	KC344107	KC343865	KC343381
D. melonis	**CBS 507.78 ***	*Glycine soja*	KC343141	KC344109	KC343867	KC343383
D. musigena	**CBS 129519***	*Musa* sp.	KC343143	KC344111	KC343869	KC343385

Table 9 (continued)

Species	Isolate	Host	GeneBank accession numbers			
			ITS	β-tubulin	TEF 1-α	CAL
D. neoarctii	**CBS 109490***	*Ambrosia trifida*	KC343145	KC344113	KC343871	KC343387
D. nothofagi	**BRIP 54801***	*Nothofagus cunninghamii*	JX862530	KF170922	JX862536	–
D. novem	**CBS 127270***	*Glycine max*	KC343155	KC344123	KC343881	KC343397
D. oxe	**CBS 133186***	*Maytenus ilicifolia*	KC343164	KC344132	KC343890	KC343406
D. paranensis	**CBS 133184***	*Maytenus ilicifolia*	KC343171	KC344139	KC343897	KC343413
D. pascoei	**BRIP 54847***	*Persea americana*	JX862532	KF170924	JX862538	–
D. perjuncta	**CBS 109745***	*Ulmus glabra*	KC343172	KC344140	KC343898	KC343414
D. pseudomangiferae	**CBS 101339***	*Mangifera indica*	KC343181	KC344149	KC343907	KC343423
D. pseudophoenicicola	**CBS 462.69***	*Mangifera indica*	KC343183	KC344151	KC343909	KC343425
D. psoraleae	**CBS 136412***	*Psoralea pinnata*	KF777158	KF777251	KF777245	–
D. psoraleae-pinnatae	**CBS 136413**	*Psoralea pinnata*	KF777159	KF777252	–	–
D. pterocarpi	**MFLUCC 10-0571***	*Pterocarpus indicus*	JQ619899	JX275460	JX275416	JX197451
D. pterocarpicola	**MFLUCC 10-0580***	*Pterocarpus indicus*	JQ619887	JX275441	JX275403	JX197433
D. pulla	**CBS 338.89***	*Hedera helix*	KC343152	KC344120	KC343878	KC343394
D. raonikayaporum	**CBS 133182***	*Spondias mombin*	KC343188	KC344156	KC343914	KC343430
D. rudis	**CBS 109291***	*Laburnum anagyroides*	KC843331	KC843177	KC843090	KC843146
D. rudis	**CBS 113201***	*Vitis vinifera*	KC343234	KC344202	KC343960	KC343476
D. saccarata	**CBS 116311***	*Protea repens*	KC343190	KC344158	KC343916	KC343432
D. salicicola	**BRIP 54825***	*Salix purpurea*	JX862531	JX862531	JX862537	–
D. schini	**CBS 133181***	*Schinus terebinthifolius*	KC343191	KC344159	KC343917	KC343433
D. sclerotioides	**CBS 296.67***	*Cucumis sativus*	KC343193	KC344161	KC343919	KC343435
D. siamensis	**MFLUCC 10-0573a***	*Dasymaschalon sp.*	JQ619879	JX275429	JX275393	–
D. terebinthifolii	**CBS 133180***	*Schinus terebinthifolius*	KC343216	KC344184	KC343942	KC343458
D. thunbergii	**MFLUCC 10-0576***	*Thunbergia grandifolia*	JQ619893	JX275449	JX275409	JX197440
D. toxica	**CBS 534.93***	*Lupinus angustifolius*	KC343220	KC344188	KC343946	KC343462
Diaporthella corylina	**CBS 121124***	*Corylus* sp.	KC343004	KC343972	KC343730	KC343246
P. lithocarpus	**CGMCC 3.15175***	*Lithocarpus glabra*	KC153104	–	KC153095	–
P. mahothocarpus	**CGMCC 3.15181***	*Lithocarpus glabra*	KC153096	–	KC153087	–
P. ternstroemia	**CGMCC 3.15183***	*Ternstroemia gymnanthera*	KC153098	–	KC153089	–

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

generic type. The delimitation of the genus has been in a state of flux since it was introduced, and detailed explanations of its taxonomy have been given by Sutton (1977), Crous and Palm (1999) and Phillips et al. (2008, 2013). Crous and Palm (1999) examined the holotype of *D. pyrenophora* and synonymised *Dothiorella* under *Diplodia* based on a broad morphological concept of *Diplodia*. That treatment was followed by Denman et al. (2000), Zhou and Stanosz (2001) and Slippers et al. (2004a). Phillips et al. (2005) re-examined the type of *D. pyrenophora* and found that the conidia become brown and 1-septate when they are still attached to the conidiogenous cells, while in *Diplodia* the conidia are hyaline and become dark and septate only after discharge from the conidiomata. Crous et al. (2006) confirmed these morphological differences by re-examining types of both *Diplodia* and *Dothiorella*. The sexual state of the species is rarely found in nature and no sexual morph was formed in culture for any of the species, except for *D. sarmentorum* and *D. iberica*. Therefore, differentiation of species is mostly derived based on the asexual morphs and cultural characteristics.

Species identification and numbers

As members of *Botryosphaeriaceae*, species of *Dothiorella* are known as endophytes, pathogens and saprobes in association with various woody plants, and species in *Dothiorella* were

Fig. 10 Phylogram generated from parsimony analysis based on combined ITS, EF1-α, β- tubulin, and CAL sequenced data of *Diaporthe*. Parsimony bootstrap support values and Bayesian posterior probabilities greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*. The tree is rooted with *Diaporthella corylina* CBS 121124

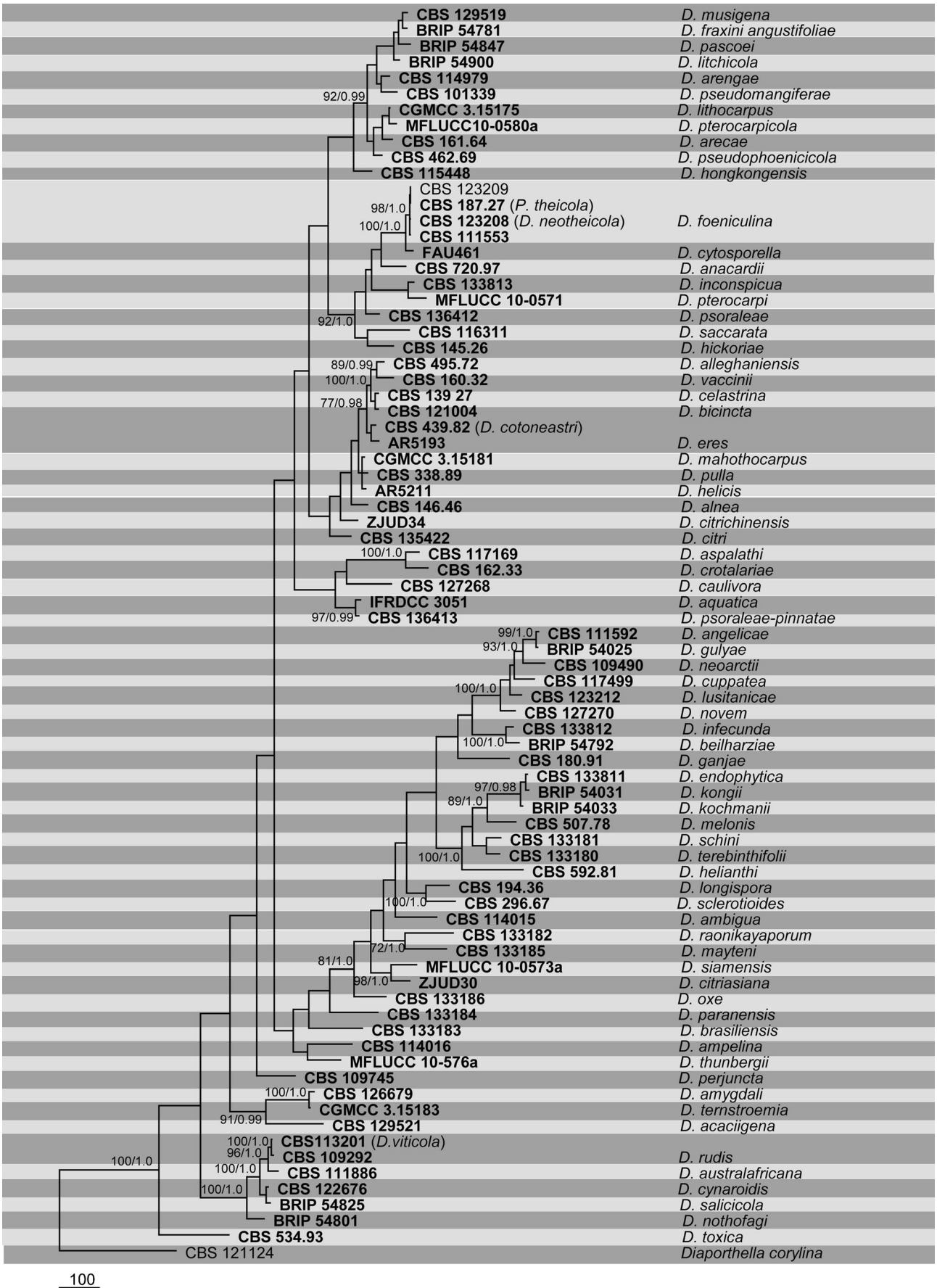

CBS 129519 D. musigena
BRIP 54781 D. fraxini angustifoliae
BRIP 54847 D. pascoei
BRIP 54900 D. litchicola
CBS 114979 D. arengae
92/0.99
CBS 101339 D. pseudomangiferae
CGMCC 3.15175 D. lithocarpus
MFLUCC10-0580a D. pterocarpicola
CBS 161.64 D. arecae
CBS 462.69 D. pseudophoenicicola
CBS 115448 D. hongkongensis
CBS 123209
98/1.0
CBS 187.27 (P. theicola)
100/1.0
CBS 123208 (D. neotheicola) D. foeniculina
CBS 111553
FAU461 D. cytosporella
CBS 720.97 D. anacardii
CBS 133813 D. inconspicua
MFLUCC 10-0571 D. pterocarpi
92/1.0
CBS 136412 D. psoraleae
CBS 116311 D. saccarata
CBS 145.26 D. hickoriae
89/0.99
CBS 495.72 D. alleghaniensis
100/1.0
CBS 160.32 D. vaccinii
77/0.98
CBS 139 27 D. celastrina
CBS 121004 D. bicincta
CBS 439.82 (D. cotoneastri)
AR5193 D. eres
CGMCC 3.15181 D. mahothocarpus
CBS 338.89 D. pulla
AR5211 D. helicis
CBS 146.46 D. alnea
ZJUD34 D. citrichinensis
CBS 135422 D. citri
100/1.0
CBS 117169 D. aspalathi
CBS 162.33 D. crotalariae
CBS 127268 D. caulivora
IFRDCC 3051 D. aquatica
97/0.99
CBS 136413 D. psoraleae-pinnatae
99/1.0
CBS 111592 D. angelicae
93/1.0
BRIP 54025 D. gulyae
CBS 109490 D. neoarctii
CBS 117499 D. cuppatea
100/1.0
CBS 123212 D. lusitanicae
CBS 127270 D. novem
CBS 133812 D. infecunda
100/1.0
BRIP 54792 D. beilharziae
CBS 180.91 D. ganjae
CBS 133811 D. endophytica
97/0.98
BRIP 54031 D. kongii
89/1.0
BRIP 54033 D. kochmanii
CBS 507.78 D. melonis
CBS 133181 D. schini
100/1.0
CBS 133180 D. terebinthifolii
CBS 592.81 D. helianthi
CBS 194.36 D. longispora
100/1.0
CBS 296.67 D. sclerotioides
CBS 114015 D. ambigua
CBS 133182 D. raonikayaporum
72/1.0
CBS 133185 D. mayteni
81/1.0
MFLUCC 10-0573a D. siamensis
98/1.0
ZJUD30 D. citriasiana
CBS 133186 D. oxe
CBS 133184 D. paranensis
CBS 133183 D. brasiliensis
CBS 114016 D. ampelina
MFLUCC 10-576a D. thunbergii
CBS 109745 D. perjuncta
100/1.0
CBS 126679 D. amygdali
CGMCC 3.15183 D. ternstroemia
91/0.99
CBS 129521 D. acaciigena
100/1.0
CBS113201 (D.viticola)
96/1.0
CBS 109292 D. rudis
100/1.0
CBS 111886 D. australafricana
100/1.0
CBS 122676 D. cynaroidis
BRIP 54825 D. salicicola
BRIP 54801 D. nothofagi
CBS 534.93 D. toxica
CBS 121124 Diaporthella corylina
100/1.0
100

Table 10 *Diplodia*. Details of the isolates used in the phylogenetic tree

Species	Isolate no.	Host	GenBank		
			ITS	TEF	β-tubulin
Diplodia africana	**CBS 120835***	*Prunus persica*	EF445343	EF445382	–
D. agrifolia	**CBS 132777***	*Quercus agrifolia*	JN693507	JQ517317	JQ411459
D. alatafructa	**CBS 124931***	*Pterocarpus angolensis*	FJ888460	FJ888444	–
D. allocellula	**CBS 130408***	*Acacia karroo*	JQ239397	JQ239384	JQ239378
D. bulgarica	**CBS 124254***	*Malus sylvestris*	GQ923853	GQ923821	–
D. corticola	**CBS 112549***	*Quercus suber*	AY259100	AY573227	DQ458853
D. cupressi	**CBS 168.87***	*Cupressus sempervirens*	DQ458893	DQ458878	DQ458861
D. fraxini	**CBS 136010***	*Fraxinus angustifolia*	KF307700	KF318747	–
D. intermedia	**CBS 124462***	*Malus sylvestris*	GQ923858	GQ923826	–
D. malorum	**CBS 124130***	*Malus sylvestris*	GQ923865	GQ923833	–
D. mutila	**CBS 112553***	*Vitis vinifera*	AY259093	AY573219	DQ458850
D. olivarum	**CBS 121887***	*Olea europaea*	EU392302	EU392279	HQ660079
D. sapinea	**CBS 393.84***	*Pinus nigra*	DQ458895	DQ458880	–
D. pseudoseriata	**CBS 124906***	*Blepharocalyx salicifolius*	EU080927	EU863181	–
D. quercivora	**CBS 133852***	*Quercus canariensis*	JX894205	JX894229	–
D. rosulata	**CBS 116470***	*Prunus africana*	EU430265	EU430267	EU673132
D. scrobiculata	**CBS 109944***	*Pinus greggii*	DQ458899	DQ458884	AY624258
D. seriata	**CBS 112555***	*Vitis vinifera*	AY259093	AY573219	DQ458856
D. subglobosa	**CBS 124133***	*Lonicera nigra*	GQ923856	GQ923824	–
D. tsugae	**CBS 418.64***	*Tsuga heterophylla*	DQ458888	DQ458873	DQ458855
Lasiodiplodia theobromae	**CBS 164.96***	Fruit along coral reef coast	AY640255	AY640258	EU673110

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

mostly described based on host association, much as for other members of *Botryosphaeriaceae*. This led to the introduction of many species names, and there are 368 epithets for *Dothiorella* in Index Fungorum (2014) and 393 species names in MycoBank (2014). Slippers et al. (2013) suggested that host association should not be considered an important factor in species definition of the *Botryosphaeriaceae*, therefore most of these names are likely synonyms. There are 19 described species with available cultures, and with the exception of *D. sarmentorum* all have been described after 2005. The phylogenetic analysis was performed based on up to date holotype or ex-epitype sequence data available in GenBank (Table 11).

Molecular phylogeny

Phillips et al. (2005) broadened the concept of *Botryosphaeria* and included *Dothiorella* in *Botryosphaeria* based on ITS analysis. Crous et al. (2006) recognised ten lineages within *Botryosphaeriaceae* corresponding to different genera based on phylogenetic analysis of 28S rDNA, and the three species *D. iberica*, *D. sarmentorum* and *D. viticola* formed a clade within *Botryosphaeriaceae*. These were assigned to *Dothidotthia*. Subsequently, Phillips et al. (2008) showed that *Do. symphoricarpa* (the type species of *Dothidotthia*) belongs in a distinct family within the *Pleosporales*, while *D. sarmentorum*, *D. iberica* and *D. viticola* fall within two separate genera in the *Botryosphaeriaceae* and a new genus, *Spencermartinsia* was introduced to accommodate *D. viticola*. Phillips et al. (2013) listed all cultures of available *Dothiorella* species, and provided a key to species, as well as a phylogenetic tree. Abdollahzadeh et al. (2014) introduced five new *Dothiorella* species which were associated with woody plants in Iran, New Zealand, Portugal and Spain. The phylogenetic tree constructed with holotype or ex-epitype sequences is presented in Fig. 12.

Recommended genetic markers

- ITS–placement within the *Botryosphaeriaceae* (the generic level), and also some specific delineation.
- TEF–the generic level and inter-specific delineation.
- β-tubulin–inter-specific delineation.

Slippers et al. (2013) suggested that all of the known species of *Dothiorella* in culture can be separated based solely on ITS, but bootstrap support values for some of the internal nodes are quite low. Due to the studies on the other members

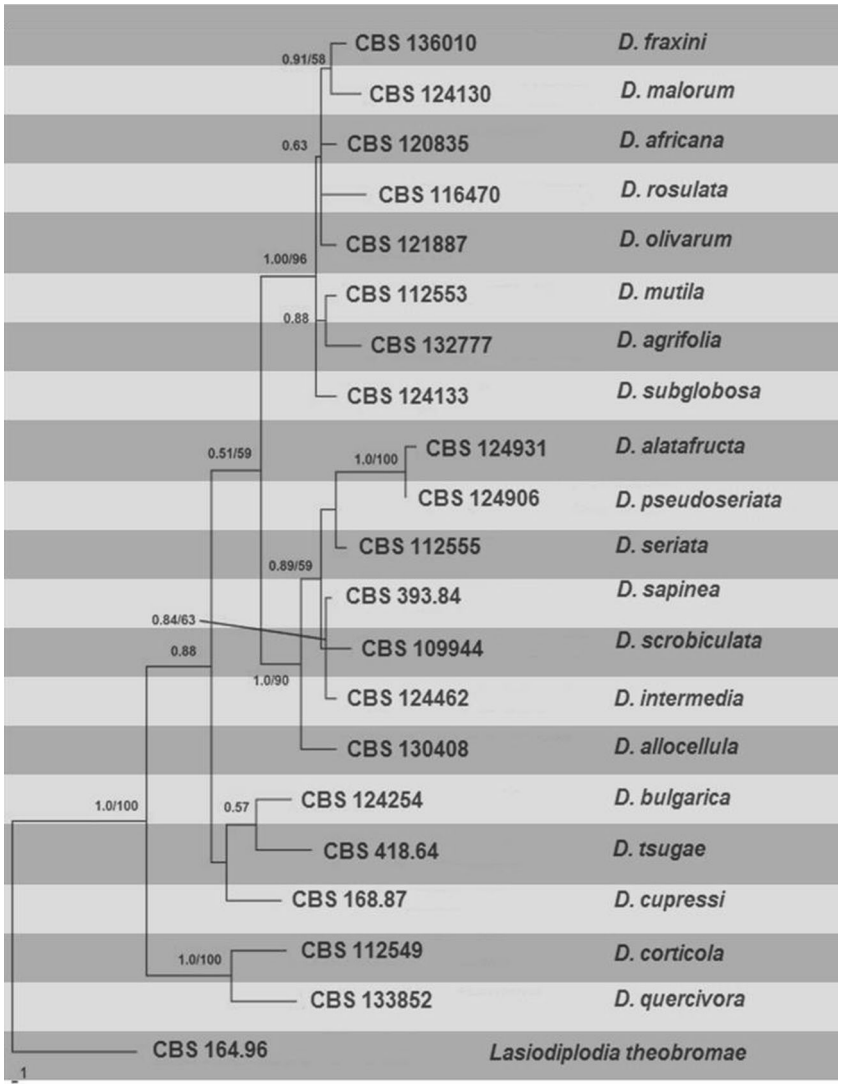


Fig. 11 Phylogram generated from parsimony analysis based on combined ITS, TEF and β-tubulin sequenced data of *Diplodia*. Parsimony bootstrap support values and Bayesian posterior probabilities greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*. The tree is rooted with *Lasiodiplodia theobromae* CBS 164.96

of *Botryosphaeriaceae*, therefore, we strongly recommend that it is necessary to combine ITS and TEF (or intended β-tubulin gene) when molecular studies are carried out on *Dothiorella*.

Fusarium

Background

The genus *Fusarium* was described by Link (1809) and later became a sanctioned name (Fries 1821). It is based on the type species *Fusarium sambucinum* (Nirenberg 1995). Species in *Fusarium* were described largely on the basis of the morphology of the canoe shaped septate conidia produced by most species as well as the shape and formation of other asexual spores Leslie and Summerell 2006). The sexual morphs (ascospores produced in perithecia) have played little role in the differentiation of most species as they are rare, if produced at all (Seifert 2001). *Fusarium* includes a number of species that are very important plant pathogens, some that are potent producers of an array of mycotoxins and several species or species complexes that are involved in diseases of humans (Leslie and Summerell 2006). There are also many species that are apparently endophytic in plants as well as species that are saprobes in soil and in organic matter.

Two species, *F. graminearum* and *F. oxysporum*, were included in an assessment of the top 10 fungal plant pathogens by Dean et al. (2012). *Fusarium graminearum* is the cause of head blight of wheat (Windels 2000), and *F. oxysporum* causes wilt diseases in a range of crops including bananas, tomatoes and other vegetables as well as cotton (Beckman 1987). Other species of *Fusarium* cause stalk and cob rots in maize and sorghum, canker diseases in woody plants and root and crown diseases across a vast spectrum of plant species (Summerell et al.

Table 11 *Dothiorella*. Details of the isolates used in the phylogenetic tree

Species name	Strain no.	Host	ITS	TEF
Dothiorella americana	**CBS 128309***	*Vitis* sp.	HQ288218	HQ288262
D. americana	CBS 128310	*Vitis* sp.	HQ288219	HQ288263
D. brevicollis	**CBS 130411***	*Acacia karroo*	JQ239403	JQ239390
D. brevicollis	CBS 130412	*Acacia karroo*	JQ239404	JQ239391
D. casuarinae	**CBS 120688***	*Casuarina* sp.	DQ846773	DQ875331
D. casuarinae	CBS 120690	*Casuarina* sp.	DQ846774	DQ875333
D. dulcispinae	**CBS 130413***	*Acacia karroo*	JQ239400	JQ239387
D. dulcispinae	CBS 130414	*Acacia karroo*	JQ239401	JQ239388
D. dulcispinae	CBS 130415	*Acacia karroo*	JQ239402	JQ239389
D. iberica	**CBS 115041***	*Quercus ilex*	AY573202	AY573222
D. iberica	CBS 113188	*Quercus ilex*	AY573198	EU673278
D. iberica	CAA 005	*Quercus ilex*	EU673312	EU673279
D. iranica	**IRAN1587C***	*Olea europaea*	KC898231	KC898214
D. longicollis	**CBS 122068***	*Lysiphyllum cunninghamii*	EU144054	EU144069
D. longicollis	CBS 122067	*Lysiphyllum cunninghamii*	EU144052	EU144067
D. moneti	**MUCC 505***	*Acacia rostellifera*	EF591920	EF591971
D. moneti	MUCC 507	*Acacia rostellifera*	EF591922	EF591973
D. parva	**IRAN1579C***	*Corylus avellana*	KC898234	KC898217
D. parva	IRAN1585C	*Corylus avellana*	KC898235	KC898218
D. pretoriensis	**CBS 130404***	*Acacia karroo*	JQ239405	JQ239392
D. pretoriensis	CBS 130403	*Acacia karroo*	JQ239406	JQ239393
D. prunicola	**IRAN1541***	*Prunus dulcis*	EU673313	EU673280
D. Santali	**MUCC 509***	*Santalum acuminatum*	EF591924	EF591975
D. santali	MUCC 508	*Santalum acuminatum*	EF591923	EF591974
D. sarmentorum	**IMI 63581b***	*Ulmus* sp.	AY573212	AY573235
D. sarmentorum	CBS 115038	*Malus pumila*	AY573206	AY573223
D. sempervirentis	IRAN1581C	*Cupressus sempervirens*	KC898237	KC898220
D. sempervirentis	**IRAN1583C***	*Cupressus sempervirens*	KC898236	KC898219
D. striata	ICMP16819	*Citrus sinensis*	EU673320	EU673287
D. striata*	**ICMP16824***	*Citrus sinensis*	EU673321	EU673288
D. thailandica	**MFLUCC 11-0438***	Unknown	JX646796	JX646861
D. thripsita	**BRIP 51876***	*Acacia harpophylla*	FJ824738	
D. uruguayensis	**CBS 124908***	*Hexalamis edulis*	EU080923	EU863180
D. vidmadera	**DAR78992***	*Vitis vinifera*	EU768874	EU768881
D. vidmadera	DAR78993	*Vitis vinifera*	EU768876	EU768882
D. vidmadera	DAR78994	*Vitis vinifera*	EU768877	EU768883
Spencermartinsia viticola	**CBS 117009***	*Vitis vinifera*	AY905554	AY905559

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

2011). Species of *Fusarium* produce a very large number of secondary metabolites, but two toxin groups, trichothecenes and fumonisins, are particularly detrimental to livestock and humans (through consumption) and as such are heavily regulated in many parts of the world (Desjardins 2005). As a result of the importance of these diseases, the genus is one of the most heavily researched of all genera of fungi and an enormous body of work on all facets of its biology exists (Leslie and Summerell 2006).

Several sexual morph genera are associated with *Fusarium*, the most important of which is *Gibberella* (Desjardins 2003). Most *Fusarium* species, particularly the plant pathogenic species, have a *Gibberella* sexual morph. Other sexual morph genera include *Albonectria, Haematonectria* and *Neocosmospora* as well as a number of other generic names (Gräfenhan et al. 2011). With the changes to the International Code of Nomenclature for Algae, Fungi and Plants providing the opportunity to have a single name for fungi of this nature there has been a strong consensus amongst the community of researchers working on *Fusarium* that this name be used for all the fungi in the so-called

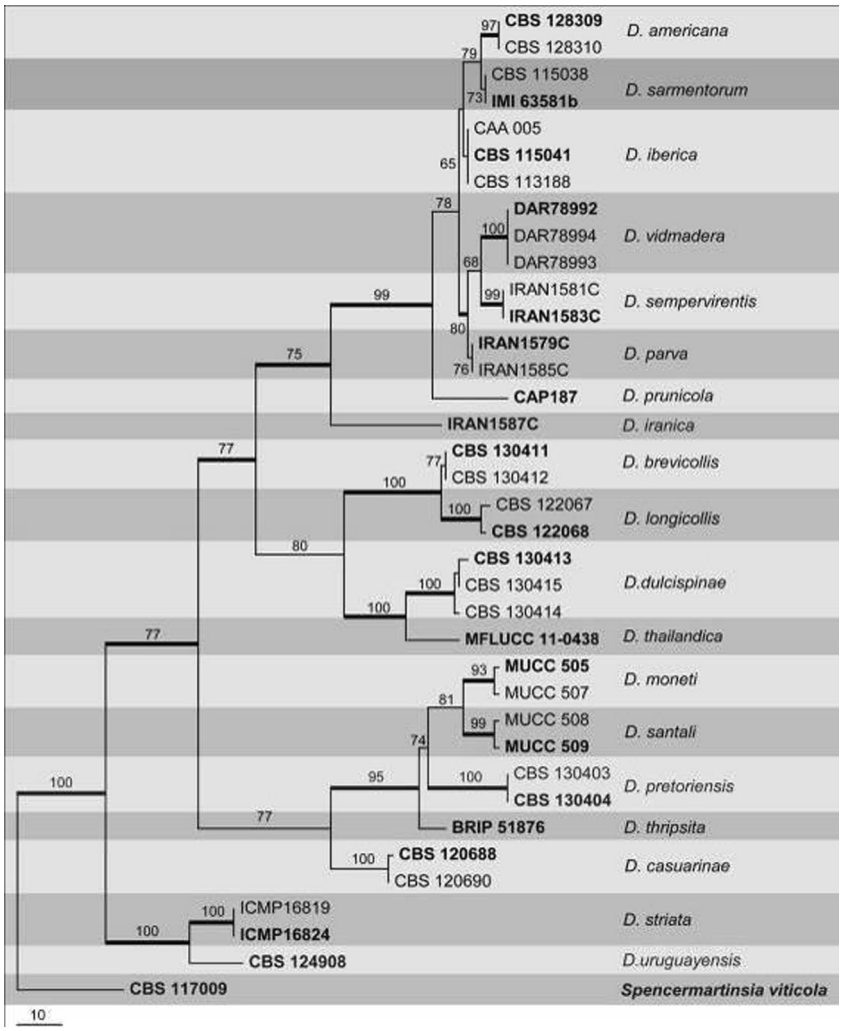


Fig. 12 Phylogram generated from parsimony analysis based on combined ITS and TEF sequenced data of *Dothiorella*. Parsimony bootstrap support values greater than 50 % are indicated above the nodes, and branches with Bayesian posterior probabilities greater than 0.95 are given in *bold*. The ex-type (ex-epitype) and voucher strains are in *bold*. The *scale bar* indicates ten changes. The tree is rooted with *Spencermartinsia viticola* CBS 117009

terminal *Fusarium* clade (Geiser *et al.* 2013). The end result of this is that species of *Fusarium* such as *F. solani, F. decemcellulare* and *F. dimerum* are included with species with *Gibberella* sexual morphs in the current generic definition of *Fusarium* (Geiser et al. 2013).

Species identification and numbers

It is difficult to accurately quantify the number of extant, currently recognized species of *Fusarium*. Over 1,500 names are listed in MycoBank; Leslie and Summerell (2006) documented 72 species, although this was not intended as a monograph, and many of species have been described in the intervening period (e.g. Jacobs et al. 2010; Laurence et al. 2011; Schroers et al. 2009; Walsh et al. 2010). Recent investigations into a number of important species (e.g. *F. graminearum*, *F. incarnatum, F. oxysporum, F. solani*) have provided evidence that they are complexes of phylogenetically distinct lineages that have been, or will eventually be described as species (Aoki et al. 2005; O'Donnell et al. 2004, 2008, 2009).

Molecular phylogeny

There has been substantial work on understanding the phylogenetic relationships within *Fusarium*, and in defining generic boundaries (e.g. Geiser et al. 2013; O'Donnell et al. 2013). This has provided refined concepts for several important plant pathogenic species (e.g. *F. graminearum*, *F. pseudograminearum*, *F. subglutinans, F. verticillioides*) and it has also shown that several important plant pathogens (especially *F. oxysporum* and *F. solani*) are in fact species complexes (Laurence et al. 2014; O'Donnell et al. 2008). A genus-wide phylogeny was inferred using the RNA polymerase largest subunit (RPB1) and RNA polymerase second largest subunit (RPB2) (O'Donnell et al. 2013), as these genes are very informative from a phylogenetic perspective across the whole genus (Table 12, Fig. 13)

Table 12 *Fusarium*. Details of the isolates used in the phylogenetic tree

Species	Isolate	GenBank accession numbers	
		RPB1	RPB2
Fusarium falciforme	NRRL 43529	JX171541	JX171653
F. solani	NRRL 45880	JX171543	JX171655
Fusarium sp.	NRRL 22436	JX171497	JX171610
F. ambrosium	NRRL 20438	JX171470	JX171584
F. phaseoli	NRRL 22276	JX171495	JX171608
F. virguliforme	NRRL 31041	JX171530	JX171643
Fusarium sp.	NRRL 22632	JX171501	JX171614
Fusarium sp.	NRRL 13444	JX171454	JX171568
Fusarium sp.	NRRL 28578	JX171526	JX171639
Fusarium sp.	NRRL 13338	JX171447	JX171561
F. aywerte	NRRL 25410	JX171513	JX171626
F. longipes	NRRL 13368	JX171448	JX171562
F. longipes	NRRL 13374	JX171450	JX171564
F. longipes	NRRL 20723	JX171483	JX171596
Fusarium cf. *compactum*	NRRL 13829	JX171460	JX171574
Fusarium sp.	NRRL 31008	JX171529	JX171642
F. sambucinum	NRRL 22187	JX171493	JX171606
F. venenatum	NRRL 22196	JX171494	JX171607
F. poae	NRRL 13714	JX171458	JX171572
F. sporotrichioides	NRRL 3299	JX171444	JX171558
F. langsethiae	NRRL 54940	JX171550	JX171662
F. armeniacum	NRRL 6227	JX171446	JX171560
F. asiaticum	NRRL 13818	JX171459	JX171573
F. graminearum	NRRL 31084	JX171531	JX171644
F. culmorum	NRRL 25475	JX171515	JX171628
F. pseudograminearum	NRRL 28062	JX171524	JX171637
F. equiseti	NRRL 13402	JX171452	JX171566
F. lacertarum	NRRL 20423	JX171567	JX171581
F. equiseti	NRRL 20697	JX171481	JX171595
Fusarium sp.	NRRL 26417	JX171522	JX171635
Fusarium sp.	NRRL 32175	JX171532	JX171645
F. subglutinans	NRRL 22016	JX171486	JX171599
F. circinatum	NRRL 25331	JX171510	JX171623
F. guttiforme	NRRL 22945	JX171505	JX171618
F. fujikuroi	NRRL 13566	JX171456	JX171570
F. proliferatum	NRRL 22944	JX171504	JX171617
F. mangiferae	NRRL 25226	JX171509	JX171622
F. sacchari	NRRL 13999	JX171466	JX171580
F. verticillioides	NRRL 20956	JX171485	JX171598
F. thapsinum	NRRL 22045	JX171487	JX171600
F. xylarioides	NRRL 25486	JX171517	JX171630
Fusarium sp.	NRRL 52700	JX171544	JX171656
F. nisikadoi	NRRL 25179	JX171507	JX171620
F. miscanthi	NRRL 26231	JX171521	JX171634
F. gaditjirrii	NRRL 45417	JX171542	JX171654
F. lyarnte	NRRL 54252	JX171549	JX171661
F. commune	NRRL 28387	JX171525	JX171638
F. inflexum	NRRL 20433	JX171469	JX171583
F. oxysporum	NRRL 25387	JX171512	JX171625
F. oxysporum	NRRL 34936	JX171533	JX171646
F. foetens	NRRL 38302	JX171540	JX171652
Fusarium sp.	NRRL 25184	JX171508	JX171621
F. redolens	NRRL 22901	JX171503	JX171616
F. hostae	NRRL 29889	JX171527	JX171640
Fusarium sp.	RBG 5116	KJ716216	HQ646395
F. burgessii	RBG 5319	KJ716217	HQ646392
F. beomiforme	NRRL 25174	JX171506	JX171619
F. concolor	NRRL 13459	JX171455	JX171569
F. anguioides	NRRL 25385	JX171511	JX171624
Fusarium sp.	NRRL 25533	JX171518	JX171631
F. babinda	NRRL 25539	JX171519	JX171632
Fusarium sp.	NRRL 22566	JX171500	JX171613
F. torulosum	NRRL 22748	JX171502	JX171615
F. flocciferum	NRRL 25473	JX171514	JX171627
F. tricinctum	NRRL 25481	JX171516	JX171629
F. nurragi	NRRL 36452	JX171538	JX171650
F. heterosporum	NRRL 20693	JX171480	JX171594
F. buharicum	NRRL 13371	JX171449	JX171563
F. sublunatum	NRRL 13384	JX171451	JX171565
F. lateritium	NRRL 13622	JX171457	JX171571
F. sarcochroum	NRRL 20472	JX171472	JX171586
F. stilbioides	NRRL 20429	JX171468	JX171582
Fusarium sp.	NRRL 54149	JX171548	JX171660
F. dimerum	NRRL 20691	JX171478	JX171592
F. lunatum	NRRL 36168	JX171536	JX171648

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

Recommended genetic markers

The recommended and most frequently used gene for identification of species of *Fusarium* is the translation elongation factor 1α gene (TEF) and this is generally used for routine identifications, effectively performing a DNA barcoding function, and forms a significant component of the FUSARIUM-ID database (http://isolate.fusariumdb.org/; Geiser et al. 2004). This database provides a similar facility to GenBank but is based on sequences from accurately identified and validated cultures held in reference collections (Geiser et al. 2004). Using a standard approach (Summerell et al. 2003), sequencing the TEF gene and comparing the sequence with the FUSARIUM-ID database makes it possible to rapidly and accurately identify most pathogenic *Fusarium* species. The ITS region is less informative in *Fusarium* from both a

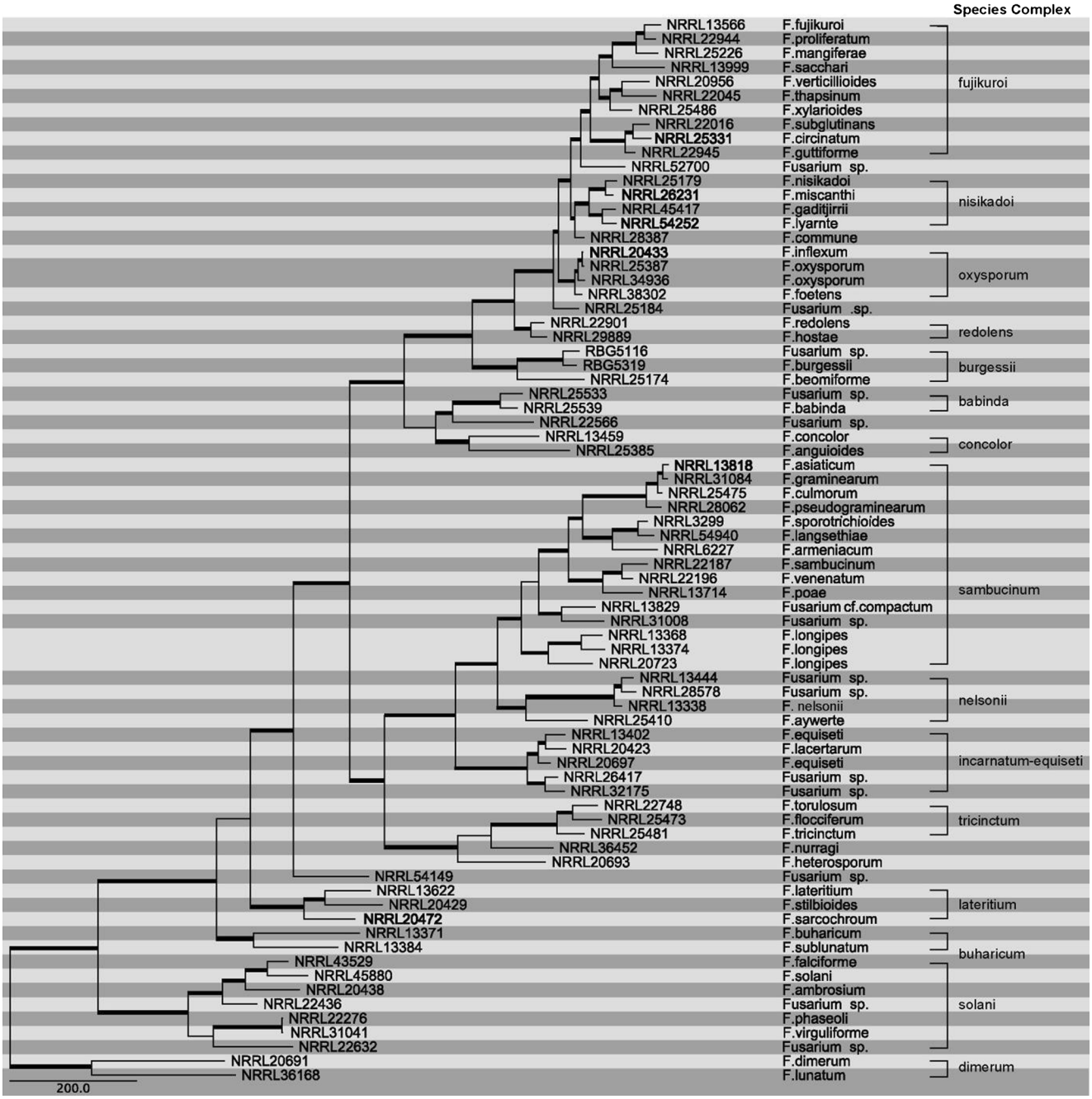


Fig. 13 *Fusarium* The single most parsimonious tree inferred from a combined *RPB1* and *RPB2* dataset indicating the phylogenetic relationships among species complexes in the genus *Fusarium*. Branches with bootstrap intervals greater than 70 % and Bayesian posterior probabilities greater than 0.95 are indicated in *bold*. The NRRL (Agricultural Research Service Culture Collection, Peoria, Illinois USA) and RBG (Royal Botanic Gardens Trust Culture Collection, Sydney, New South Wales, Australia) *numbers* are indicated for all reference taxa

barcoding and phylogenetic perspective and as a result it has not been used extensively. This is primarily because there are nonorthologous copies of ITS2 that are incongruent with species phylogenies derived from other unlinked loci in species of economic importance {O'Donnell and Cigelnik (1997) #1278}. As a consequence it is not recommended that ITS be used for differentiation or identification of *Fusarium* species (Summerell et al. 2003).

Gilbertella

Background

The monotypic genus *Gilbertella* belongs to the family *Choanephoraceae* and subfamily *Gilbertelloideae* (Mucorales, former Zygomycota). It was established by Hesseltine (1960) for species described earlier as *Choanephora persicaria* by Eddy

(1925), and consequently the type species of the genus is *Gilbertella persicaria*. Benny (1991) proposed a new family, *Gilbertellaceae* to accommodate this genus. Currently, the genus belongs to the family *Choanephoraceae* and subfamily *Gilbertelloideae* that can be distinguished from *Choanephoroideae* (Voigt and Kirk 2012) by ornamented zygospores and opposed suspensors (Voigt 2012). Although *G. persicaria* was originally described as *Choanephora persicaria* (Eddy 1925), its separate position within the family has been confirmed in several studies (Papp et al. 2003; Hoffmann et al. 2013).

In tropical and subtropical regions *Gilbertella* is a common postharvest pathogen, causing rots of pears (Mehrotra 1963a), peaches (Hesseltine 1960; Mehrotra 1963b; Ginting et al. 1996) and tomatoes (Mehrotra 1966). It was reported by Butler et al. (1960) and Hesseltine (1960) from mulberry (*Morus* sp.) in USA. It was also recently isolated from pitaya fruits (*Hylocereus undatus*, *Cactaceae*) in Japan (Taba et al. 2011) and China (Guo et al. 2012).

Species identification and numbers

Currently, *Gilbertella persicaria* is the only species within the genus. Although another species–*Gilbertella hainanensis*–has been described (Cheng and Hu 1965), after recent molecular studies of its ITS sequence, it is not currently recognized as a separate species (Walther et al. 2013). Two varieties of *G. persicaria* have been described: *G. persicaria* var. *persicaria* and *G. persicaria* var. *indica*, however only the former was accepted in the monograph published by Benny (1991).

Gilbertella persicaria produces sporangia with a persistent wall that ruptures at preformed sutures in two halves. Ellipsoid, smooth-walled, hyaline sporangiospores with polar appendages are released in droplet of fluid. Light brown ornamented zygospores are formed on opposed suspensors (Hesseltine 1960). Examination of morphology is usually enough for correct species identification. Moreover, the morphological identification may be easily confirmed by ITS sequencing (Table 13, Fig. 14).

Molecular phylogeny

The phylogenetic relationships based on the complete ITS region of *Gilbertella* representatives and related *Mucorales* taxa was completed by Papp et al. (2003). All *Gilbertella* cultures available in the CBS culture collection have been sequenced for their ITS region and were included in a molecular analysis by Walther et al. (2013). These studies showed that the universal fungal DNA barcoding marker–the ITS region (Schoch et al. 2012)–is sufficient for *Gilbertella* species identification (Fig. 16). The multi-marker phylogenetic analysis including representatives of this genus performed by Hoffmann et al. (2013), confirmed a distinct, well-supported position of *Gilbertella* within *Choanephoraceae* family.

Recommended genetic markers

- The internal transcribed spacer (ITS) region–generic and species level
- The large and small subunits (LSU and SSU) of nrDNA–placement within the *Mucorales* order, higher-level phylogeny

Lasiodiplodia

Background

Lasiodiplodia (*Botryosphaeriaceae*) was introduced by Ellis in 1894 with *L. tubericola* as the type species. Clendenin (1896) provided a description of the genus and the species, but did not refer to any type or other specimens of the genus or

Table 13 *Gilbertella*. Details of the isolates used in the phylogenetic tree

Species	Isolate	Host	GenBank no
Gilbertella persicaria	**CBS 190.32***	***Prunus persica***	**HM999958**
G. persicaria	CBS 785.97	–	JN206218
G. persicaria	CBS 442.64	–	JN206219
G. persicaria	CBS 325.71A	*Saccharum officinarum*	JN206220
G. persicaria	CBS 403.51	–	JN206221
G. persicaria	CBS 246.59	Trickling filter plant system	JN206222
G. persicaria	CBS 421.77	Soil	JN206223
G. persicaria	CBS 532.77	Dung of mouse	JN206224
G. persicaria	CBS 325.71D	Wood	JN206225
G. persicaria	CBS 565.91	Dung of swine	JN206226
Choanephora cucurbitarum	CBS 120.25	–	JN206231
C. cucurbitarum	CBS 150.51	–	JN206232

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

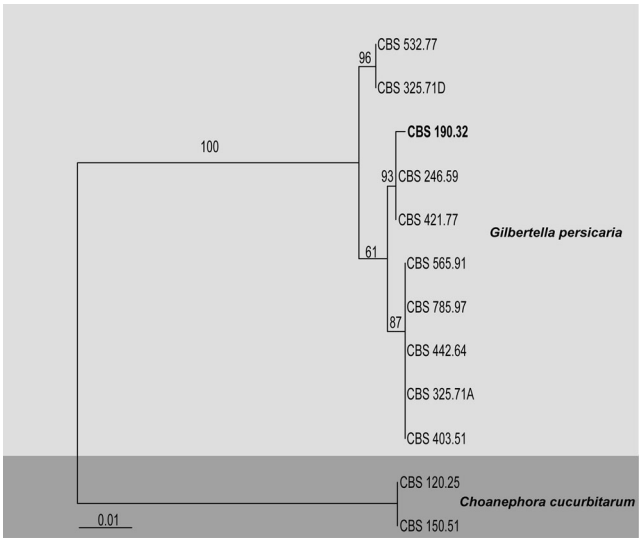


Fig. 14 Phylogram generated from Maximum likelihood analysis based on ITS sequenced data of *Gilbertella*. Bootstrap support values greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*

species. Pavlic et al. (2004) could not locate the types, nor find any specimens from the original hosts or origins, but gave a clear concept of the genus and the type. A new status for the type species of *Lasiodiplodia* has been proposed by Phillips et al. (2013) and they designated CBS 164.96 as ex-neotype culture, and deposited a dried specimen as neotype with convincing reasons, although this specimen was collected from an unidentified fruit in Papua New Guinea, whereas the type was collected in Ecuador on cocoa plant. Twenty new species have been described since 2004; however the generic application of the name, *L. theobromae*, has not been resolved.

Species identification and numbers

Lasiodiplodia differs from *Diplodia* species in having striations on the conidia, and differs from *Neodeightonia* as *Lasiodiplodia* has conidiomatal paraphyses. *Barriopsis* differs as it has unique striate conidia, with the striations present on immature, hyaline conidia. A sexual morph has been reported for *L. theobromae,* which has been linked to *Botryodiplodia rhodina* (Cooke) Arx, but this link has not been unequivocally proven (Alves et al. 2008; Phillips et al. 2008). Phillips et al. (2013) transferred *Auerswaldia lignicola* (Liu et al. 2012) to *Lasiodiplodia*, and this is the only species where the asexual morph and sexual have been definitively linked. There are 30 epithets of *Lasiodiplodia* recorded in Index Fungorum (2014) and 32 species names in MycoBank (March 2014), and 24 species are currently kept in culture. Species can be differentiated based on conidial morphology (especially dimensions) and morphology of the paraphyses. The phylogenetic analysis was performed based on up to date holotype or ex-epitype sequence data available in GenBank (Table 14).

Molecular phylogeny

Denman et al. (2000) suggested that *Lasiodiplodia* could be a possible synonym of *Diplodia* based on the ITS data analysis. However, phylogenetic studies by Zhou and Stanosz (2001), Slippers et al. (2004a) and Phillips et al. (2008) show that it clusters separately from *Diplodia*. As more genes and molecular data have become available, more complex sections within *Botryosphaeriaceae* have been resolved. By combining TEF and β-tubulin genes with ITS, Phillips et al. (2005, 2008) reinstated the genus *Neodeightonia* in the *Diplodia*/*Lasiodiplodia* complex and also showed that the latter asexual genera are morphologically and phylogenetically distinct. Most of the known species with available cultures have been described based on at least two genetic markers (ITS, TEF/ β-tubulin). The phylogenetic tree constructed with holotype or ex-epitype sequences is presented in Fig. 15.

Recommended genetic markers

- ITS–placement within the *Botryosphaeriaceae* (the generic level), and also some species-level delineation.
- TEF–generic level and inter-specific delineation.
- β-tubulin–generic level and inter-specific delineation, mostly for inter-specific delineation.

In most cases, a combination of ITS and TEF will separate all species and a minimal requirement for *Lasiodiplodia* species separation. However, for some groups, such as *L. theobromae*, β-tubulin is needed.

Mucor

Background

The genus *Mucor* belongs to the *Mucoraceae*, which is the largest and the most diverse family within *Mucorales* (former Zygomycota; Hoffmann et al. 2013). It was described by Fresenius (1850). The type species of the genus is *Mucor mucedo*, although the name *Mucor* had been used long before also by other authors to describe species currently classified as *Rhizopus stolonifer* (syn. *Mucor mucedo* L. 1753 or *Mucor mucedo* (Tode) Pers. 1801).

There has been no comprehensive molecular phylogenetic study in the genus *Mucor* and consequently its taxonomy is still widely based on morphological characters. *Mucor* representatives produce nonapophysate sporangia arising directly from the substrate and they do not form stolons. Rhizoids

Table 14 *Lasiodiplodia*. Details of the isolates used in the phylogenetic tree

Species name	Strain no.	Host	ITS	TEF
Diplodia mutila	**CBS 112553***	*Vitis vinifera*	AY259093	AY573219
Lasiodiplodia brasiliense	**CMM 4015***	*Mangifera indica*	JX464063	JX464049
L. brasiliense	CMM 2320	*Mangifera indica*	KC484814	KC481544
L. brasiliense	CMM 2319	*Mangifera indica*	KC484798	KC481529
L. brasiliense	CMM 2314	*Mangifera indica*	KC484813	KC481543
L. citricola	**CBS 124707***	*Citrus* sp.	GU945354	GU945340
L. citricola	CBS 124706	*Citrus* sp.	GU945353	GU945339
L. crassispora	**CBS 118741***	*Santalum album*	DQ103550	EU673303
L. crassispora	WAC 12534	*Eucalyptus urophylla*	DQ103551	DQ103558
L. egyptiacae	**CBS 130992***	*Mangifera indica*	JN814397	JN814424
L. egyptiacae	BOT 29	*Mangifera indica*	JN814401	JN814428
L. euphorbicola	**CMM3609***	*Jatropha curcas*	KF234543	KF226689
L. euphorbicola	CMM3652	*Jatropha curcas*	KF234554	KF226715
L. gilanensis	**CBS 124704***	Unknown	GU945351	GU945342
L. gilanensis	CBS 124705	Unknown	GU945352	GU945341
L. gonubiensis	**CBS 115812***	*Syzigium cordatum*	AY639595	DQ103566
L. gonubiensis	CBS 116355	*Syzigium cordatum*	AY639594	DQ103567
L. hormozganensis	**CBS 124709***	*Olea* sp.	GU945355	GU945343
L. hormozganensis	CBS 124708	*Mangifera indica*	GU945356	GU945344
L. iraniensis	**CBS 124710***	*Salvadora persica*	GU945346	GU945334
L. jatrophicola	CMM3610	*Jatropha curcas*	KF234544	KF226690
L. lignicola	**MFLUCC 11-0435***	Unknown	JX646797	JX646862
L. lignicola	MFLUCC 11-0656	Unknown	JX646798	JX646863
L. macrospora	**CMM3833***	*Jatropha curcas*	KF234557	KF226718
L. mahajangana	**CBS 124927***	*Terminalia catappa*	FJ900597	FJ900643
L. mahajangana	CBS 124925	*Terminalia catappa*	FJ900595	FJ900641
L. margaritacea	**CBS 122519***	*Adansonia gibbosa*	EU144050	EU144065
L. margaritacea	CBS 122065	*Adansonia gibbosa*	EU144051	EU144066
L. marypalme	**CMM 2275***	*Carica papaya*	KC484843	KC481567
L. marypalme	CMM 2274	*Carica papaya*	KC484841	KC481565
L. marypalme	CMM 2272	*Carica papaya*	KC484842	KC481566
L. marypalme	CMM 2271	*Carica papaya*	KC484844	KC481568
L. missouriana	**CBS 128311***	*Vitis vinifera*	HQ288225	HQ288267
L. missouriana	CBS 128312	*Vitis vinifera*	HQ288226	HQ288268
L. parva	**CBS 456.78***	*Cassava*-field soil	EF622083	EF622063
L. parva	CBS 494.78	*Cassava*-field soil	EF622084	EF622064
L. plurivora	**CBS 120832***	*Prunus salicina*	EF445362	EF445395
L. plurivora	CBS 121103	*Prunus salicina*	AY343482	EF445396
L. pseudotheobromae	**CBS 116459***	*Gmelina arborea*	EF622077	EF622057
L. pseudotheobromae	CBS 447.62	*Citrus aurantium*	EF622081	EF622060
L. rubropurpurea	**CBS 118740***	*Eucalyptus grandis*	DQ103553	EU673304
L. rubropurpurea	WAC 12536	*Eucalyptus grandis*	DQ103554	DQ103572
L. subglobose	**CMM3872***	*Jatropha curcas*	KF234558	KF226721
L. subglobosa	CMM4046	*Jatropha curcas*	KF234560	KF226723
L. theobromae	**CBS 164.96***	Fruit on coral reef coast	AY640255	AY640258
L. theobromae	CBS 111530	Unknown	EF622074	EF622054
L. venezuelensis	**CBS 118739***	*Acacia mangium*	DQ103547	EU673305
L. venezuelensis	WAC 12540	*Acacia mangium*	DQ103548	DQ103569
L. viticola	**CBS 128313***	*Vitis vinifera*	HQ288227	HQ288269
L. viticola	CBS 128315	*Vitis vinifera*	HQ288228	HQ288270

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

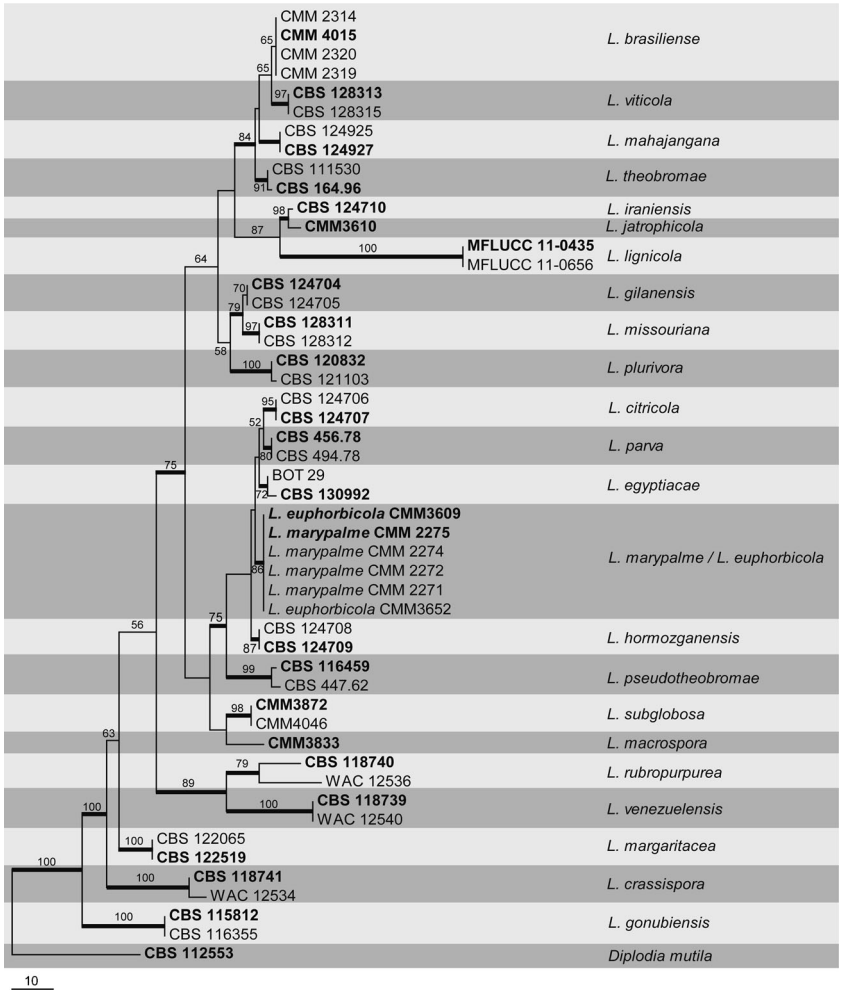


Fig. 15 Phylogram generated from parsimony analysis based on combined ITS and TEF sequenced data of *Lasiodiplodia*. Parsimony bootstrap support values greater than 50 % are indicated above the nodes, and branches with Bayesian posterior probabilities greater than 0.95 are given in *bold*. The ex-type (ex-epitype) and voucher strains are in *bold*. The *scale bar* indicates ten changes. The tree is rooted with *Diplodia mutila* CBS 112553

were also considered to be absent in *Mucor,* but it is now known that they can be produced under certain conditions (Walther et al. 2013).

Mucor representatives are saprotrophs that can be found mainly in soil or on plant debris. They are also known as postharvest plant pathogens, e.g. *M. mucedo* (Moline and Millner 1981) and *M. piriformis* (Michailides and Spotts 1990a). In case of peach and nectarine rots, Michailides and Spotts (1990b), Spotts (1990) and Michailides et al. (1992) regarded flies (especially *Drosophila melanogaster*) and nitidulid beetles (*Carpophilus hemipterus* and *C. freemani*) as effective vectors. *Mucor* rot symptoms include softening of juicy decayed tissue, often with a sweet odour, lesions with a sharp margin and eventually developing of grey mycelium with sporangia. *Mucor* isolated from several different plant hosts, angiosperms and gymnosperms, monocots as well as dicotyledons. USDA Fungus-Host Database reports 375 cases of *Mucor* infections from plants from approximately 40 countries in Europe, Central and South-East Asia, Australia, Africa, and North and South America (Farr and Rossman 2014). *Mucor circinelloides* causes rots in tomatoes (Smith et al. 1976), mangoes (Johnson 2008), yam (Amusa et al. 2003) and peaches (Restuccia et al. 2006). *Mucor hiemalis* can be pathogenic on guavas (Kunimoto et al. 1977), carrots and cassava (Snowdon 1991). *Mucor piriformis* is a destructive pathogen of fresh strawberries (Snowdon 1990; Pitt and Hocking 2009) and a major cause of rotting of cold-stored pears, apples, peaches, nectarines and tomatoes (Smith et al. 1979; Bertrand and Saulie-Carter 1980; Michailides and Spotts 1986; Michailides 1991; Mari et al. 2000; Pitt and Hocking 2009; Ukeh and Chiejina 2012), plums (Børve and Vangdal 2007), sweet persimmons (Kwon et al. 2004) and yams (Amusa and Baiyewu 1999; Iwama 2006). *Mucor piriformis* may infect the stem, calyx or wounds on the skin of fruits (Michailides and Spotts 1990a, b). *Mucor mucedo* was reported as important postharvest pathogen of strawberries (Dennis and Davis 1977), and from tomatoes (Moline and Kuti 1984). *Mucor racemosus* was noted causing soft rot of cherry tomato fruits in Korea (Kwon and Hong 2005). Some *Mucor* species (e.g. *M. circinelloides*) are also human opportunistic pathogens, especially dangerous to immunodeficient patients (Walther et al. 2013).

Species identification and numbers

The last extensive studies of the genus *Mucor* (Schipper 1973, 1975) are from the pre-molecular era. Based on morphological features and mating experiments Schipper (1976, 1978) recognized 39 species, 4 varieties and 11 formae. In the following years further species were described (e.g. Watanabe 1994; Zalar et al. 1997). Molecular phylogenetic analyses of the entire *Mucorales* revealed the polyphyly of the genus (Voigt and Wöstemeyer 2001; O'Donnell et al. 2001). The study of Walther et al. (2013) on the genetic diversity within the *Mucorales* based on sequences of the nuclear ribosomal internal transcribed spacer region (ITS) and the large ribosomal subunit (LSU) strongly supported the polyphyly of *Mucor*. The genus was split into several morphological groups differing in the size of the sporangia and the branching mode of the sporangiophores that are widely in agreement with the intrageneric classification of Schipper (1973). However, ?in molecular analyses these groups are intermingled by other sporangia-forming genera such as *Pilaira* und *Pirella* and sporangiola-forming genera such as *Ellisomyces*, *Chaetocladium*, *Helicostylum* and *Thamnidium* (Walther et al. 2013). The position of the *Mycotyphaceae* and the *Choanephoraceae* in relation to the *Mucoraceae* is still not resolved (Hoffmann et al. 2013).

Recently, the introduction of new species or changes of the taxonomic status were supported by sequence analyses of the ITS and/or rDNA genes (Jacobs and Botha 2008; Budziszewska et al. 2010; Álvarez et al. 2011; Madden et al. 2011). Several studies on certain species or species complexes (Li et al. 2011; Lu et al. 2013) or a particular ecological group (Hermet et al. 2012) used multi-marker approaches for phylogenetic species recognition in the genus *Mucor*. However, a comprehensive study on the entire genus is still lacking. As a consequence, species and even generic boundaries are still unclear for *Mucor*. Currently 58 species are recognised within the genus (Walther et al. 2013) (Table 15, Fig. 16).

Molecular phylogeny

The ITS region allows identification to species level for most mucoralean representatives (Walther et al. 2013). Detailed molecular species identification is currently not possible for species complexes such as *M. circinelloides* or *M. flavus* because of unclear species boundaries (Walther et al. 2013).

Along with the ITS region for species identification, the LSU (e.g. Fig. 16, Álvarez et al. 2011) or the SSU (e.g. Budziszewska et al. 2010) genes have frequently been used in molecular phylogenetic analyses of *Mucor* because the ITS is too variable to be confidently aligned across the entire genus (Walther et al. 2013). In addition, the RNA polymerase subunit gene (rpb1) was successfully used for multi-marker studies at the species level (Li et al. 2011; Hermet et al. 2012; Lu et al. 2013). Hermet et al. (2012) also used the fragment of a mini-chromosome maintenance protein (MCM7) and of the 20 S rRNA accumulation protein (tsr1). The multi-marker analysis of the entire *Mucorales* including representatives of genus *Mucor* by Hoffmann et al. (2013) were based on partial genes of actin and the translation elongation factor 1-alpha in addition to the rRNA genes.

Recommended genetic markers

- The internal transcribed spacer (ITS)–genus and species level
- The RNA polymerase II largest subunit gene (RPB1)–species level
- The large and small subunits (LSU and SSU) of nrDNA–placement within the *Mucorales* order, higher-level phylogeny
- The mini-chromosome maintenance proteins gene (MCM7–higher-level phylogeny)

Neofusicoccum

Background

Pennycook and Samuels (1985) listed *Fusicoccum parvum* as the asexual morph when they described *Botryosphaeria parvum*. *Neofusicoccum* was introduced by Crous et al. (2006) for species that have an asexual morph that occurs with a "Dichomera" like synanamorph (morphologically similar, but phylogenetically distinct from *Botryosphaeria*). They suggested the name as it provides more information of the morphological state.

Species identification and numbers

On the basis of conidial dimensions and pigmentation, pigment production in media and ITS sequence data, 22 species are currently recognized in *Neofusicoccum,* although some of these characters have recently been questioned (Abdollahzadeh et al. 2013). Four new species, *N. batangarum*, *N. cordaticola*, *N. kwambonambiense* and *N. umdonicola* were identified in this complex based on congruence between genealogies of multiple genes (Pavlic et al. 2009a, b; Begoude et al. 2010). Though many species of *Neofusicoccum* are morphologically similar and can be very difficult to distinguish from one another, an attempt has been made to differentiate all species in a key by Phillips et al. (2013) (Table 16).

Table 15 *Mucor.* Details of the isolates used in the phylogenetic tree

Species	Isolate	Country of collection	GenBank accession no
Mucor abundans	CBS 521.66	Germany	JN206457
M. aligarensis	**CBS 993.70***	**UK**	**JN206461**
M. amphibiorum	**CBS 763.74***	**Germany**	**HM849688**
M. ardhlaengiktus	**CBS 210.80***	**India**	**JN206504**
M.azygosporus	**CBS 292.63***	**USA**	**JN206497**
M. bacilliformis	**CBS 251.53***	**USA**	**JN206451**
M. bainieri	**CBS 293.63***	**India**	**JN206424**
M. brunneogriseus[1]	CBS 129.41	Netherlands	
M. circinelloides f. circinelloides	**CBS 195.68***	**Netherlands**	**HM849680**
M. circinelloides f. griseocyanus	CBS 116.08	Norway	JN206421
M. circinelloides f. janssenii	**CBS 205.68***	**South Africa**	**JN206425**
M.circinelloides f. lusitanicus	CBS 968.68	–	JN206419
M. ctenidius	CBS 293.66	USA	JN206417
M. durus	**CBS 156.51***	**Ukraine**	**JN206456**
M. endophyticus	**CBS 385.95***	**China**	**JN206448**
M. exponens	**CBS 141.20***	**Germany**	**JN206441**
M. falcatus	**CBS 251.35***	**Germany**	**JN206509**
M. flavus	**CBS 234.35***	**Germany**	**JN206468**
M. fuscus	CBS 282.78	France	JN206442
M.fusiformis	**CBS 336.68***	**Finland**	**JN206447**
M. genevensis	**CBS 114.08***	**Switzerland**	**JN206435**
M.gigasporus	**CBS 566.91***	**China**	**JN206494**
M. guiliermondii	**CBS 174.27***	**Russia**	**JN206475**
M.heterogamus	**CBS 405.58***	–	**JN206487**
M. hiemalis f. corticola	CBS 362.68	Norway	JN206449
M. hiemalis f. hiemalis	**CBS 201.65***	**USA**	**HM849683**
M. inaequisporus	**CBS 255.36***	**Ghana**	**JN206502**
M. indicus	**CBS 226.29***	**Switzerland**	**HM849690**
M.irregularis	CBS 103.93	India	HM849684
M. japonicus	**CBS 154.69***	**Russia**	**JN206446**
M. lanceolatus	CBS 638.74	France	JN206443
M. laxorrhizus	**CBS 143.85***	**United Kingdom**	**JN206444**
M. luteus[1]	**CBS 243.35***	**Germany**	
M. megalocarpus	**CBS 215.27***	**France**	**JN206489**
M. microsporus[1]	**CBS 204.28**	**France**	
M. minutes	CBS 586.67	India	JN206463
M. moelleri	**CBS 444.65***	**USA**	**HM849682**
M. mousanensis	**CBS 999.70***	**India**	**JN206434**
M. mucedo	**CBS 640.67***	**Netherlands**	**HM849687**
M. multiplex	**CBS 110662***	**China**	**JN206484**
M. nederlandicus	CBS 735.70	–	JN206503
M. odoratus	**CBS 130.41***	**Denmark**	**JN206495**
M. parviseptatus	CBS 417.77	Australia	JN206453
M. piriformis	**CBS 169.25***	–	**HM849681**
M. plasmaticus	CBS 275.49	Netherlands	JN206483
M. plumbeus	CBS 634.74	Germany	HM849677
M. prayagensis	CBS 652.78	India	JN206498
M. racemosus f. racemosus	**CBS 260.68***	**Switzerland**	**HM849676**
M. racemosus f. sphaerosporus	**CBS 115.08***	**Norway**	**JN206433**
M. ramosissimus	**CBS 135.65***	**Uruguay**	**HM849678**

Table 15 (continued)

Species	Isolate	Country of collection	GenBank accession no
M. saturninus	**CBS 974.68***	**Netherlands**	**JN206458**
M. silvaticus	**CBS 249.35***	**Denmark**	**JN206455**
M. strictus	CBS 100.66	Austria	JN206477
M. ucrainicus	CBS 674.88	Ukraine	JN206507
M. variisporus	**CBS 837.70***	**India**	**JN206508**
M. zonatus	**CBS 148.69***	**Germany**	**JN206454**
M. zychae	**CBS 416.67***	**India**	**JN206505**
Backusella lamprospora	CBS 195.28	USA	JN206530
B. grandis	**CBS 186.87***	**India**	**JN206527**

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

Molecular phylogeny

Crous et al. (2006) proposed new combinations for 13 species based on the sequence data from cultures. Based on DNA sequence data for five nuclear markers, Pavlic et al. (2009a, b) identified three new species of *Neofusicoccum* within the *N. parvum/N. ribis* species complex in South Africa. *N. batangarum* was described from *Terminalia catappa* by Begoude et al. (2010). Analysis of TEF, β-tubulin and LSU gene sequences (Alves et al. 2008; Abdollahzadeh et al. 2010) and Genealogical Sorting Index (GSI) has been used to resolve the asexual morph of *Neofusicoccum* (Sakalidis et al. 2011) (Fig. 17).

Recommended genetic markers

- LSU, SSU and ITS–genus level
- β-tubulin and TEF–species level

Common genetic markers that are used for the identification of *Botryosphaeriaceae* species are ITS, TEF, β- tubulin, LSU and SSU. Recent studies have shown that the combination of TEF, ITS and β- tubulin is sufficient to characterize species in this lineage. However, even when using only the TEF gene, it is possible to identify distinct species. The unavailability of the TEF sequence of several type species makes species identification using molecular phylogeny problematic. Therefore, in future research, it is recommended to use the combination of TEF, ITS and β- tubulin for better species level delimitation.

Pestalotiopsis

Background

Pestalotiopsis is an appendage-bearing conidial asexual coelomycetous genus in the family *Amphisphaeriaceae*, *Xylariales*, Sordariomycetes (Ascomycota) (Barr 1975; Kang et al. 1998) that is common in tropical and temperate ecosystems (Maharachchikumbura et al. 2011, 2012). The sexual state is *Pestalosphaeria* and only 13 species are known as compared to the asexual state (253 species names). Species of *Pestalotiopsis* cause a variety of disease in plants, including canker lesions, shoot dieback, leaf spots, needle blight, tip blight, grey blight, scabby canker, severe chlorosis, fruit rots and leaf spots (Espinoza et al. 2008; Maharachchikumbura et al. 2013a, b; Tagne and Mathur 2001). Species belonging to the genus *Pestalotiopsis* are thought to be a rich source for bioprospecting, and chemical exploration of endophytic *Pestalotiopsis* species is on the increase (Aly et al. 2010; Xu et al. 2010, 2014). *Pestalotiopsis* species have been recorded as saprobes where they are recyclers of dead plant material (Maharachchikumbura et al. 2012) and are also known to cause human and animal infections (*Pestalotiopsis clavispora*) (Monden et al. 2013).

Most *Pestalotiopsis* names in the literature are described based on host association. However, molecular data have shown that the genus needs revision (Maharachchikumbura et al. 2011, 2012; Zhang et al. 2013c), and many of the traditional species may be spurious. There are also numerous cryptic species, very few distinct species, species with wide host ranges, those with cosmopolitan distribution and some species being opportunistic pathogens. This calls for critical re-examination of the genus, using both morphological studies and a multi-marker phylogeny based on ex-type and ex-epitype cultures (Maharachchikumbura et al. 2012, 2013c).

Species identification and numbers

According to Index Fungorum (2014) there are 253 *Pestalotiopsis* names, while in MycoBank (2014) there are 264 names. The reason for the large number of names is historical and may not reflect the actual number of species (Jeewon et al. 2004). Kohlmeyer and Kohlmeyer (2001) described *P. juncestris,* which was isolated from the host *Juncus roemerianus*; this species is morphologically similar to *P. versicolor* and several other species of *Pestalotiopsis*, but

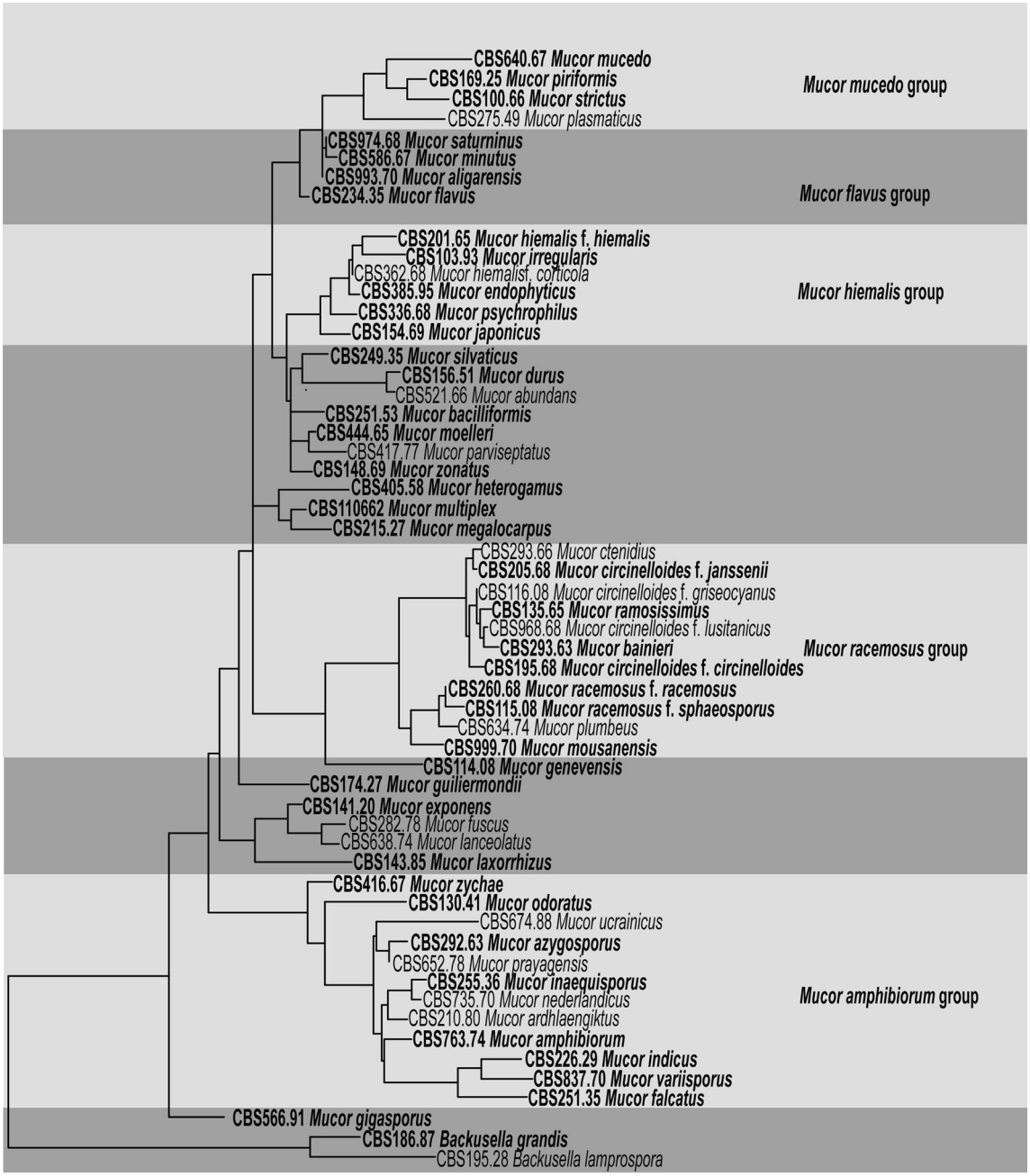


Fig. 16 Maximum likelihood tree based on partial LSU sequences for *Mucor* species and main groups within the genus. Detailed phylogenetic trees for each group may be found in Walther et al. (2013)

the taxon was described as a new species based on the host occurrence. However, recent molecular data have shown that host association and geographical location is less informative for distinguishing taxa (Jeewon et al. 2004; Hu et al. 2007). Isolation of endophytic *Pestalotiopsis* strains for bioprospecting for new biochemical compounds has shown that the same species can be found in a range of hosts. It has been shown that most of the key conidial characters used in species level separation are not stable and vary with host range, generation, culture and other environmental conditions (Hu et al. 2007). Furthermore, the arrangement of species by Steyaert (1949) and Guba (1961) in various coloured groupings is problematic because this character has been shown to be variable within a species (Liu et al. 2010). Thus, most species in the above arrangements may be confused and many species are probably synonyms. Therefore, most of the species recorded in checklists and the literature may not reflect what actually occurs. Thus, many names assigned to *Pestalotiopsis* probably lack any accurate taxonomic basis, leaving the taxonomy of the genus markedly confused. Until 1990,

Table 16 *Neofusicoccum*. Details of the isolates used in the phylogenetic tree

Species	Isolate	GenBank accession numbers				
		SSU	ITS	LSU	TEF	β-tubulin
Neofusicoccum andinum	**CBS 117453***	N/A	AY693976	N/A	AY693977	N/A
N. arbuti	**CBS 116131***	KF531814	AY819720	DQ377915	KF531792	KF531792
N. australe	**CMW 6837***	N/A	AY339262	N/A	AY339270	AY339254
N. batangarum	**CBS 124924***	N/A	FJ900607	N/A	FJ900653	FJ900634
N. cordaticola	**CBS 123634***	N/A	EU821898	N/A	EU821868	EU821838
N. corticosae	**CBS 120081***	N/A	DQ923533	N/A	N/A	N/A
N. eucalypticola	**CBS 115679***	N/A	AY615141	N/A	AY615133	AY615125
N. grevilleae	**CBS 129518***	N/A	JF951137	JF951157	N/A	N/A
N. kwambonambiense	**CBS 123639***	N/A	EU821900	N/A	EU821870	EU821840
N. luteum	**CBS 110299***	EU673148	AY259091	AY928043	AY573217	DQ458848
N. macroclavatum	**CBS 118223***	N/A	DQ093196	N/A	DQ093217	DQ093206
N. mangiferae	**CBS 118532***	EU673154	AY615186	DQ377921	DQ093220	AY615173
N. mediterraneum	**CBS 121718***	N/A	GU251176	N/A	GU251308	GU251836
N. nonquaesitum	**CBS 126655***	N/A	GU251163	N/A	GU251295	GU251823
N. occulatum	**CBS 128008***	N/A	EU301030	N/A	EU339509	EU339472
N. parvum	**CMW 9081***	EU673151	AY236943	AY928045	AY236888	AY236917
N. pennatisporum	**WAC 13153***	N/A	EF591925	EF591942	EF591976	EF591959
N. protearum	**CBS 114176***	N/A	AF452539	N/A	N/A	N/A
N. ribis	**CBS 115475***	N/A	AY236935	N/A	AY236877	AY236906
N. umdonicola	**CBS 123645***	N/A	EU821904	N/A	EU821874	EU821844
N. viticlavatum	**CBS 112878***	N/A	AY343381	N/A	AY343342	N/A
N. vitifusiforme	**CBS 110887***	N/A	AY343383	N/A	AY343343	N/A
Spencermartinsia viticola	**CBS 117009***	EU673165	AY905554	DQ377873	AY905559	EU673104

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

phylogenetic understanding of the taxonomy associated with *Pestalotiopsis* and allied genera was based mainly on conidial characters (Steyaert 1949; Guba 1961; Nag Rag 1993), conidiogenesis (Sutton 1980) and sexual state association (Barr 1975). More recently, some new species have been introduced based on host occurrence, plus morphological and molecular data (Maharachchikumbura et al. 2012, 2013a, b; Strobel et al. 2000). Furthermore, currently only 36 *Pestalotiopsis* species have either ex-type or ex-epitype sequences.

Molecular phylogeny

Recently, many *Pestalotiopsis* species have been defined using ITS sequence data, however, there are only a few type cultures available for *Pestalotiopsis*. For example, *Pestalotiopsis clavispora, P. disseminata, P. microspora, P. neglecta, P. photiniae, P. theae, P. virgatula* and *P. vismiae* have numerous ITS sequences in GenBank. However, in phylogenetic studies all these species scattered throughout the phylogram and there appears to be no living ex-type strain for any of these species (Maharachchikumbura et al. 2011). Therefore it is unwise to use GenBank sequences to represent any of these names. Rapid development in molecular phylogeny has had a great impact on *Pestalotiopsis* taxonomy. For example, random amplification of polymorphic DNA (RAPD) can be used to detect genetic diversity in the genus (Tejesvi et al. 2007). Watanabe et al. (2012) evaluated the use of the ITS2 region and showed that it is conserved at the level of secondary structure rather than the level of primary sequence, which can be used for classification of the *Pestalotiopsis*. Hu et al. (2007) showed that the ITS region is less informative than the β-tubulin gene in differentiating endophytic species of *Pestalotiopsis* in *Pinus armandii* and *Ribes* spp. A combination of β-tubulin and ITS gave improved phylogenetic resolution, and they suggested that at least two genetic markers should be used to resolve the phylogeny of species of *Pestalotiopsis*. However, Liu et al. (2010) disagreed with above statement concerning the ITS region as being less informative when compared to the β-tubulin region. They indicated that alignment of the ITS region can be a useful character in grouping *Pestalotiopsis* to different types of pigmentation, which can be used as a key character for

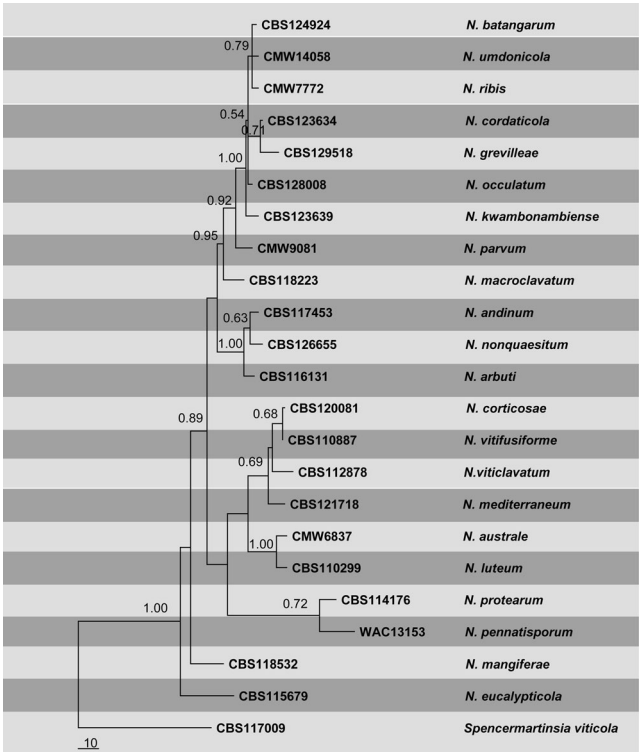


Fig. 17 Phylogram generated from parsimony analysis based on combined ITS, TEF, β- tubulin, LSU and SSU sequenced data of *Neofusicoccum*. Parsimony bootstrap support values and Bayesian posterior probabilities greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*. The *scale bar* indicates ten changes. The tree is rooted with *Spencermartinsia viticola* CBS 117009

the phylogeny of the species. In order to select suitable markers for better species resolution, Maharachchikumbura et al. (2012) analyzed a combined ACT, β-tubulin, CAL, GPDH, GS, ITS, LSU, RPB 1, SSU and TEF dataset. They compared the morphological data versus the sequence data from each gene to establish which characters satisfactorily resolve the species. They narrowed down the 10 gene regions to three most applicable regions (ITS, β-tubulin and TEF), which were tested individually and in combination, to evaluate the differences between species. The species sequenced with ITS had a high PCR and sequence success rate and β-tubulin and TEF gene regions proved to be favourable taxonomic markers for *Pestalotiopsis* since they resolved the taxonomic relationships of most species studied. Further, TEF had better PCR amplification success rates and was found to be superior to β-tubulin. TEF is therefore a powerful tool to resolve lineages within *Pestalotiopsis*. Because of the better PCR and sequencing success rate and fewer difficulties with alignment, editing and better resolution, the TEF gene appears to be a very good molecular marker for phylogenetic investigation of *Pestalotiopsis*. Furthermore, a combination of ITS, β-tubulin and TEF gene data gave the best resolution as compared to any single marker (Table 17, Fig. 18). In addition to the above three markers, the authors also tested LSU, SSU, ACT and GPDH (low resolution), GS and RPB1 (cannot be synthesized using available primers or multiple copies) and CAL (species resolution is high, PCR success rate low).

Recommended genetic markers

- The large subunits of nrDNA (LSU)–placement within the *Amphisphaeriaceae* (generic level)
- The internal transcribed spacer (ITS), β-tubulin and TEF–species level (as outlined in Maharachchikumbura et al. 2012)

Phyllosticta

Background

Phyllosticta is an important plant pathogenic genus with coelomycetes asexual states. It was previously placed in *Botryosphaeriaceae*, *Botryosphaeriales*, Dothideomycetes, Ascomycota. However following phylogenetic analysis, Wikee et al. (2013c) placed this genus in *Phyllostictaceae* which is sister to the *Botryosphaeriaceae*. *Phyllosticta* species are known to cause leaf spots and various fruit diseases worldwide on a diverse range of hosts including some economically important crops and ornamentals such as citrus, banana, apple, grapes, cranberry, orchids, mai dong and maple (Uchida and Aragaki 1980; Paul and Blackburn 1986; Baayen et al. 2002; McManus 1998; Olatinwo et al. 2003; Paul et al. 2005; Liu et al. 2009b; Wikee et al. 2011, 2012; Shivas et al. 2013b). Some species such as *P. capitalensis* are endophytes and weak pathogens (Baayen et al. 2002; Glienke et al. 2011; Wikee et al. 2013a), while others such as *P. cocoicola* are saprobes (Punithalingam 1974; Taylor and Hyde 2003). *Phyllosticta* species have been also used as bio-control agents and produce novel bioactive metabolites such as phyllostine and phyllostoxin (Yan et al. 2011; Evidente et al. 2008a, b; Wikee et al. 2011, 2013b).

The sexual state of *Phyllosticta* was named *Guignardia* which comprises 353 records in MycoBank (Hyde 1995; Crous et al. 1996; Hyde et al. 2010). *Phyllosticta* species have sometimes been named in *Leptodothiorella* after their spermatial state (Van der Aa 1973). Most species of *Phyllosticta* and *Guignardia* have been described independently, and only a few *Phyllosticta* species have been linked to their *Guignardia* sexual morphs (Wulandari et al. 2010). On the other hand, the host ranges of many diseases are poorly understood (Van der Aa and Vanev 2002; Wikee et al. 2011). It has been recommended that *Phyllosticta* which is the older, more commonly used and more species-rich, should

Table 17 *Pestalotiopsis*. Details of the isolates used in the phylogenetic tree

Species	Isolates	Host	GenBank accession number		
			ITS	β -tubulin	TEF
Pestalotiopsis adusta	ICMP6088*	On refrigerator door PVC gasket	JX399006	JX399037	JX399070
P. adusta	MFLUCC10-146	*Syzygium* sp.	JX399007	JX399038	JX399071
P. anacardiacearum	**IFRDCC2397***	*Mangifera indica*	KC247154	KC247155	KC247156
P. asiatica	**MFLUCC12-0286***	Unidentified tree	JX398983	JX399018	JX399049
P. camelliae	**MFLUCC12-0277***	*Camellia japonica*	JX399010	JX399041	JX399074
P. camelliae	MFLUCC12-0278	*Camellia japonica*	JX399011	JX399042	JX399075
P. chrysea	**MFLUCC12-0261***	Dead plant	JX398985	JX399020	JX399051
P. chrysea	MFLUCC12-0262	Dead plant	JX398986	JX399021	JX399052
P. clavata	**MFLUCC12-0268***	*Buxus* sp.	JX398990	JX399025	JX399056
P. clavispora	MFLUCC12-0280	*Magnolia* sp.	JX398978	JX399013	JX399044
P. clavispora	**MFLUCC12-0281***	*Magnolia* sp.	JX398979	JX399014	JX399045
P. coffeae–arabicae	**HGUP4015***	*Coffeae arabica*	KF412647	KF412641	KF412644
P. coffeae–arabicae	HGUP4019	*Coffeae arabica*	KF412649	KF412643	KF412646
P. diversiseta	**MFLUCC12-0287***	*Rhododendron* sp.	JX399009	JX399040	JX399073
P. ellipsospora	**MFLUCC12-0283***	Dead plant	JX398980	JX399016	JX399047
P. ellipsospora	MFLUCC12-0284	Dead plant	JX398981	JX399015	JX399046
P. ericacearum	**IFRDCC2439***	*Rhododendron delavayi*	KC537807	KC537821	KC537814
P. foedans	CGMCC3.9178	*Neodypsis decaryi*	JX398989	JX399024	JX399055
P. foedans	**CGMCC3.9123***	Mangrove leaves	JX398987	JX399022	JX399053
P. foedans	CGMCC3.9202	*Calliandra haematocephala*	JX398988	JX399023	JX399054
P. furcata	**MFLUCC12-0054***	*Camellia sinensis*	JQ683724	JQ683708	JQ683740
P. gaultheria	**IFRD411-014***	*Gaultheria forrestii*	KC537805	KC537819	KC537812
P. inflexa	**MFLUCC12-0270***	Unidentified tree	JX399008	JX399039	JX399072
P. intermedia	**MFLUCC12-0259***	Unidentified tree	JX398993	JX399028	JX399059
P. licualacola*	**HGUP4057***	*Licuala grandis*	KC436006	KC481683	KC481684
P. linearis	**MFLUCC12-0271***	*Trachelospermum* sp.	JX398992	JX399027	JX399058
P. magna	**MFLUCC12-652***	*Pteridium* sp.	KF582795	KF582793	KF582791
P. rhododendri	**IFRDCC2399***	*Rhododendron sinogrande*	KC537804	KC537818	KC537811
P. rhodomyrtus	**HGUP4230***	*Rhodomyrtus tomentosa*	KF412648	KF412642	KF412645
P. rosea	**MFLUCC12-0258***	*Pinus* sp.	JX399005	JX399036	JX399069
P. samarangensis	**MFLUCC12-0233***	*Syzygium samarangense*	JQ968609	JQ968610	JQ968611
P. saprophyta	**MFLUCC12-0282***	*Litsea rotundifolia*	JX398982	JX399017	JX399048
P. simitheae	**MFLUCC12-0121***	*Pandanus odoratissimus*	KJ503812	KJ503815	KJ503818
P. simitheae	MFLUCC12-0125	*Pandanus odoratissimus*	KJ503813	KJ503816	KJ503819
P. shorea	**MFLUCC12-0314***	*Shorea obtuse*	KJ503811	KJ503814	KJ503817
P. steyaertii	**IMI192475***	*Eucalyptus viminalis*	KF582796	KF582794	KF582792
P. theae	**MFLUCC12-0055***	*Camellia sinensis*	JQ683727	JQ683711	JQ683743
P. theae	SC011	*Camellia sinensis*	JQ683726	JQ683710	JQ683742
P. trachicarpicola	MFLUCC12-0263	Unidentified tree	JX399000	JX399031	JX399064
P. trachicarpicola	MFLUCC12-0264	*Chrysophyllum* sp.	JX399004	JX399035	JX399068
P. trachicarpicola	MFLUCC12-0265	*Schima* sp.	JX399003	JX399034	JX399067
P. trachicarpicola	MFLUCC12-0266	*Sympolocos* sp.	JX399002	JX399033	JX399066
P. trachicarpicola	MFLUCC12-0267	Unidentified tree	JX399001	JX399032	JX399065
P. trachicarpicola	IFRDCC2403	*Podocarpus macrophyllus*	KC537809	KC537823	KC537816
P. trachicarpicola	**OP068***	*Trachycarpus fortunei*	JQ845947	JQ845945	JQ845946
P. umberspora	**MFLUCC12-0285***	Unidentified tree	JX398984	JX399019	JX399050
P. unicolor	MFLUCC12-0275	Unidentified tree	JX398998	JX399029	JX399063

Table 17 (continued)

Species	Isolates	Host	GenBank accession number		
			ITS	β -tubulin	TEF
P. unicolor	**MFLUCC12-0276***	*Rhododendron* sp.	JX398999	JX399030	–
P. verruculosa	**MFLUCC12-0274***	*Rhododendron* sp.	JX398996	–	JX399061
Seiridium sp.	SD096	–	JQ683725	JQ683709	JQ683741

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

have priority over *Guignardia* (Zhang et al. 2013a, b, c; Wikee et al. 2013c).

Phyllosticta species have been historically indentified based on morphology, culture characters as well as host association, which has resulted in several taxonomic revisions (Van der Aa 1973; Van der Aa and Vanev 2002). Fresh collections and future molecular analyses should help resolve species relationships (Hyde et al. 2010). Phylogenetic analysis has been routinely used in species identification, in combination with morphological characters (Crous and Groenewald 2005; Hyde et al. 2010; Wikee et al. 2013c). To create a stable and workable taxonomy, neo- or epitypification are required for many species of *Phyllosticta* (Hyde et al. 2010; Wikee et al. 2013c).

Species identification and numbers

The genus *Phyllosticta* was first introduced as the generic name for *Sphaeria lichenoides* by Persoon (1818). Desmazieres (1847) re-defined *Phyllosticta*, in which he did not restrict the genus to species with one-celled conidia. Consequently, many fungi with one-celled or septate conidia were named as *Phyllosticta* (Desmazieres 1847; Van der Aa 1973). Saccardo (1878) however, restricted *Phyllosticta* to species with one-celled conidia, and after that *Phyllosticta* was further restricted to leaf inhabiting species (Saccardo 1878, 1884; Van der Aa 1973; Petrak and Sydow (1927) published a compilation of *Phyllosticta* names, and gave extensive descriptions of 28 species. Van der Aa (1973) proposed a morphological identification criterion for the genus and detailed 46 *Phyllosticta* species based mostly on material collected in Europe and North America. The genus was revised by Van der Aa and Vanev (2002) and they accepted 141 species. The currently used generic circumscription of *Phyllosticta* is: "*pycnidia globose, subglobose or tympaniform, conidiogenous cells holoblastic, with percurrent proliferation, conidia hyaline, 1-celled, ovoid, overate, ellipsoid, short cylindrical, or globose to subglobose, usually bearing a slime layer and an apical appendage*" (Van der Aa 1973; Van der Aa and Vanev 2002). During 2002–2014, about 30 new species were described (Motohashi et al. 2008; Wulandari et al. 2009, 2010; Glienke et al. 2011; Wang et al. 2012; Su and Cai 2012; Wong et al. 2012; Wikee et al. 2012, 2013c; Zhang et al. 2013b; Shivas et al. 2013b), with the currently accepted species possibly being more than 171. Unfortunately, molecular data are currently available for about only 69 species (Table 18).

Molecular phylogeny

Phylogenetic analysis has become a standard approach in fungal identification and has been well applied in several other coelomycetous genera such as *Colletotrichum* (Cai et al. 2009; Crouch et al. 2009b, c; Hyde et al. 2009a, b) and *Phoma* (Aveskamp et al. 2008, 2010; de Gruyter et al. 2010). Recent reports on *Phyllosticta* have shown that molecular phylogenetic tools have significantly improved species identification and delimitation; similarly it has improved the resolution in species complexes (Wulandari et al. 2009; Glienke et al. 2011; Wicht et al. 2012).

Baayen et al. (2002) evaluated the *P. citricarpa sensu lato* from *Citrus* and associated hosts based on ITS sequence analysis and found that two phylogenetically distinct groups existed: a slowly growing pathogenic group and morphologically similar but fast-growing, non-pathogenic group which latter proved to be *P. capitalensis*. Wicht et al. (2012) used a polyphasic approach including morphological, molecular and proteomic techniques to analyze samples of *G. bidwellii* collected from grapevine cultivars and ornamental plants of various geographic origins, and showed that *P. ampelicida* isolated from grapevine cultivars should be split into two species.

Recent studies have provided clear phylogenetic relationships in the group. These efforts primarily used intron-dominated genes (ITS, ACT, TEF), and highly conserved gene coding regions (LSU, GPDH) that can recognize cryptic species in traditionally morphologically circumscribed species complexes, e.g. *P. citricarpa* on citrus, *P. musarum* on banana, *P. vaccinii* on

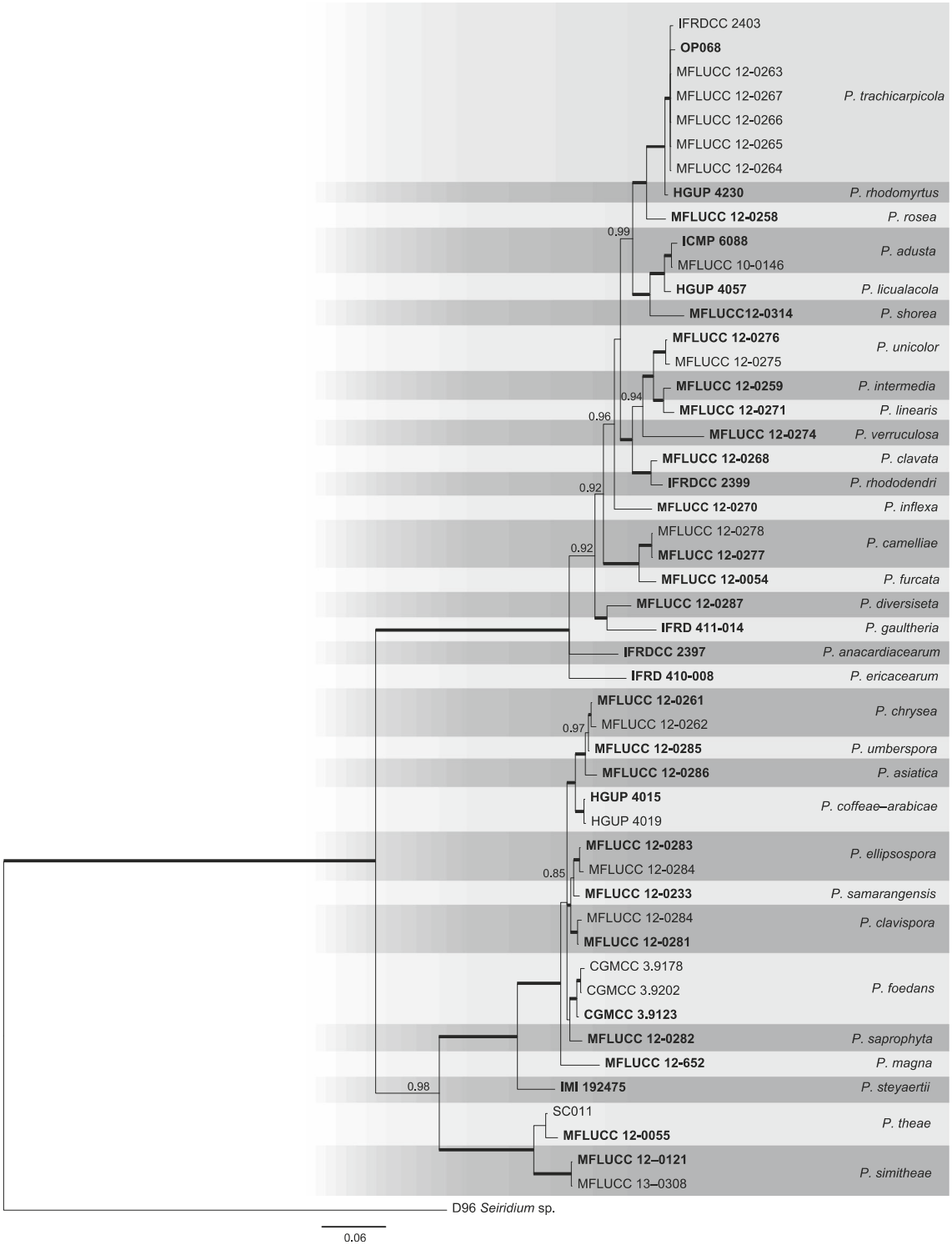


Fig. 18 Strict consensus combined (ITS + β-tubulin + TEF) tree from Bayesian analysis of the analyzed *Pestalotiopsis*. *Thickened lines* indicate Bayesian posterior probabilities (PP) of 100 %. Strain accession numbers (ex-type are in *bold*) are followed by the species name. The *scale bar* represents the expected changes per site. The tree is rooted to *Seiridium* spp. (D96)

Vaccinium, G. philoprina on *Rhododendron*, *Hedera*, *Ilex, Magnolia* and *Taxus* (Glienke *et al*. 2011; Wang et al. 2012; Wulandari et al. 2009; Wikee et al. 2013c, a, b, c; Wong et al. 2012; Zhang et al. 2013a) (Fig. 19).

Recommendations

- The large and small subunits of nrDNA (LSU and SSU)–placement within the ascomycetes (generic and family level)

Table 18 *Phyllosticta*. Details of the voucher and extype isolates used in the phylogenetic tree

Species	Strain no.	Host	Locality	GenBank accession number			
				ITS	ACT	TEF	GPDH
Botryosphaeria obtusa	CMW8232	Conifers	South Africa	AY972105	AY972111	DQ280419	
Guignardia alliacea	**MUCC0014***	*Allium fistulosum*	Japan	AB454263			
G. bidwellii	NBRC9757	*Parthenocissus tricuspidata*	Japan	AB095510			
G. gaultheriae	**CBS447.70***	*Gaultheria humifusa*	USA	JN692543	JN692519	JN692531	JN692508
G. mangiferae	**IMI260.576***	*Manifera indica*	India	JF261459	JF343641	JF261501	JF343748
G. philoprina	**CBS447.68***	*Taxus baccata*	Netherlands	AF312014			
G. vaccinii	**CBS126.22***	*Oxycoccus macrocarpos*	USA	FJ538353			
Phyllosticta abieticola	**CBS112067***	*Abies concolor*	Canada	KF170306	KF289238		
P. aloeicola	**CPC21020***	*Aloe ferox*	South Africa	KF154280	KF289311	KF289193	KF289124
P. ampelicida	**ATCC200578***	*Vitis riparia*	USA	KC193586	KC193581		KC193584
P. ardisiicola	**NBRC102261***	*Ardisia crenata*	Japan	AB454274			
P. aspidistricola	**NBRC102244***	*Aspidistra elatior*	Japan	AB454260			
P. beaumarisii	**CBS535.87=IMI 298910** *	*Muehlenbekia adpressa*	Australia	AY042927	KF306232	KF289170	KF289074
P. bifrenariae	**CBS128855***	*Bifrenaria harrisoniae*	Brazil	JF343565	JF343649	JF343586	JF343744
P. brazilianiae	**CBS126270***	*Mangifera indica*	Brazil	JF343572	JF343656	JF343593	JF343758
P. capitalensis	**CBS128856***	*Stanhopea* sp.	Brazil	JF261465	JF343647	JF261507	JF343776
	CPC16592	*Citrus limon*	Argentina	KF206187	KF289273	KF289178	KF289092
P. cavendishii	**BRIP554196***	*Musa* cv. Formosana	Taiwan	JQ743562			
P. citriasiana	**CBS 120486***	*Citrus maxima*	Thailand	FJ538360	FJ538476	FJ538418	JF343686
P. citribraziliensis	**CBS100098***	*Citrus limon*	Brazil	FJ538352	FJ538468	FJ538410	JF343691
P. citricarpa	**CBS127454***	*Citrus limon*	Australia	JF343583	JF343667	JF343604	JF343771
	CPC16603	*Citrus limon*	Uruguay	KF170295	KF289274	KF289213	KF289147
P. citrichinaensis	**ZJUCC200956***	*Citrus reticulata*	China	JN791620	JN791533	JN791459	
P. citrimaxima	**CBS136059***	*Citrus maxima*	Thailand	KF170304	KF289300	KF289222	KF289157
P. concentrica	**CBS 937.7***	*Hedera helix*	Italy	FJ538350	KF289257	FJ538408	JF411745
P. cordylinophila	**CPC20261***	*Cordyline fruticosa*	Thailand	KF170287	KF289295	KF289172	KF289076
P. cornicola	CBS111639	*Cornus florida*	USA	KF170307	KF289234		
P. cussoniae	**CBS136060***	*Cussonia* sp.	South Africa	JF343578	JF343662	JF343599	JF343764
P. ericarum	**CBS132534***	*Erica gracilis*	South Africa	KF206170	KF289291	KF289227	KF289162
P. fallopiae	**NBRC102266***	*Fallopia japonica*	Japan	AB454307			
P. foliorum	**CBS 447.68**	*Taxus baccata*	Netherlands	KF170309	KF289247	KF289201	KF289132
P. hamamelidis	MUCC149	*Hamamelis japonica*	Japan	KF170289	KF289309		
P. hostae	**CGMCC3.14355***	*Hosta plantaginea*	China	JN692535	JN692511	JN692523	JN692503
P. hubeiensis	**CGMCC3.14986***	*Viburnum odoratissimim*	China	JX025037	JX025032	JX025042	JX025027
P. hymenocallidicola	**CBS 131309***	*Hymenocallis littoralis*	Australia	JQ044423	KF289242	KF289211	KF289142
P. hypoglossi	**CBS 434.92***	*Ruscus aculeatus*	Italy	FJ538367	FJ538483	FJ538425	JF343695
P. ilicis-aquifolii	**CGMCC3.14358***	*Ilex aquifolium*	China	JN692538	JN692514	JN692526	
P. kerriae	**NBRC102251***	*Kerria japonica*	Japan	AB454266			
P. leucothoicola	**CBS136073***	*Leucothoe catesbaei*	Japan	AB454370	KF289310		
P. ligustricola	**MUCC0024***	*Ligustrum obtusifolium*	Japan	AB454269	AB704212		
P. maculate	**CPC18347***	*Musa* cv. Goly-goly pot-pot	Australia	JQ743570			
P. mangifera-indica	**CPC20264***	*Mangifera indica*	Thailand	KF170305	KF289296	KF289190	KF289121
P. minima	**CBS 585.84***	*Acer rubrum*	USA	KF206176	KF289249	KF289204	KF289135
P. musarum	**BRIP55434***	Hill banana	India	JQ743584			
P. musicola	**CBS123405***	*Musa acuminata*	Thailand	FJ538334	FJ538450	FJ538392	

Table 18 (continued)

Species	Strain no.	Host	Locality	GenBank accession number			
				ITS	ACT	TEF	GPDH
P. neopyrolae	**CPC21879***	*Pyrola asarifolia*	Japan	AB454318	AB704233		
P. owaniana	**CBS776.97***	*Brabejum stellatifolium*	South Africa	FJ538368	KF289254	FJ538426	JF343767
P. pachysandricola	**MUCC0124***	*Pachysandra terminalis*	Japan	AB454317	AB704232		
P. parthenocissi	**CBS111645***	*Parthenocissus quinquefolia*	USA	EU683672	JN692518	JN692530	
P. paxistimae	**CBS112527***	*Paxistima mysinites*	USA	KF206172	KF289239	KF289209	KF289140
P. philoprina	CBS616.72	*Ilex aquifolium*	Germany	KF154279	KF289251	KF289205	KF289136
P. podocarpi	CBS111647	*Podocarpus lanceolata*	South Africa	KF154276	KF289235	KF289232	KF289168
P. podocarpicola	**CBS728.79***	*Podocarpus maki*	USA	KF206173	KF289252	KF289203	KF289134
P. pseudotsugae	CBS111649	*Pseudotsuga menziesii*	USA	KF154277	KF289236	KF289231	KF289167
P. rhaphiolepidis	**MUCC0432***	*Rhaphiolepis indica*	Japan	AB454349	AB704242		
P. schimae	**CGMCC3.14354***	*Schima superb*	China	JN692534	JN692510	JN692522	JN692506
P. speewahensis	BRIP58044	Orchids	northern Australia	KF017269		KF017268	
P. spinarum	CBS292.90	*Chamaecyparis pisifera*	France	JF343585	JF343669	JF343606	JF343773
P. styracicola	**CGMCC3.14985***	*Styrax grandiflorus*	China	JX025040	JX025035	JX025045	JX025030
P. telopeae	**CBS777.97***	*Telopea speciosissima*	Tasmania	KF206205	KF289255	KF289210	KF289141
P. vaccinii	**ATCC46255***	*Vaccinium macrocarpon*	USA	KC193585	KC193580	KC193582	KC193583
P. vacciniicola	**CPC18590***	*Vaccinium macrocarpum*	USA	KF170312	KF289287	KF289229	KF289165
P. yuccae	CBS117136	*Yucca elephantipes*	New Zealand	JN692541	JN692517	JN692529	JN692507

Ex-type strains are bolded and marked with an * and voucher stains are bolded

- The internal transcribed spacer (ITS)–generic level
- Combined ITS, TEF, GPDH and ACT–inter-specific delineation

Phytophthora

Background

While resembling Eumycotan fungi with the production of hyphae, the genus is placed in the kingdom Straminipila, class Oomycetes, order *Peronosporales*, and family Peronosporacae. The type species is *P. infestans* described by de Bary in 1876. Since this time over 128 species have been described, many of which are important plant pathogens capable of significantly impacting agricultural production and natural ecosystems. Some species have a rather narrow host range (*P. infestans, P. lateralis, P. sojae*) while others are capable of infecting a wide range of plant host species (*P. cinnamomi, P. nicotianae, P. ramorum*). From a historical perspective, most investigations on the genus have focused on the impact of the genus on agricultural production systems, however, more recently there has been an increased interest in investigating the role this genus plays in natural ecosystems as exemplified by the number of publications concerning species such as *P. ramorum* and *P. alni*, as well as the description of many new species recovered from environmental sampling (Martin et al. 2012).

Although *Phytophthora* species resemble Eumycotan fungi with the production of hyphae, evolutionarily they are more closely related to chromophyte algae and plats than to Eumycotan fungi (Wainright et al. 1993). They have cell walls that are primarily cellulose rather than chitin as observed in fungi and they are incapable of synthesizing β-hydroxysterols (which are required for synthesis of hormones regulating sexual reproduction). In addition, Oomycetes are diploid throughout their life cycle in contrast to most true fungi.

An excellent overview of the ecology, biology and taxonomy of the genus (although missing more recently described species) can be found in Erwin and Ribeiro (1996), a review of the recent taxonomic status in Kroon et al. (2012) and an overview of the genus, including molecular identification and diagnostics, in Martin et al. (2012). There are several publically available databases that provide a wealth of up to date information on the genus, along with sequences useful for species identification via BLAST analysis, including the *Phytophthora* Database (www.phytophthoradb.org), *Phytophthora* ID (www.phytophthora-id.org) and Q-Bank (www.q-bank.eu). Cline et al. (2008) have published an online list of *Phytophthora* spp. with a hyperlink for each species to the USDA SMML database that includes host range, distribution and supporting literature.

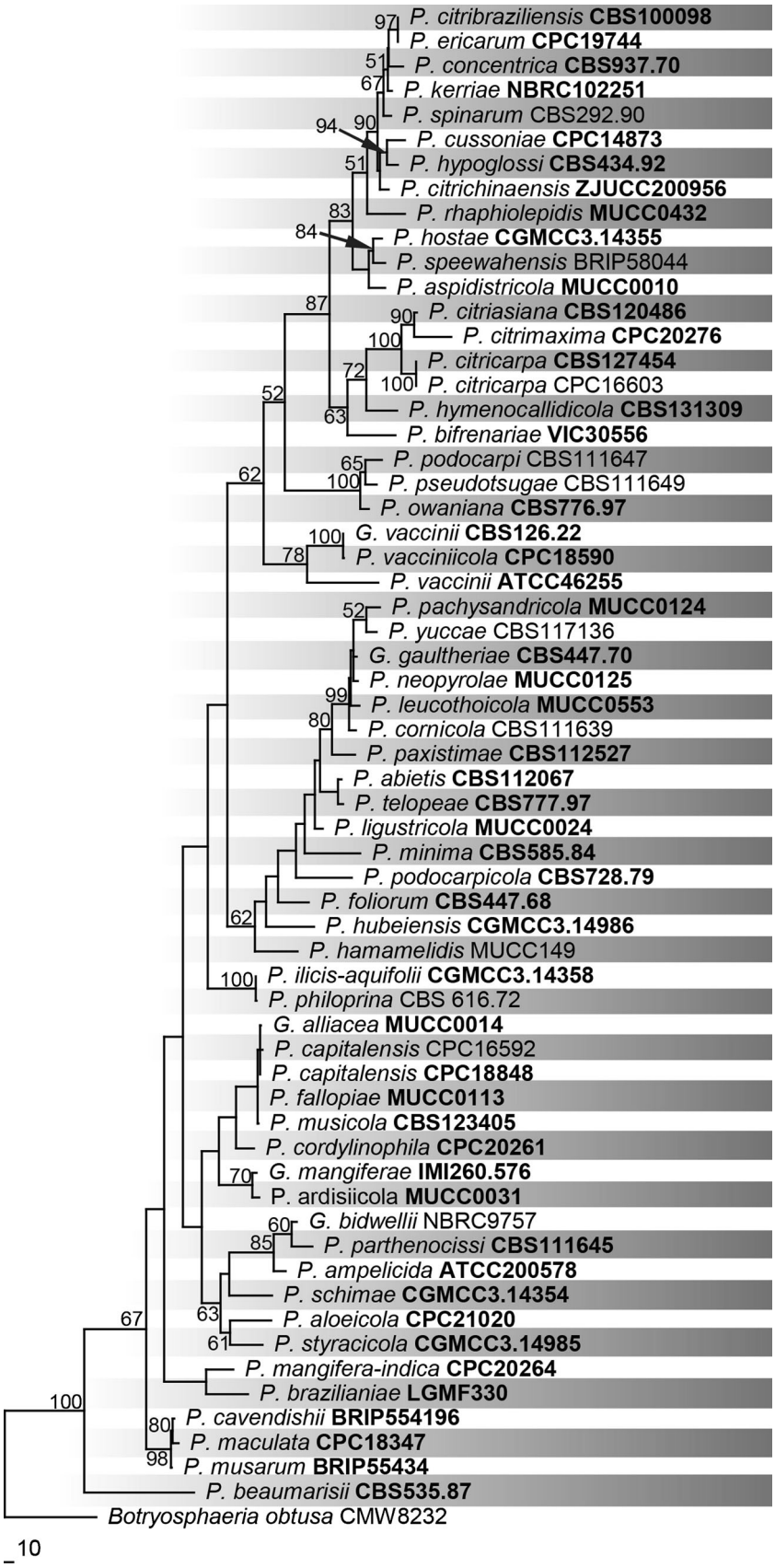


Fig. 19 Phylogram generated from parsimony analysis based on combined ITS, TEF, GPDH and ACT sequenced data of *Phyllosticta*. Parsimony bootstrap support values greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*

Species identification and numbers

A complicating factor when trying to identify *Phytophthora* species or investigate phylogenetic relationships is hybridization among distinct evolutionary lineages. While this does not appear to be a common occurrence, several stable hybrid species have been identified, e.g. *P. andina* (Goss et al. 2011; Blair et al. 2012); *P. alni* (Brasier et al. 1999); *P. x pelgrandis* (Nirenberg et al. 2009); *P. x serindipita* (Man in 't Veld et al. 2012) as well as hybrid clade 1 species recovered from the field (Man in 't Veld et al. 1998, 2007; Hurtado-Gonzales et al. 2009; Bonants et al. 2000). While conducting a detailed evaluation of clade 6 *Phytophthora* spp. from natural ecosystems in Australia, Burgess et al. (2010) observed 'hybrid swarms' that contained mixtures of parent, offspring, and intermediate isolates with high tendencies for back-crossing and out crossing. The authors' concluded that the presence of such hybrid swarms was indicative of sexual and somatic hybridization events; the high proportion of these variant isolates within the population also suggested that these hybridization events were not uncommon. Recently four interspecific hybrid clade 6 species have been recovered from riparian ecosystems in Australia and South Africa that reflect outcrossing between *P. amnicola*, *P. thermophila* and *P.* taxon PgChlamydo (Nagel et al. 2013). Additional putative interspecific hybrids from riparian ecosystems in Australia were reported by Hüberli et al. (2013). Hybridization is a topic that requires a more detailed investigation as it could have a profound influence on gene flow among species and the evolution of new species with an expanded host range that could impact agricultural and natural ecosystems (as observed with *P. alni*).

Traditional classification to species level has been based on morphological characterization of reproductive structures (reviewed in Martin et al. 2012). This includes the sporangium (asexual) and oospore (sexual) as well as the production of chlamydospores (asexual structure not produced by all species). Important features of the sporangium include their dimensions (length and breadth), shape, thickening at the terminus (papilla), length of stalk (pedicle), whether or not the sporangium can be easily dislodged from the sporangiophore (caducity), and proliferation of sporangia (internal, external or nested).

The sexual reproductive structures consist of the antheridium and oogonium (paternal and maternal gametangia, respectively) and are produced when cultures are grown on the appropriate sterol-containing medium. Their fusion leads to the formation of an oogonium that matures into a thick-walled resting structure referred to as an oospore. While most species are homothallic and form oospores in single culture, there are heterothallic species where pairing with opposite mating types is essential to stimulate production of sexual reproductive structures. Since *Phytophthora* is sexually dimorphic (an isolate of a heterothallic species can function either as the maternal or paternal parent depending on the isolate it is paired with) it is advisable to pair self-sterile isolates with two tester isolates of opposite mating type. While the use of tester isolates of the same species is advisable, isolates of other heterothallic species (such as *P. cryptogea* or *P. cambivora*) may also be used. Characteristics such as the diameter of the oogonium and oospore, thickness of the oospore wall, whether or not the oospore fills the oogonium (plerotic), ornamentation on the oogonial wall, and mode of attachment of the antheridium are useful for species classification.

In an effort to simplify isolate identification and establish groupings of isolates for comparison of morphological features (but not phylogenetic relationships), Waterhouse (1963) introduced the concept of morphological groups I through VI based on a number of characteristics, and is still useful today. Unfortunately a dichotomous key that includes recently described species is not available for identification of isolates but there are several recent efforts to simplify morphological identification of species, including a manual for identification of 60 species of *Phytophthora* by integration of a dichotomous key with a DNA fingerprinting technique based on PCR-single strand conformational polymorphism (SSCP) (Gallegly and Hong 2008). A LUCID key for identification of 55 common *Phytophthora* spp. is available (Ristaino 2011) and an expanded LUCID key including most described species should be available on a dedicated website in the near future (G. Abad and Y. Balci, personal communication). A tabular presentation of morphological features enabling comparison among 117 species may be found in Martin et al. (2012; a downloadable file of the table alone is available on the journal website).

In 1999 the number of described species in the genus *Phytophthora* was approximately 55 (Brasier 2007) but since then there has been a significant increase., Brasier (2007) reported a doubling in number to 105 described species, with this number recently increasing to 117 (Martin et al. 2012). Additional species have recently been described; *P. lacustris* (Nechwatal et al. 2012) *P. pluvialis* (Reeser et al. 2013), *P. mississippiae* (Yang et al. 2013), *P. cichorii, P. dauci* and *P. lactucae* (Bertier et al. 2013), *P. pisi* (Heyman et al. 2013), *P. stricta and P. macilentosa* (Yang et al. 2014) and the hybrid species *P.* x *serendipita* and *P.* x *pelgrandis* (Man in 't Veld et al. 2012), bringing the total to at least 128 described species. With the number of provisional species names used in the literature, and research efforts to evaluate the distribution of this genus in natural ecosystem, this number is likely to continue to increase in the future.

Molecular phylogeny

Historically the genus *Phytophthora* has been placed in the *Pythiales*with *Pythium* and related genera but more recent

phylogenetic analysis with the large (LSU) or small (SSU) rDNA sequences or *cox2* gene has indicated a closer affiliation with downy mildews and white rusts (*Albugo*.) in the *Peronosporales* (Beakes and Sekimoto 2009; Thines et al. 2009). However, additional multigene analyses with a larger number of downy mildew species is needed to better characterize this relationship and the placement of *Phytophthora* spp. in clade 9 and 10 (Blair et al. 2008). The relationship between the *Peronosporales* and *Pythium* (*Pythiales*) needs clarification as well. A new genus, *Phytopythium*, was erected to accommodate an inconsistency between taxonomic and phylogenetic grouping for certain "intermediate" *Pythium* species (Bala et al. 2010), and it is likely that additional taxonomic revisions of the Peronosporomycetidae will be needed to fully resolve taxonomic conflicts.

Early efforts to understand phylogenetic relationships in *Phytophthora* focused on the use of the nuclear encoded rDNA, primarily the ITS region (Förster et al. 2000; Cooke and Duncan 1997; Crawford et al. 1996). Cooke et al. (2000) published the first comprehensive phylogenetic analysis of the genus using the ITS region to examine the phylogeny of 50 species. Most isolates grouped within eight primary clades (numbered 1 to 8) with several other species placed in two additional clades (clades 9 and 10). Kroon et al. (2004) expanded this analysis using two nuclear (translation elongation factor 1α, β-tubulin) and two mitochondrial (*cox1* and *nad1*) genes. While in general the results were congruent with those reported by Cooke et al. (2000), there were some notable differences in the grouping of some species. Subsequent analysis by Blair et al. (2008) using seven nuclear genes (60S ribosomal protein L10, ß-tubulin, enolase, heat shock protein 90, large subunit rDNA, TigA gene fusion and translation elongation factor 1α) representing 8.1 kb of sequence data for 82 *Phytophthora* spp. clarified these differences. This larger, multi-marker analysis supported the observations of Cooke et al. (2000) with eight main clades plus two additional closely affiliated clades (clades 9 and 10) as the sister clades to the rest of the genus. More recently, Martin et al. (2014) expanded on this analysis by adding four mitochondrial genes (*cox2, nad9, rps10* and *secY*) and additional species. The resulting phylogeny from this 11-marker analysis (10,828 bp per isolate) was similar to the prior observations of Blair et al. (2008) and subsequent analysis indicated that similar results could be obtained when using only five markers (LSU, β-tubulin, *cox2, nad9* and *rps10*).

While the ITS region may be useful for species identification (see below), length variation among species makes it impossible to construct an unambiguous alignment across the entire genus, thus hampering the utility of this marker for phylogenetic analysis. Likewise, the translation elongation factor 1α has been used for phylogenetic analysis, but recent analysis of *Phytophthora* genomic data indicates that the gene is duplicated; divergence among duplicates may complicate phylogenetic interpretations of species evolution (J. E. Blair, unpublished).

While the above noted phylogenetic analyses have provided insight into the broader evolutionary relationships within the genus, there is still ambiguity when examining some closely related species and species complexes. Significant progress has been made with the clarification of the *P. megasperma* complex and other clade six species (Brasier et al. 2003; Durán et al. 2008; Hansen et al. 2009; Jung et al. 2011a, b) but there are still several provisional species awaiting more comprehensive analysis (for example, *P. taxon* PgChlamydo, *P. taxon* raspberry, *P. taxon* canalensis, *P. taxon* erwinii, *P. taxon* hungarica, *P. taxon* oregonsis and *P. taxon* paludosa). While there have been advances in understanding the relationships among some clade 2 species, there is need for additional analysis to clarify species complexes such as *P. citricola* and *P. citrophthora*. One clade 8 species complex where phylogenetic resolution has been elusive is *P. cryptogea* and the closely related species *P. drechsleri*. The multigene analysis of Mostowfizadeh-Ghalamfarsa et al. (2010) confirmed that while *P. drechsleri* was monophyletic, the *P. cryptogea* complex formed three well-defined phylogenetic groups with group I closely affiliated with *P. erythroseptica* and group II and III as a separate clade (group III isolates have been reported as the provisional species, *P.* sp. *kelmania*; Martin et al. 2014). Some isolates were placed intermediate between groups II and III and exhibited a greater amount of heterozygosity than the other isolates, suggesting possible outcrossing between these groups. Using a parsimony-based ancestral recombination graph and genealogies inferred from the β-tubulin and translation elongation factor 1-α genes from greenhouse recovered isolates, Olson et al. (2011) suggested that divergence between *P. cryptogea* and *P. drechsleri* was recent and that speciation is still in progress.

In addition to the choice of markers to use for phylogenetic analysis, another important consideration is the type of analysis used for estimating phylogenetic relationships or for the description of new species. While traditional methods of phylogenetic analysis (maximum likelihood, neighbour-joining, Bayesian) have adequately described relationships among most species, they have been unable to fully resolve the deeper relationships among the ten *Phytophthora* clades or among related genera. A recent study by Martin et al. (2014) used a novel variation of a multispecies coalescent approach to evaluate the ten clades; in general support was higher than that observed in the phylogenetic analysis for the recovered relationships, but the position of certain clades (Clade 3 and the unique grouping of *P.* sp. *ohioensis* and *P. quercina*) remained ambiguous. Here we present an analysis using a more powerful and complex Bayesian method (Drummond et al. 2012) with five genetic markers (Fig. 20), and recover strong support for basal relationships among the clades that are quite similar to

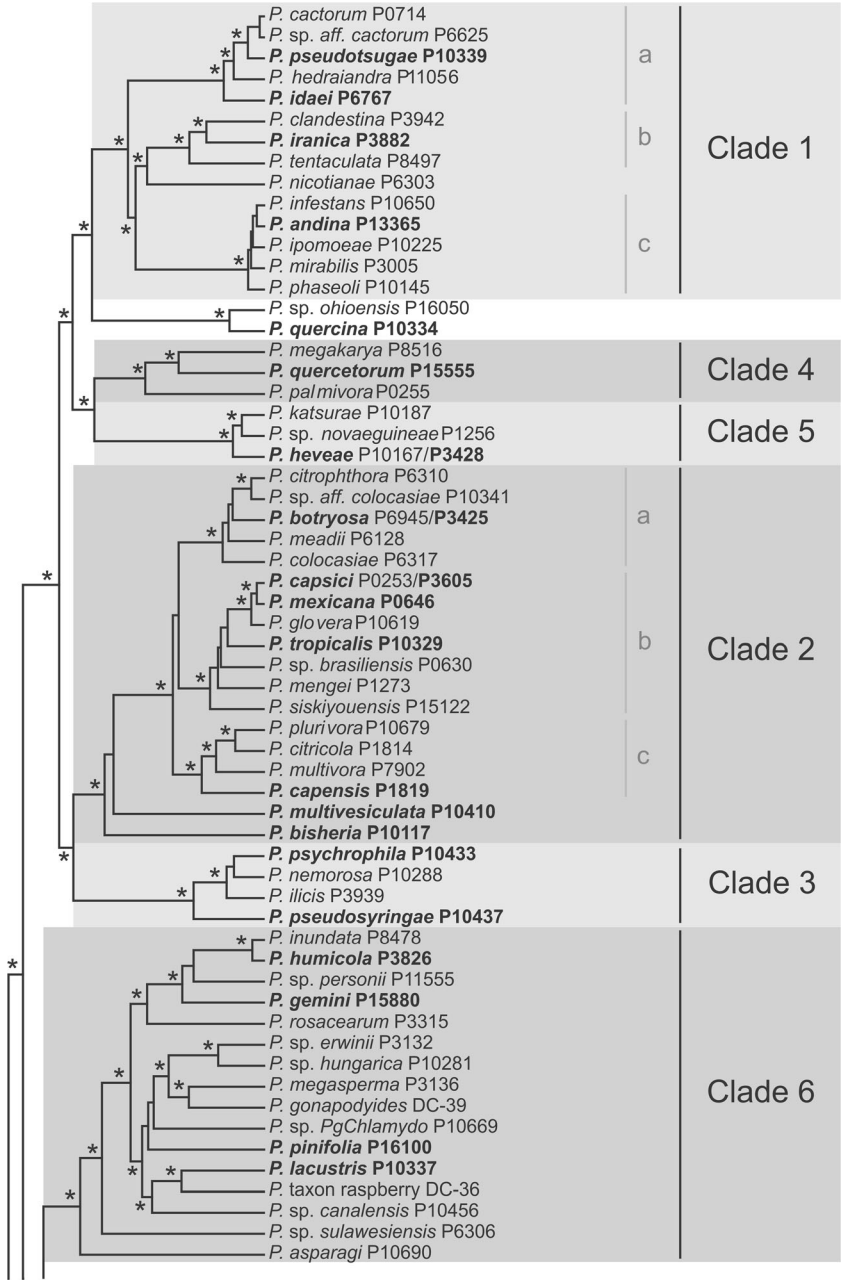


Fig. 20 Bayesian analysis of phylogenetic relationships within *Phytophthora*. *Asterisks* on nodes indicate posterior probabilities greater than 0.95 (95 %) generated from an analysis of five genes (nuclear LSU and β-tubulin; mitochondrial *cox2, nad9, rps10*). Evolutionary rates were estimated under a GTR + I + G model for nuclear markers and an HKY + I + G model for mitochondrial gene; each marker was treated as a separate partition. The analysis was run twice with 50 million generations under a strict clock model in BEAST v1.7.5. A 20 % burn in was removed before the maximum clade credibility tree was constructed. Ex-type isolates are shown in *bold*. Separate isolate numbers are shown for those few species that did not have sequence data available for both nuclear and mitochondrial genes from a single isolate

the 11-marker study of Martin et al. (2014). Newer phylogenetic methods may allow for more complex modelling of the evolutionary process, however they are still sensitive to the accuracy of *a priori* information provided by the user. Additional studies will be needed to provide more basic information on the tempo of molecular evolution within this group.

The description of new species is also an area were traditional phylogenetic methods may not accurately describe species relatedness. Aside from morphological characterization, recent species descriptions typically contain molecular evidence from one or a few genetic markers (primarily ITS and perhaps *cox1* or *2*). However, as described above, alignment ambiguity and the presence of intraspecific polymorphisms can seriously impact the recovered phylogeny; recent hybridization events and incomplete lineage sorting of ancestral polymorphisms also violate the assumptions made by

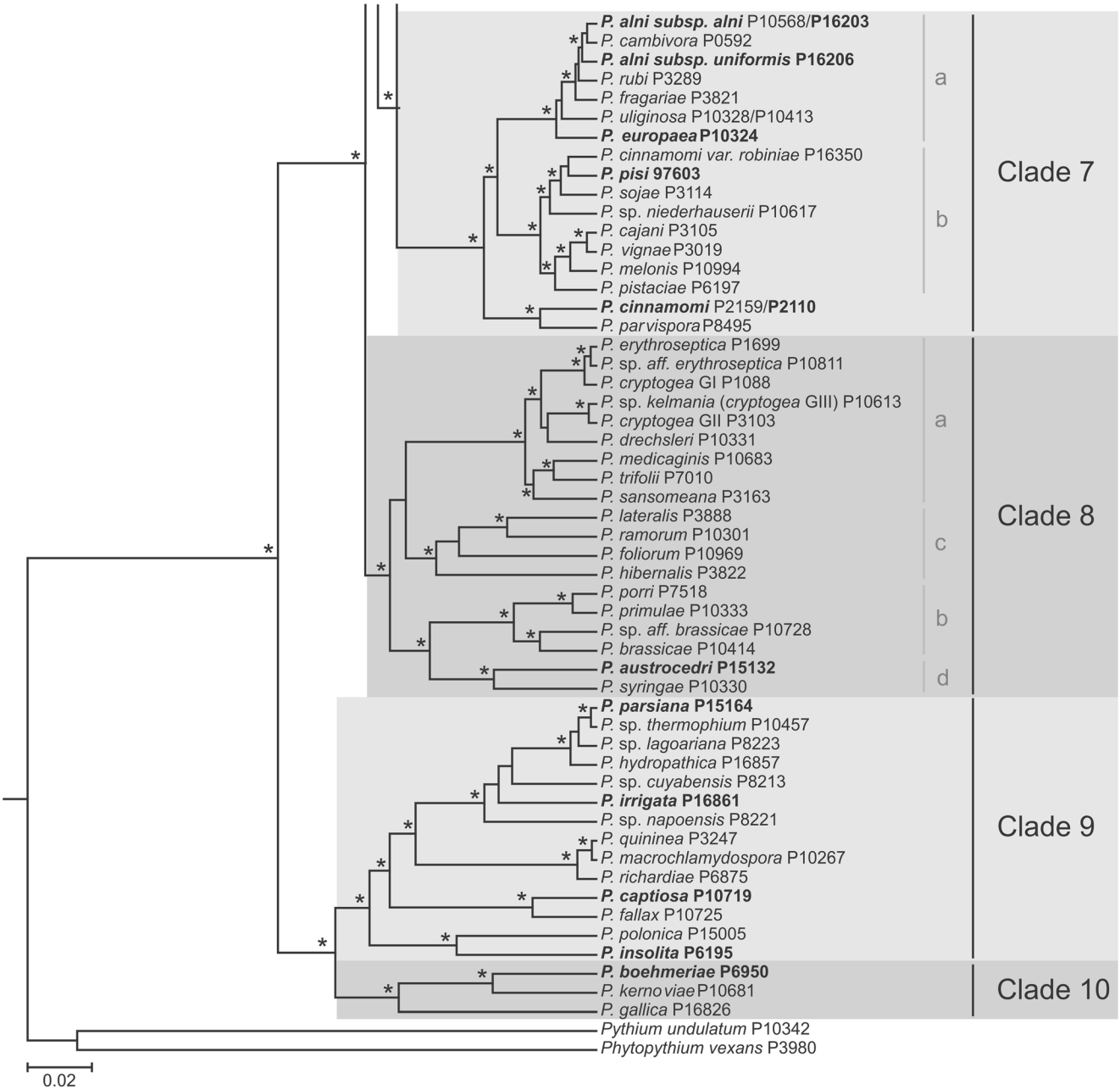


Fig. 20 (continued)

traditional phylogenetic methods. The use of coalescent-based approaches to estimate species trees from a collection of gene trees has been gaining popularity among many other taxonomic groups, but has seen little attention in *Phytophthora* or oomycete research in general. The recent description of *P. pisi* (Heyman et al. 2013) employed a multispecies coalescent approach, which confirmed the individual analyses of ITS and *cox2* data. In addition, a recent study of the hybrid species *P. andina* (Blair et al. 2012) used several coalescent methods to determine the likely parental lineages of this species, one of which was clearly *P. infestans*. In the future, the use of more complex phylogenetic methods as well as coalescent-based approaches will be needed to clarify relationships at both ends of the spectrum, from deep basal nodes to recently evolved and potentially interbreeding species complexes.

A common observation among all phylogenetic studies is there is no consistent correlation between phylogenetic grouping and morphological features (Cooke et al. 2000; Kroon et al. 2004, 2012; Blair et al. 2008; Martin et al. 2014). While there is some correlation with sporangial type (clade 4, 5, and 10 have primarily papillate sporangia while clade 3 has primarily semipapillate sporangia and clades 6, 7, and 9 primarily nonpapillate sporangia), other clades show combinations of these

features (clade 1, 2 and 8). Characteristics such as oogonial ornamentation, heterothallism, and mode of antheridial attachment are all polyphyletic.

Because of the large number of species, intraspecific variation of some morphological features, and overlapping morphology among closely related species, traditional methods of species identification can be challenging and require some level of expertise to be effective. The use of molecular criteria has simplified this task and provides a tool for delineating distinct taxa within morphologically similar species complexes. The most accurate molecular method for species identification is sequence analysis of specific markers. The internal transcribed spacer (ITS) region of the nuclear ribosomal DNA (rDNA) has been widely used and a large number of sequences are currently available in public databases. However, this marker may not be ideal for the identification of all species, especially those that are closely related. For example, many clade 1C species (*P. infestans, P. mirabilis*) cannot be distinguished using this marker alone, nor can *P. fragariae* and *P. rubi*. More recently a portion of the *cox1* gene, along with the ITS region, have been proposed as the markers to use in the Barcode of Life Database (www.boldsystems.org) and representative sequences for all described and some provisional species have been deposited (Robideau et al. 2011).

Several nuclear (60S ribosomal protein L10, β-tubulin, enolase, heat shock protein 90, large subunit rRNA, TigA gene fusion, translation elongation factor 1α; (Blair et al. 2008; Kroon et al. 2004; Villa et al. 2006)) and mitochondrial (*cox1, nad1, cox2, nad9, rps10* and *secY*; (Kroon et al. 2004; Martin 2008; Martin and Tooley 2003a, b; Martin et al. 2014) markers have been sequenced for phylogenetic analysis of *Phytophthora* and can also be used for species identification. Background information for amplification and sequencing of many of these markers, as well as the capability for BLAST searches against a curated database for isolate identification, may be found at the *Phytophthora* Database (www.phytophthoradb.org). A dataset for ITS and *cox1* and *2* spacer sequences is also available at *Phytophthora* ID ((Grünwald et al. 2011), www.phytophthora-id.org) and sequence data for several markers (ITS, β-tubulin, elongation factor 1 alpha, and *cox1*), along with pictures of morphological features, may be found at Q-Bank (www.q-bank.eu).

There are several caveats to consider when using BLAST analysis to identify isolates to species level to prevent misidentification (Kang et al. 2010; Nilsson et al. 2012). BLAST scores are dependent on the length of the aligned sequences as well as the level of sequence identity; instances where high levels of sequence identity occur for only a portion of the target sequence may result in incorrect species identification. Also, it is common to encounter situations where scores are similar among multiple species, making it difficult to draw conclusions about an isolate's identity (this can be especially problematic for isolates within or related to species complexes). In addition, the use of markers known to contain intraspecific polymorphisms may lead to inaccurate species identifications due to potentially lower similarities among closely related sequences. Heterozygosity in nuclear markers may also complicate identification efforts; while the presence of distinct alleles may indicate outcrossing (as *Phytophthora* is a known diploid), heterozygosity may also result from hybridization events between distinct lineages (as described above). Phylogenetic analysis of several markers is therefore suggested to confirm species identification, especially when working with species complexes. Additional gel based techniques, such as PCR-RFLP, SSCP, random amplified polymorphic DNAs (RAPDs), amplified fragment length polymorphisms (AFLP) and simple sequence repeat (SSR) analysis, for species identification and population analysis are reviewed in Martin et al. (2012).

Recommended genetic markers

The following genetic markers have been found to amplify well across all species and provided a similar level of phylogenetic resolution as a concatenated dataset of seven nuclear and four mitochondrial genes (Martin et al. 2014). Information on amplification and sequencing primers for these genes may be found at the *Phytophthora* Database (www.phytophthoradb.org).

Nuclear genes–LSU, β-tubulin

Mitochondrial–*cox2, nad9, rps10*

Phytophthora Data

Sequence alignments of the seven nuclear and four mitochondrial markers used in Martin et al. (2014) and Fig. 20 may be downloaded at TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S14595). A table with additional information on isolates used in the analysis may be found in Martin et al. (2014) with GenBank accession numbers listed in the supplementary material of this citation. These sequences can also be downloaded from the *Phytophthora* Database (www.phytophthoradb.org).

Pythium

Background

Pythium is classified as belonging to the family *Pythiaceae sensu lato* (*s.l.*), order *Peronosporales s.l.*, class Peronosporomycetes, phylum Oomycota, and kingdom

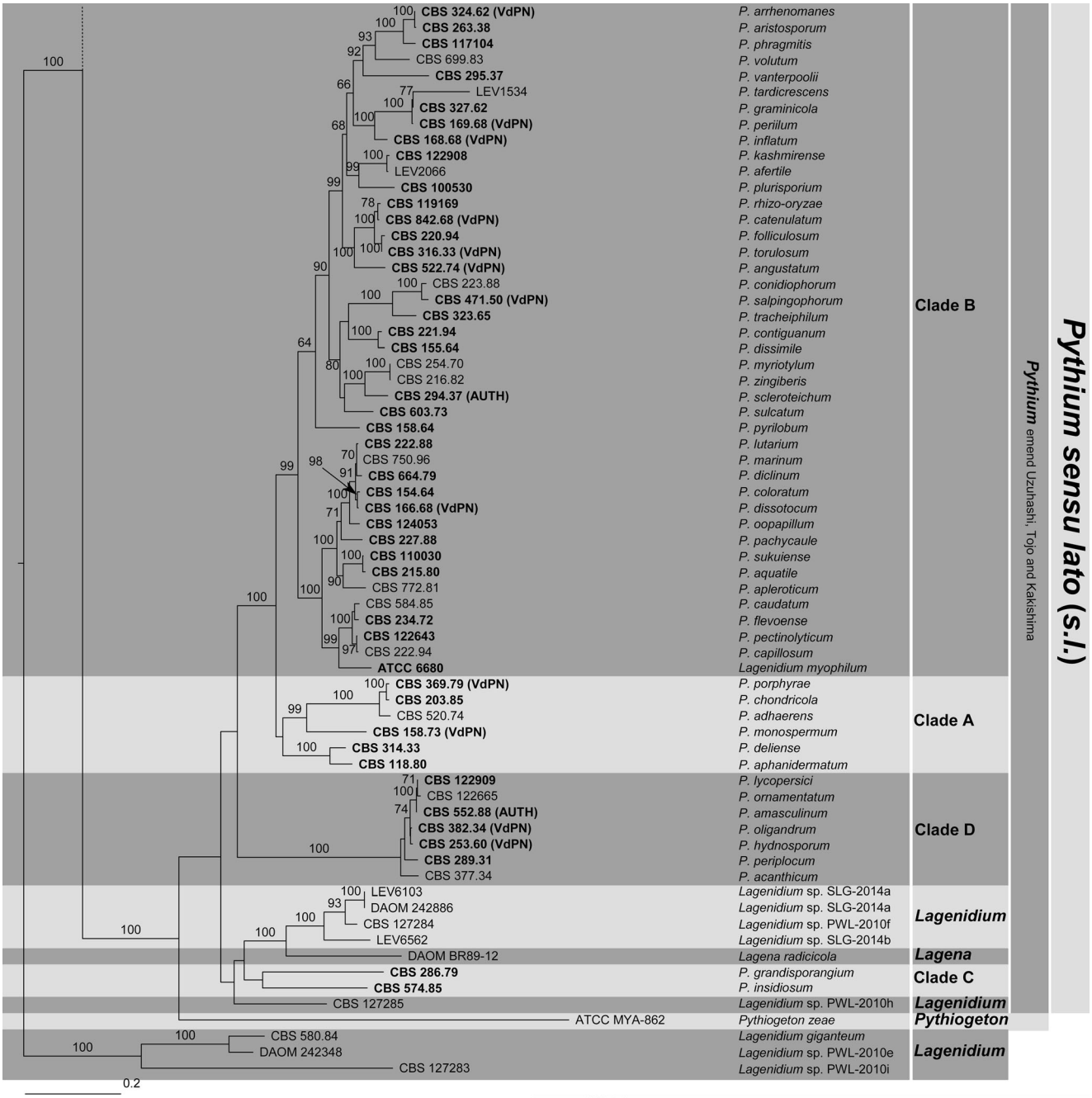
Straminipila (Beakes et al. 2014). Although many species are considered to be saprobes, the genus is known primarily for its parasitic interactions with plants. Several species also parasitize algae (green and red), fungi, other oomycetes, nematodes, insects, crustaceans, and fish. One species, *P. insidiosum*, is the causal agent of pythiosis in mammals, including humans (Van der Plaats-Niterink 1981; de Cock et al. 1987). Plant pathogenic *Pythium* species often target young below-ground plant parts such as fine roots, germinating seeds and emerging growth, resulting in damping-off, root rot and poor crop stands with stunted plants and reduced yield. Some species can also cause fruit rot, and at least one species, *P. vexans*, has been associated with trunk cankers of rubber trees (Van der Plaats-Niterink 1981; Zeng et al. 2005). Although some species have a limited host range, such as *P. arrhenomanes* that seems to be exclusively associated with gramineous crops, species like *P. aphanidermatum*, *P. irregulare* and *P. ultimum* are known for being highly virulent on an extensive range of plant hosts (Van der Plaats-Niterink 1981). However, not all *Pythium* species have a negative impact on the plants they are associated with. Besides saprobes, others can benefit plants by acting as biocontrol agents that parasitize pathogenic fungi and/or induce host resistance, e.g. *Pythium oligandrum* (Benhamou et al. 1997). Other species of *Pythium* have also been reported to stimulate plant growth (Mazzola et al. 2002). Recent genome sequencing of six *Pythium* species found high levels of variation in the number of CRN ("Crinkler") effectors found in the different species, possibly suggesting species-specific infection strategies (Adhikari et al. 2013) that may contribute to the range of interactions of *Pythium* species with their hosts. Such species-specific host-interactions along with the ubiquitous nature of the genus in soils all over the world make accurate species identification necessary to facilitate disease diagnosis and management.

Debates regarding possible genera within *Pythium* were initially sparked by differences in sporangial morphology. Based on these characters some of the novel genera that have been proposed are *Nematosporangium* (for species with filamentous zoosporangia), *Rheosporangium* (species with lobulate zoosporangia), and *Sphaerosporangium* (species with ovoid, spherical or citriform sporangia) (Schröter 1897; Sparrow 1931). The legitimacies of these genera have been questioned for various reasons (Sideris 1931a; Sparrow 1932; Van der Plaats-Niterink 1981), and aside from some attempts at transferring *Pythium* species to *Nematosporangium* (Jaczewski and Jaczewski 1931; Sideris 1931b) the scientific community has stuck with the generic classification of *Pythium* versus these genera. As molecular taxonomy became a more popular approach to studying systematics, the paraphyletic nature of *Pythium* became apparent and the debate on splitting the genus was rekindled. Early sequence-based phylogenies provided strong arguments for *P. vexans* to be part of a separate genus (Briard et al. 1995; Cooke et al. 2000). The ITS and 28S phylogenies of Lévesque and de Cock (2004) divided *Pythium* into 11 clades (A-K) of which clade K (including *P. vexans*) is more closely related to *Phytophthora* than to the rest of the *Pythium* clades (Villa et al. 2006). A new genus, *Phytopythium*, was subsequently erected to include all clade K species, with *Phytopythium sindhum* as type species (Bala et al. 2010), although the official transfer of all clade K *Pythium* species to *Phytopythium* has not yet been published. The remaining ten clades (A-J) can be divided into two groups: species with filamentous zoosporangia (clades A-D) and species with globose zoosporangia (clades E-J) (Lévesque and de Cock 2004), calling to mind early suggestions of splitting the genus based on this character (Schröter 1893; Sparrow 1931). This division is echoed to varying degrees by phylogenies of the 28S rRNA, ITS, cytochrome c oxidase subunits 1 and 2 (*cox1* and *cox2*), and β-tubulin, although the different gene trees are often incongruent and support for internal nodes low or absent (Martin 2000; Riethmüller et al. 2002; Villa et al. 2006; Hulvey et al. 2010; Robideau et al. 2011). Despite the shortcomings of these gene regions, Uzuhashi et al. (2010) used 28S and *cox2* phylogenies to divide *Pythium* into five genera: *Pythium* (clades A-D), *Globisporangium* (clades E-G, I and J), *Elongisporangium* (clade H), *Ovatisporangium* (clade K, syn. *Phytopythium*), and *Pilasporangium* (distinct from any of the aforementioned 11 clades). Although this division is more or less in agreement with previous phylogenetic studies, it is problematic with regards to a lack of bootstrap support for the *Pythium* and *Globisporangium* clades, and the relationship and distinction between *Elongisporangium* and *Globisporangium* is not resolved with support (Fig. 21, Uzuhashi et al. 2010). Additionally, the genera *Pythiogeton* and *Lagena* seem to be phylogenetically situated within, or closely related to *Pythium* emend Uzuhashi, Tojo and Kakishima (Fig. 21, Huang et al. 2013a), so even this revised version of *Pythium* is paraphyletic. For these reasons investigators have generally been slow to adopt the proposed genera. Following this trend references to "*Pythium*" in this manuscript refer to *Pythium s.l.* (*i.e. Pythium* Pringsheim) unless stated otherwise.

Species identification and numbers

A combined list of *Pythium* species in MycoBank (2014) and Index Fungorum (2014) includes a total of

Fig. 21 Maximum likelihood phylogeny of *Pythium s.l.* and related genera based on the concatenated 18S rRNA, ITS, 28S rRNA, cytochrome c oxidase subunit 2 (*cox2*), and β-tubulin regions. Bootstrap support values below 60 % are not indicated. Strains in *bold* typeface represent type-derived material, authentic strains or strains used by Van der Plaats-Niterink (1981) for descriptions. The 11 clades (A–K) of Lévesque and de Cock (2004) and the genera erected by Bala et al. (2010) and Uzuhashi et al. (2010) are indicated on the right along with related taxa such as *Phytophthora*, *Lagenidium*, *Lagena*, and *Pythiogeton*



328 names of which several are either synonyms, orthographic variants or varieties that are rarely referred to and are possibly synonyms of other species (i.e. all varieties excluding varieties of *P. ultimum*). Excluding such cases along with putative synonyms based on cox1 and ITS sequence homology as identified by Robideau et al. (2011) leaves more or less 230 species of *Pythium*. Undoubtedly this number still includes species that should be synonymized and/or transferred to genera other than *Pythium* (Van der Plaats-Niterink 1981; Dick 1990, 2001), but for now this should serve as a rough estimate of the number of actual *Pythium* species discovered to date. Of these species 152 (66 %) are known to be represented by sequence(s) in GenBank, including at least 123 (53 %) species for which type-material, ex-type strains or strains described by Van der Plaats-Niterink (1981) were used to generate sequence data (Table 19, Fig. 21).

Identification of *Pythium* isolates to the species level is generally straightforward when comparing both ITS and cox1 sequences to that of ex-type, authentic or other reliable representative strains. For this purpose the sequences

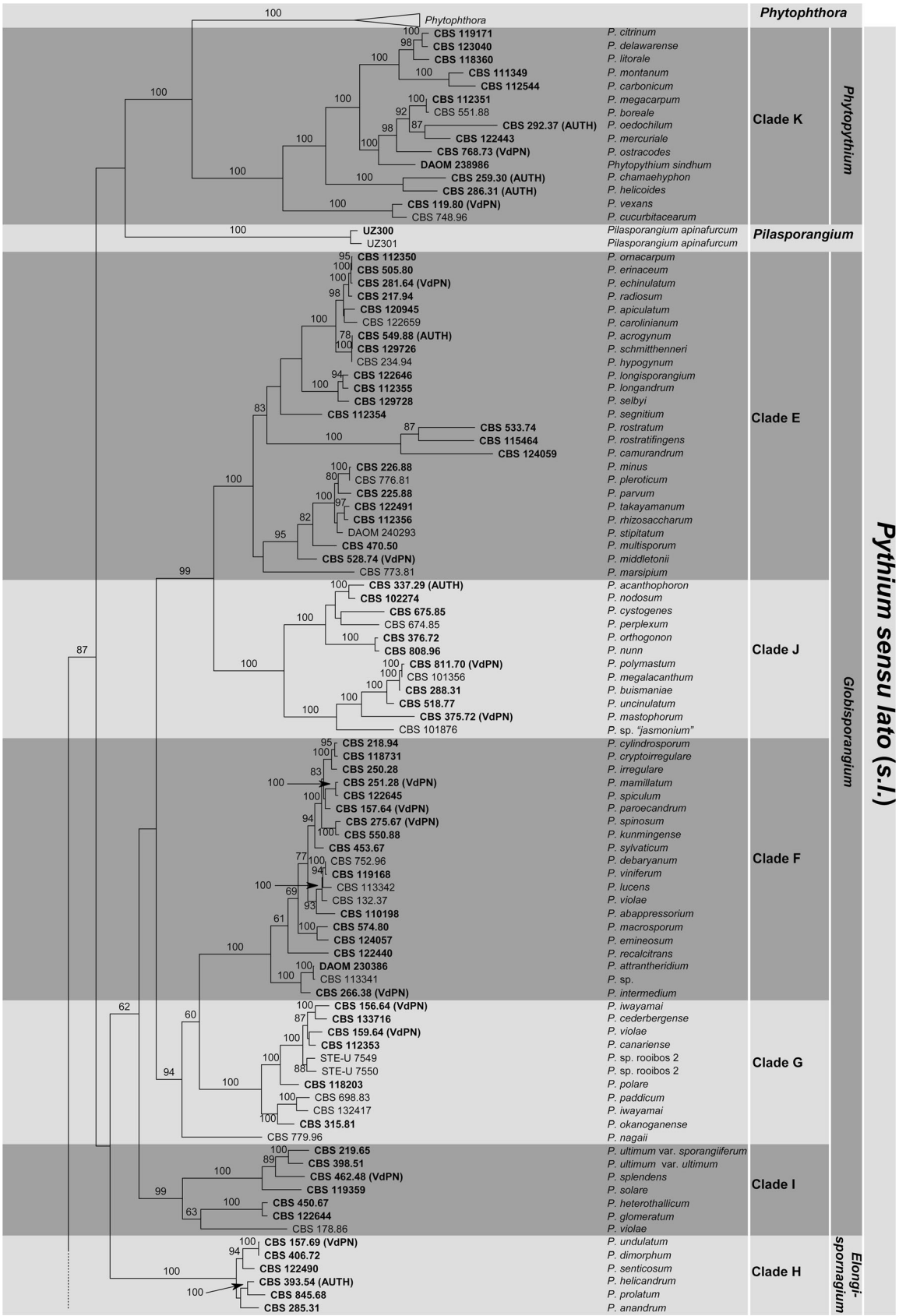


Fig. 21 (continued)

Table 19 *Pythium*. Strain numbers, host information and GenBank accession numbers for species included in Fig. 21

Species	Isolate	Host	GenBank accession numbers				
			SSU	ITS	LSU	*cox2*	β- tubulin
Lagena radicicola	DAOM BR89-12	*Triticum aestivum*	KJ716869	KJ716869	KJ716869	KJ595434	N/A
Lagenidium giganteum	CBS 580.84	Mosquito larva	KJ716868	KJ716868	KJ716868	KJ595392	KJ595516
Lagenidium myophilum	**ATCC 6680**	*Pandalus borealis*	AB284577	AB285498	AB285220	AF290311	N/A
Lagenidium sp. PWL-2010e	DAOM 242348	Soil nematode	KJ716871	KJ716871	KJ716871	KJ595438	KJ595561
Lagenidium sp. PWL-2010f	CBS 127284	Soil nematode	HQ343198	HQ111472	HQ395652	HQ605945	N/A
Lagenidium sp. PWL-2010h	CBS 127285	Soil nematode	HQ343197	HQ111470	HQ395651	HQ660435	N/A
Lagenidium sp. PWL-2010i	CBS 127283	Soil nematode	HQ343199	HQ111471	HQ395653	HQ680580	N/A
Lagenidium sp. SLG-2014a	DAOM 242886	Soil nematode	N/A	KJ716872	KJ716872	KJ595442	KJ595565
Lagenidium sp. SLG-2014a	LEV6103	Soil nematode	KJ716870	KJ716870	KJ716870	KJ595441	KJ595564
Lagenidium sp. SLG-2014b	LEV6562	*Oedogonium* sp.	KJ716873	KJ716873	N/A	KJ595443	KJ595566
Phytophthora capsici	P1319	*Capsicum annuum*	JN635215	FJ801727	EU079741	GU221958	EU079737
Phytophthora cinnamomi	P8495	*Beaucamea* sp.	JN635088	FJ802007	EU079953	GU221971	EU079949
Phytopythium sindhum	**DAOM 238986**	Soil (*Musa* sp.)	HQ643396	HQ643396	HQ643396	KJ595436	KJ595559
Pilasporangium apinafurcum	**UZ300**	Soil	N/A	AB458660	AB458651	AB458820	N/A
Pilasporangium apinafurcum	UZ301	Soil	N/A	AB458657	AB458652	AB458818	N/A
Pythiogeton zeae	ATCC MYA-862	*Zea mays*	N/A	HQ643405	HQ665310	N/A	N/A
Pythium abappressorium	**CBS 110198**	*Triticum aestivum*	HQ643408	HQ643408	HQ643408	KJ595409	KJ595533
P. acanthicum	CBS 377.34	*Solanum tuberosum*	AY598617	AY598617	AY598617	KJ595380	KJ595504
P. acanthophoron	**CBS 337.29 (AUTH)**	*Ananas sativus*	AY598711	AY598711	AY598711	KJ595376	KJ595500
P. acrogynum	**CBS 549.88 (AUTH)**	Soil (*Spinacia oleracea*)	N/A	AY598638	AY598638	AB362324	KJ595458
P. adhaerens	CBS 520.74	Soil	AY598619	AY598619	AY598619	KJ595386	KJ595510
P. afertile	LEV2066	Turf grass	N/A	HQ643416	HQ643416	KJ595440	KJ595563
P. amasculinum	**CBS 552.88 (AUTH)**	soil (vegetable garden)	AY598671	AY598671	AY598671	KJ595390	KJ595514
P. anandrum	**CBS 285.31**	*Rheum rhaponticum*	AY598650	AY598650	AY598650	AB362328	KJ595450
P. angustatum	**CBS 522.74 (VdPN)**	Soil	AY598623	AY598623	AY598623	KJ595387	KJ595511
P. aphanidermatum	**CBS 118.80**	Unknown	AY598622	AY598622	AY598622	KJ595344	KJ595472
P. apiculatum	**CBS 120945**	soil (*Vitis* sp.)	HQ643443	HQ643443	HQ643443	KJ595422	KJ595547
P. apleroticum	CBS 772.81	*Nymphyoides peltata*	AY598631	AY598631	AY598631	KJ595400	KJ595524
P. aquatile	**CBS 215.80**	Soil	AY598632	AY598632	AY598632	KJ595355	KJ595481
P. aristosporum	**CBS 263.38**	*Triticum aestivum*	AY598627	AY598627	AY598627	AB507410	DQ071297
P. arrhenomanes	**CBS 324.62 (VdPN)**	*Zea mays*	AKXY02050628	AY598628	AY598628	AKXY02053172	KJ595451
P. attrantheridium	**DAOM 230386**	*Prunus serotina*	HQ643476	HQ643476	HQ643476	AB512889	AB512822
P. boreale	CBS 551.88	Soil	AY598662	AY598662	AY598662	EF408876	EF408882

Table 19 (continued)

Species	Isolate	Host	GenBank accession numbers				
			SSU	ITS	LSU	*cox2*	β- tubulin
P. buismaniae	**CBS 288.31**	*Linum usitatissimum*	AY598659	AY598659	AY598659	KJ595368	KJ595493
P. camurandrum	**CBS 124059**	*Hordeum vulgare*	GQ244426	GQ244426	GQ244426	KJ595433	KJ595558
P. canariense	**CBS 112353**	Soil	HQ643482	HQ643482	HQ665069	JX397983	JX397969
P. capillosum	CBS 222.94	Soil	AY598635	AY598635	AY598635	KJ595360	KJ595485
P. carbonicum	**CBS 112544**	Soil (spoil heap)	HQ643373	HQ643373	HQ643373	AB690678	KJ595464
P. carolinianum	CBS 122659	soil	N/A	HQ643484	HQ665111	KJ595427	KJ595551
P. catenulatum	**CBS 842.68 (VdPN)**	Turf grass	AY598675	AY598675	AY598675	KJ595404	KJ595528
P. caudatum	CBS 584.85	*Xiphinema rivesi*	HQ643136	HQ643136	HQ665277	AF290309	KJ595459
P. cederbergense	**CBS 133716**	*Aspalathus linearis*	N/A	JQ412768	KJ716864	JQ412805	JQ412781
P. chamaehyphon	**CBS 259.30 (AUTH)**	*Carica papaya*	AY598666	AY598666	AY598666	AB257280	KJ595448
P. chondricola	**CBS 203.85**	*Chondrus crispus*	N/A	AY598620	AY598620	KJ595354	KJ595480
P. citrinum	**CBS 119171**	Soil (*Vitis* sp.)	HQ643375	HQ643375	HQ643375	AB690679	KJ595465
P. coloratum	**CBS 154.64**	Soil (tree nursery)	AY598633	AY598633	AY598633	KJ595346	KJ595474
P. conidiophorum	CBS 223.88	Soil	AY598629	AY598629	AY598629	KJ595361	KJ595486
P. contiguanum	**CBS 221.94**	Soil (salt marsh)	HQ643514	HQ643514	HQ665162	KJ595358	KJ595483
P. cryptoirregulare	**CBS 118731**	*Euphorbia pulcherrima*	HQ643515	HQ643515	HQ643515	GU071763	GU071888
P. cucurbitacearum	CBS 748.96	Unknown	AY598667	AY598667	AY598667	AB690680	KJ595460
P. cylindrosporum	**CBS 218.94**	Soil	AY598643	AY598643	AY598643	GU071762	GU071877
P. cystogenes	**CBS 675.85**	*Vicia faba*	HQ643518	HQ643518	HQ643518	KJ595396	KJ595520
P. debaryanum	CBS 752.96	*Tulipa* sp.	AY598704	AY598704	AY598704	KJ595399	KJ595523
P. delawarense	**CBS 123040**	*Glycine max*	KF853241	EU339312	KF853240	KJ595430	KJ595555
P. deliense	**CBS 314.33**	*Nicotiana tabacum*	AY598674	AY598674	AY598674	KJ595372	KJ595497
P. diclinum	**CBS 664.79**	*Beta vulgaris*	N/A	AY598690	HQ665282	KJ595394	KJ595518
P. dimorphum	**CBS 406.72**	*Pinus taeda*	AY598651	AY598651	AY598651	AB362331	KJ595454
P. dissimile	**CBS 155.64**	*Pinus radiata*	AY598681	AY598681	AY598681	KJ595347	KJ595475
P. dissotocum	**CBS 166.68 (VdPN)**	*Triticum aestivum*	AY598634	AY598634	AY598634	KJ595351	KJ595479
P. echinulatum	**CBS 281.64 (VdPN)**	Soil (forest nursery)	AY598639	AY598639	AY598639	AB362327	KJ595449
P. emineosum	**CBS 124057**	*Juniperus communis*	N/A	GQ244427	GQ244427	KJ595432	KJ595557
P. erinaceum	**CBS 505.80**	Soil	N/A	AY598694	HQ665243	AB362326	KJ595456
P. flevoense	**CBS 234.72**	Soil	AY598691	AY598691	AY598691	KJ595363	KJ595488
P. folliculosum	**CBS 220.94**	Soil	AY598676	AY598676	HQ665160	N/A	N/A
P. glomeratum	**CBS 122644**	Soil	N/A	HQ643542	HQ665097	KJ595424	KJ595548
P. graminicola	**CBS 327.62**	*Saccharum officinarum*	AY598625	AY598625	AY598625	AF196593	KJ595452

Table 19 (continued)

Species	Isolate	Host	GenBank accession numbers				
			SSU	ITS	LSU	*cox2*	β- tubulin
P. grandisporangium	**CBS 286.79**	Decaying leaf (*Zostera marina*)	AY598692	AY598692	AY598692	KJ595367	KJ595492
P. helicandrum	**CBS 393.54 (AUTH)**	*Rumex acetosella*	AY598653	AY598653	AY598653	AB362329	KJ595453
P. helicoides	**CBS 286.31 (AUTH)**	*Phaseolus vulgaris*	AY598665	AY598665	AY598665	DQ071377	AB511994
P. heterothallicum	**CBS 450.67**	Soil (*Sambucus*)	AY598654	AY598654	AY598654	AB512919	AB512850
P. hydnosporum	**CBS 253.60 (VdPN)**	Unknown	AY598672	AY598672	AY598672	KJ595364	KJ595489
P. hypogynum	CBS 234.94	Soil	AY598693	AY598693	AY598693	AB362325	KJ595447
P. inflatum	**CBS 168.68 (VdPN)**	*Saccharum officinarum*	AY598626	AY598626	AY598626	KJ595352	N/A
P. insidiosum	**CBS 574.85**	*Equus ferus*	AF289981	AY598637	AY598637	KJ595391	KJ595515
P. intermedium	**CBS 266.38 (VdPN)**	*Agrostis stolonifera*	AY598647	AY598647	AY598647	AB507410	AB512836
P. irregulare	**CBS 250.28**	*Phaseolus vulgaris*	AY598702	AY598702	AY598702	GU071760	GU071886
P. iwayamai	CBS 132417	*Poa annua*	AKYA02013211, AKYA02014361, AKYA02012602	AKYA02012602, AKYA02013659	AKYA02013659, AKYA02016578, AKYA02016542	AKYA02009930, AKYA02012077	AKYA02004337
P. iwayamai	**CBS 156.64 (VdPN)**	Soil (*Pinus* sp.)	AY598648	AY598648	AY598648	JX397979	JX397965
P. kashmirense	**CBS 122908**	Soil	HQ643671	HQ643671	HQ643671	KJ595429	KJ595553
P. kunmingense	**CBS 550.88**	Soil (*Vicia faba*)	AY598700	AY598700	HQ665259	KJ595389	KJ595513
P. litorale	**CBS 118360**	Soil (*Phragmites australis*)	HQ643386	HQ643386	HQ643386	KJ595418	KJ595543
P. longandrum	**CBS 112355**	Soil	HQ643679	HQ643679	HQ665071	KJ595413	KJ595538
P. longisporangium	**CBS 122646**	Soil (*Vitis* sp.)	N/A	HQ643680	HQ665099	KJ595426	KJ595550
P. lucens	CBS 113342	*Triticum*	HQ643681	HQ643681	HQ643681	KJ595415	KJ595540
P. lutarium	**CBS 222.88**	Soil	HQ643682	HQ643682	HQ665163	KJ595359	KJ595484
P. lycopersici	**CBS 122909**	Soil (*Lycopersicum esculentum*)	N/A	HQ643683	HQ665119	KJ595343	KJ595554
P. macrosporum	**CBS 574.80**	Flower bulb	AY598646	AY598646	AY598646	AB512916	AB512842
P. mamillatum	**CBS 251.28 (VdPN)**	*Beta vulgaris*	AY598703	AY598703	HQ665173	AB362325	AB512844
P. marinum	CBS 750.96	Soil	N/A	AY598689	AY598689	KJ595398	KJ595522
P. marsipium	CBS 773.81	*Nymphyoides peltata*	N/A	AY598699	HQ665297	KJ595401	KJ595525
P. mastophorum	**CBS 375.72 (VdPN)**	*Apium graveolens*	AY598661	AY598661	AY598661	KJ595378	KJ595502
P. megacarpum	**CBS 112351**	Soil (*Vitis* sp.)	HQ643388	HQ643388	HQ643388	AB690665	KJ595536
P. megalacanthum	CBS 101356	*Chrysanthemum*	N/A	HQ643693	KJ716865	KJ595435	N/A
P. mercuriale	**CBS 122443**	*Macadamia integrifolia*	KF853243	DQ916363	KF853236	AB690666	KJ595466
P. middletonii	**CBS 528.74 (VdPN)**	Soil	N/A	AY598640	AY598640	AB362318	KJ595457
P. minus	**CBS 226.88**	Soil	HQ643696	HQ643696	HQ665168	AB362320	KJ595446
P. monospermum	**CBS 158.73 (VdPN)**	Soil	HQ643697	HQ643697	HQ643697	KJ595350	KJ595478
P. montanum	**CBS 111349**	Soil (*Picea abies*)	HQ643389	HQ643389	HQ643389	KJ595410	KJ595534

Table 19 (continued)

Species	Isolate	Host	GenBank accession numbers				
			SSU	ITS	LSU	*cox2*	β- tubulin
P. multisporum	**CBS 470.50**	Soil	AY598641	AY598641	AY598641	AB362319	KJ595455
P. myriotylum	CBS 254.70	*Arachis hypogaea*	AY598678	AY598678	AY598678	KJ595365	KJ595490
P. nagaii	CBS 779.96	Soil	AY598705	AY598705	AY598705	KJ595402	KJ595526
P. nodosum	**CBS 102274**	Soil	N/A	HQ643709	HQ665055	KJ595407	KJ595531
P. nunn	**CBS 808.96**	Soil	AY598709	AY598709	AY598709	AF196609	DQ071325
P. oedochilum	**CBS 292.37 (AUTH)**	Unknown	AY598664	AY598664	AY598664	AB108011	EF408883
P. okanoganense	**CBS 315.81**	*Triticum aestivum*	AY598649	AY598649	AY598649	KJ595373	KJ595498
P. oligandrum	**CBS 382.34 (VdPN)**	*Viola* sp.	AY598618	AY598618	AY598618	KJ595381	KJ595505
P. oopapillum	**CBS 124053**	*Cucumis sativus*	N/A	FJ655174	FJ655174	KJ595431	KJ595556
P. ornacarpum	**CBS 112350**	Soil	HQ643721	HQ643721	HQ643721	KJ595411	KJ595535
P. ornamentatum	CBS 122665	Soil	N/A	HQ643722	HQ665117	KJ595428	KJ595552
P. orthogonon	**CBS 376.72**	*Zea mays*	AY598710	AY598710	HQ665221	KJ595379	KJ595503
P. ostracodes	**CBS 768.73 (VdPN)**	Soil	AY598663	AY598663	AY598663	AB690668	EF408880
P. pachycaule	**CBS 227.88**	Soil	AY598687	AY598687	HQ665169	KJ595362	KJ595487
P. paddicum	CBS 698.83	*Triticum* and *Hordeum*	AY598707	AY598707	AY598707	JX397982	JX397968
P. paroecandrum	**CBS 157.64 (VdPN)**	Soil	AY598644	AY598644	AY598644	DQ071391	DQ071332
P. parvum	**CBS 225.88**	Soil	AY598697	AY598697	AY598697	AB362322	KJ595445
P. pectinolyticum	**CBS 122643**	Soil	HQ643739	HQ643739	HQ643739	N/A	KJ595469
P. periilum	**CBS 169.68 (VdPN)**	Soil	AY598683	AY598683	HQ665141	N/A	KJ595444
P. periplocum	**CBS 289.31**	*Citrullus vulgaris*	AY598670	AY598670	AY598670	KJ595369	KJ595494
P. perplexum	CBS 674.85	*Vicia faba*	AY598658	AY598658	AY598658	KJ595395	KJ595519
P. phragmitis	**CBS 117104**	Soil (*Phragmites australis*)	HQ643746	HQ643746	HQ665081	AJ890351	EU152854
P. pleroticum	CBS 776.81	*Nymphyoides peltata*	AY598642	AY598642	AY598642	AB362321	KJ595461
P. plurisporium	**CBS 100530**	*Agrostis*	AY598684	AY598684	AY598684	KJ595405	KJ595529
P. polare	**CBS 118203**	*Sanionia uncinata*	KJ716858	AB299390	KJ716859	KJ595417	KJ595542
P. polymastum	**CBS 811.70 (VdPN)**	*Lactuca sativa*	AY598660	AY598660	AY598660	KJ595403	KJ595527
P. porphyrae	**CBS 369.79 (VdPN)**	*Porphyra yezoensis*	AY598673	AY598673	AY598673	KJ595377	KJ595501
P. prolatum	**CBS 845.68**	*Rhododendron* sp.	AY598652	AY598652	AY598652	AB362330	KJ595462
P. pyrilobum	**CBS 158.64**	*Pinus radiata*	AY598636	AY598636	AY598636	KJ595349	KJ595477
P. radiosum	**CBS 217.94**	Soil	N/A	AY598695	HQ665156	KJ595356	N/A
P. recalcitrans	**CBS 122440**	Soil (*Vitis vinifera*)	N/A	DQ357833	KJ716861	KJ595423	EF195143
P. rhizo-oryzae	**CBS 119169**	Soil	HQ643757	HQ643757	HQ643757	KJ595420	KJ595545
P. rhizosaccharum	**CBS 112356**	Soil (*Saccharum officinarum*)	N/A	HQ643760	HQ665072	AB362323	KJ595463

Table 19 (continued)

Species	Isolate	Host	GenBank accession numbers				
			SSU	ITS	LSU	*cox2*	β- tubulin
P. rostratifingens	**CBS 115464**	Soil (*Malus* sp.)	HQ643761	HQ643761	HQ643761	KJ595416	KJ595541
P. rostratum	**CBS 533.74**	Soil	AY598696	AY598696	AY598696	KJ595388	KJ595512
P. salpingophorum	**CBS 471.50 (VdPN)**	*Lupinus angustifolius*	AY598630	AY598630	AY598630	KJ595384	KJ595508
P. schmitthenneri	**CBS 129726**	*Glycine max*	N/A	JF836869	KJ716862	JF895530	KJ595470
P. scleroteichum	**CBS 294.37 (AUTH)**	*Ipomoea batatas*	AY598680	AY598680	AY598680	KJ595370	KJ595495
P. segnitium	**CBS 112354**	Soil	HQ643772	HQ643772	HQ643772	KJ595412	KJ595537
P. selbyi	**CBS 129728**	*Zea mays*	N/A	JF836871	KJ716863	JF895532	KJ595471
P. senticosum	**CBS 122490**	Soil (forest)	HQ643773	HQ643773	HQ643773	AB362317	KJ595467
P. solare	**CBS 119359**	*Phaseolus vulgaris*	N/A	EF688275	KJ716860	KJ595421	KJ595546
P. sp.	CBS 113341	Soil	KF853244	KF853244	KF853244	KJ595414	KJ595539
P. sp. *"jasmonium"*	CBS 101876	*Arabidopsis thaliana*	HQ643778	HQ643778	HQ643778	KJ595406	KJ595530
P. sp. rooibos 2	STE-U 7549	*Aspalathus linearis*	N/A	JQ412770	KJ716867	JQ412783	JQ412807
P. sp. rooibos 2	STE-U 7550	*Aspalathus linearis*	N/A	JQ412777	N/A	JQ412813	JQ412789
P. spiculum	**CBS 122645**	Soil (*Vitis* sp.)	KF853242	KF853242	KF853242	KJ595425	KJ595549
P. spinosum	**CBS 275.67 (VdPN)**	Compost	AY598701	AY598701	AY598701	KJ595366	KJ595491
P. splendens	**CBS 462.48 (VdPN)**	Unknown	AY598655	AY598655	AY598655	AB512921	AB512852
P. stipitatum	DAOM 240293	Soil	N/A	KJ716866	KJ716866	KJ595437	KJ595560
P. sukuiense	**CBS 110030**	Soil	N/A	HQ643836	HQ665059	KJ595408	KJ595532
P. sulcatum	**CBS 603.73**	*Daucus carota*	AY598682	AY598682	HQ665281	KJ595393	KJ595517
P. sylvaticum	**CBS 453.67**	Soil	AY598645	AY598645	AY598645	KJ595383	KJ595507
P. takayamanum	**CBS 122491**	Soil	HQ643854	HQ643854	HQ643854	AB362315	KJ595468
P. tardicrescens	LEV1534	Turf grass	N/A	HQ643855	HQ643855	KJ595439	KJ595562
P. torulosum	**CBS 316.33 (VdPN)**	Grass	AY598624	AY598624	AY598624	KJ595374	KJ595499
P. tracheiphilum	**CBS 323.65**	*Lactuca sativa*	N/A	AY598677	HQ665207	KJ595375	N/A
P. ultimum* var. *sporangiiferum	**CBS 219.65**	*Chenopodium album*	AKYB02045405	AY598656	AY598656	KJ595357	KJ595482
P. ultimum* var. *ultimum	**CBS 398.51**	*Lepidium sativum*	AY598657	AY598657	AY598657	KJ595382	KJ595506
P. uncinulatum	**CBS 518.77**	*Lactuca sativa*	AY598712	AY598712	AY598712	KJ595385	KJ595509
P. undulatum	**CBS 157.69 (VdPN)**	Soil (*Pinus* sp.)	AY598708	AY598708	AY598708	KJ595348	KJ595476
P. vanterpoolii	**CBS 295.37**	*Triticum aestivum*	AY598685	AY598685	AY598685	KJ595371	KJ595496
P. vexans	**CBS 119.80 (VdPN)**	Soil	HQ643400	HQ643400	HQ643400	GU133518	EF426556
P. viniferum	**CBS 119168**	Soil (*Vitis* sp.)	HQ643956	HQ643956	HQ643956	KJ595419	KJ595544
P. violae	CBS 132.37	*Viola tricolor*	AY598717	AY598717	AY598717	KJ595345	KJ595473
P. violae	**CBS 159.64 (VdPN)**	Soil	AY598706	AY598706	AY598706	JX397980	JX397966

Table 19 (continued)

Species	Isolate	Host	GenBank accession numbers				
			SSU	ITS	LSU	*cox2*	β- tubulin
P. violae	CBS 178.86	*Daucus carota*	AY598715	AY598715	HQ665143	KJ595353	N/A
P. volutum	CBS 699.83	*Triticum* and *Hordeum*	AY598686	AY598686	AY598686	KJ595397	KJ595521
P. zingiberis	CBS 216.82	*Zingiber mioga*	N/A	AY598679	HQ665155	N/A	N/A

Species names of type strains (including ex-type, type, neotype, holotype, isotype, and paratype material), authentic strains (AUTH), and strains used by Van der Plaats-Niterink (1981) for descriptions (VdPN) are indicated in bold. Details regarding amplification and sequencing are included in GenBank records for sequence data generated *de novo* for this analysis

generated by Lévesque and de Cock (2004) and Robideau et al. (2011) are excellent resources. Using only the ITS region would more often than not allow suitably accurate species identification, but some species are indistinguishable using ITS and require *cox1* sequences for further identification (see Text S1A of Robideau et al. 2011). Several other species are indistinguishable even when both ITS and *cox1* sequences are compared (see Text S1B of Robideau et al. 2011), and many of these should probably be formally synonymized pending more thorough investigations with multiple hypervariable genes. This approach should also resolve species complexes found in the group formed by *P. irregulare*, *P. paroecandrum*, *P. cylindrosporum*, *P. cryptoirregulare* and *P. mamillatum* (Barr et al. 1997; Matsumoto et al. 2000; Garzón et al. 2007; Spies et al. 2011a), the varieties of *P. ultimum* (Barr et al. 1996), and the *P. vexans* and *P. cucurbitacearum* group (Spies et al. 2011b). Some species epithets have been applied to multiple phylogenetic species due to imprecise species descriptions and/or misidentifications. Examples of these include *P. iwayamai*, *P. okanoganense* and *P. violae* (Lévesque and de Cock 2004; McLeod et al. 2009; Bahramisharif et al. 2013). Mislabelling or contamination of reference strains and/or data cause similar problems, as illustrated by the case of *P. terrestre* (published as "*terrestris*") of which the holotype strain ITS sequence published with the description suggests phylogenetic placement in clade E (Paul 2002), while the ITS and *cox1* sequences generated for the ex-type strain available from the Centraal Bureau voor Schimmelcultures (CBS) suggests phylogenetic placement in clade F (Robideau et al. 2011). Species identification within genetically diverse species complexes (see Text S1C of Robideau et al. 2011 for a partial list) can also be tricky, more due to uncertain species boundaries than due to the ineffectiveness of ITS and/or *cox1* as barcoding regions. The onus is on the investigator to keep such issues in mind when identifying strains to the species level and to consider the identification in context of the taxonomic history of the species and its closest relatives.

Molecular phylogeny

The first molecular phylogenies of *Pythium* were inferred from sequences of the 28S, ITS, and *cox2* regions respectively, and although each analysis included only a few species, the observed variation merited speculation regarding the polyphyletic nature of *Pythium* at least for the ITS and 28S phylogenies (Briard et al. 1995; Cooke et al. 2000; Martin 2000). The first study to provide an extensive DNA sequence based phylogeny of *Pythium* was that of Lévesque and de Cock (2004) who sequenced the 28S region of 51 species and complete ITS region (ITS1-5.8S rRNA-ITS2) region of 116 species. Although a two-marker phylogeny of the ITS-28S region was presented by

Lévesque and de Cock (2004), these markers are adjacent multi-copy markers that might not accurately represent the evolutionary relationships in *Pythium*. Villa et al. (2006) used multiple markers (ITS, *cox2*, β-tubulin) in individual phylogenetic analyses with 39 species and confirmed previous suggestions of an intermediate evolutionary position of clade K species between *Pythium* and *Phytophthora*, but also suggested that clade H species (represented by *Phytophthora undulata* ≡ *Pythium undulatum*) occupy a similar intermediate position, which contrasted the position of this clade nestled among clades E, F, G, I, and J as suggested by Lévesque and de Cock (2004). The multi-marker phylogeny (18S-ITS-28S, *cox2* and β-tubulin) of 152 *Pythium* species and some related taxa presented here confirms the association of clade K with *Phytophthora*, but fails to provide support for the evolutionary association of clade H with any of the other recognized groups within *Pythium* (Fig. 21). Furthermore, organisms such as the obligate root pathogen *Lagena radicicola* and strains resembling *Lagenidium* form an unresolved cluster of taxa related to clade C (Fig. 21). In itself this phylogenetic placement of the genus *Lagena* necessitates a further taxonomic revision of the genus *Pythium* that can only be achieved once the internal nodes of the *Pythium* phylogeny have been resolved with support. Despite the fact that the phylogeny in Fig. 21 represents the most extensive sampling of taxa and genetic markers in a multi-marker phylogeny of *Pythium* to date, it still fails to achieve this goal. Phylogenetic markers additional or alternative to those currently used in *Pythium* systematics are needed to resolve these issues and elucidate taxon boundaries.

Recommended genetic markers

- The 18S (small subunit, SSU) and 28S (large subunit, LSU) nuclear rRNA genes–generic level phylogenies within *Pythium s.l.*
- The internal transcribed spacers (ITS including ITS1, 5.8S rRNA, and ITS2), cytochrome c oxidase subunit 2 (*cox2*)–sub-generic, inter- and intra-specific level phylogenies
- ITS and *cox1*–non-phylogenetic species identification

Mitochondrial regions such as *cox1* and *cox2* should be used with consideration of the fact that they mainly reflect evolution of maternal lineages and can produce incongruent phylogenies. This is especially true for *cox1*, which is why this region was not included in Fig. 21. The β-tubulin region has also been used to a limited extent in *Pythium* phylogenies (Villa et al. 2006; Belbahri et al. 2008; Spies et al. 2011a, b). Although this region fails to resolve *Pythium* into the genera observed when using the dataset from Fig. 21 (data not shown) and has limited power in resolving species-level phylogenies (Spies et al. 2011a, b), it amplifies and sequences well for most *Pythium* species and is an easy resource for use in concatenated datasets (e.g. Bahramisharif et al. 2013; Fig. 21).

Pyrenophora

Background

Pyrenophora represents a genus of plant pathogenic fungi associated with a wide variety of substrates. Fries (1849) list the genus as *Pyrenophora* typified with *Pyrenophora phaeocomes*. The genus *Pyrenophora* clusters in the suborder Pleosporineae of the family *Pleosporaceae* (Berbee 1996; Zhang and Berbee 2001; Hyde et al. 2013a, b; Zhang et al. 2012; Ariyawansa et al. 2014). Recent studies using multigene analysis and some coupled with morphology have provided the groundwork for classification of species in *Pyrenophora* (Berbee 1996; Zhang and Berbee 2001; Hyde et al. 2013a, b; Zhang et al. 2012).

Pyrenophora has been linked to asexual morphs in *Drechslera. Pyrenophora* species are important plant pathogens as well as saprobes. Many species cause disease on their graminicolous hosts and are usually present in their asexual state (*Drechslera*) (Zhang and Berbee 2001). Species of *Pyrenophora* are serious plant pathogens (Zhang and Berbee 2001). *Pyrenophora teres* (*Drechslera teres*) is a necrotrophic pathogen of economically important crops, such as barley (Gupta and Loughman 2001; Kingsland 1991). *Pyrenophora graminea* (*Drechslera graminea*) causes barley stripe resulting in significant yield losses (Tekauz 1983, 1990). *Pyrenophora graminea* lives within barley kernels as mycelium, and when seeds germinate, hyphae enter the seedling through the coleorrhiza, causing a systemic infection (Platenkamp 1976; Porta-Puglia et al. 1986). *Pyrenophora tritici-repentis* causes tan spot of wheat (Lamari and Bernier 1989) which occurs in all the major wheat-growing areas of the world and causes 3 to 50 % yield losses (Ballance et al. 1996). Its prevalence has increased recently.

Some *Pyrenophora* species have been used as biocontrol agents. *Bromus tectorum* is a dominant winter annual weed in cold deserts of the western United States (Meyer et al. 2007). Together with other annual brome grasses it has invaded many ecosystems of the western United States creating near-monocultures in which the native vegetation cannot compete (Meyer et al. 2007). *Pyrenophora semeniperda* has be used as a biocontrol agent to kill the dormant seeds of *Bromus tectorum* (Meyer et al. 2007). Several studies have assessed chemical production by *Pyrenophora* species. A new phytotoxic sesquiterpenoid penta-2,4-dienoic acid (pyrenophoric acid) was isolated from solid wheat seed culture of *P. semeniperda*.

Species identification and numbers

Pyrenophora is characterized by immersed, erumpent to nearly superficial ascomata, indefinite pseudoparaphyses, clavate to saccate asci usually with a large apical ring, and muriform terete ascospores. Morphologically, the terete ascospores of *Pyrenophora* can be easily distinguished from *Clathrospora* and *Platyspora*. The indefinite pseudoparaphyses and smaller ascospores of *Pyrenophora* can be clearly separated from those of *Pleospora* (Sivanesan 1984). *Pyrenophora* species can easy be distinguished from species in *Cochliobolus* and *Setosphaeria* on the basis of the shape, septation and colour of the ascospores (Zhang and Berbee 2001). *Drechslera* species were initially categorized in *Helminthosporium* on the basis of their dark colour, transversely septate conidia and a graminicolous habitat (Shoemaker 1959). Consequently, graminicolous *Helminthosporium* species were segregated into three genera, *Bipolaris, Drechslera*, and *Exserohilum,* defined based on their association with their sexual states *Cochliobolus, Pyrenophora*, or *Setosphaeria*, respectively (Zhang and Berbee 2001). Currently 198 species of *Pyrenophora* and 135 species of *Drechslera* are listed in Index Fungorum (2014).

Molecular phylogeny

Rapid identification of diseases caused by *Pyrenophora* has been determined via different DNA markers. Identification of molecular genetic markers in *Pyrenophora teres* f. *teres* associated with low virulence on 'Harbin' barley was assessed by random amplified polymorphic DNA (RAPD) (Weiland et al. 1999) and five RAPD markers were obtained that were associated in coupling with low virulence. The data suggested that the RAPD technique can be used to tag genetic determinants for virulence in *P. teres* f. *teres* (Weiland et al. 1999). Specific polymerase chain reaction (PCR) primers were developed from amplified fragment length polymorphism (AFLP) fragments of *P. teres*, in order to distinguish the two forms, *P. teres* f. *teres* (which cause net form blotch on barley leaves) and *P. teres* f. *maculata* (which causes spot form); the two forms are morphologically very similar in culture (Leisova et al. 2005). The PCR assay was certified with 60 samples of *Pyrenophora* species. The amplification with four designed PCR primer pairs provided *P. teres* form-specific products. No cross-reaction was observed with DNA of several other species, such as *P. tritici-repentis* and *P. graminea* (Leisova et al. 2005). *Pyrenophora graminea* is the causal agent of barley leaf stripe disease (Mokrani et al. 2012). Two leaf stripe isolates PgSy3 (exhibiting high virulence on the barley cultivar 'Arabi Abiad') and PgSy1 (exhibiting low virulence on Arabi Abiad), were mated and 63 progeny were isolated and phenotyped for the reaction on Arabi Abiad (Mokrani et al. 2012). From 96 AFLP markers, three AFLP markers, E37M50-400, E35M59-100 and E38M47-800 were linked to the virulence locus VHv1 in isolate PgSy3. Lubna et al. (2012) suggested that the three markers are closely linked to VHv1 and are unique to isolates carrying the virulence locus. Pecchia et al. (1998) developed an efficient PCR protocol for amplification of the IGS region in *P. graminea* and to characterize this region by restriction fragment analysis. During the study based on the length of the IGS-PCR product, ca. 3.8 or 4.4 kb, two groups of isolates were identified from six cultures i.e. I3/88 (Italy; CBS 100862), I7/88 (Italy; CBS100861), 60/93 (Austria; CBS 100866), I10/95 (Tunisia; CBS 100863), I28/95 (Tunisia; CBS 100864), I33/95 (Tunisia; CBS 100865). The RFLP patterns of isolates obtained with the 6-base cutting enzymes *ApaI*, *BglII*, *DraI*, *EcoRV*, *HindIII* and *SacI* were similar within each group and different between the two groups (Pecchia et al. 1998). Restriction patterns of IGS-PCR products digested with the 4-base cutting enzyme *AluI* were polymorphic among isolates in spite of their IGS-PCR product length (Pecchia et al. 1998).

Molecular studies of *Pyrenophora*/*Drechslera* species have detailed the taxonomic placement of the genus. Initially the 18S rRNA gene was used for the classification of *Pyrenophora*/*Drechslera* and related genera (Berbee 1996). Phylogenetic analysis based on 18S rRNA showed *Pyrenophora* to cluster within the *Pleosporaceae* (Zhang and Berbee 2001) rather than in *Pyrenophoraceae* (Zhang and Berbee 2001). Later, phylogenetic analysis of the ITS and *gdp* data showed that *Pyrenophora* is monophyletic (Zhang and Berbee 2001), and the asexual state *Drechslera* clustered with their predicted sexual relatives (Table 20, Fig. 22).

Recommended genetic markers

- Large small subunits of nrDNA (LSU)–generic level
- ITS and *gdp*–inter-specific delineation

Based on our phylogeny, we observed that *gdp* gives high resolution compared to ITS and LSU, such that it can be readily used to determine the placement of *Pyrenophora* species.

Puccinia

Background

Puccinia is the type genus of the family *Pucciniaceae* in the order of rust fungi, *Pucciniales* (Basidiomycota). *Puccinia* has approximately 4,000 named species (Kirk et al. 2008), and is a widespread genus of plant pathogens that has shaped history. For example, *Puccinia graminis*, the type species of *Puccinia*,

Table 20 *Pyrenophora*. Details of the isolates used in the phylogenetic tree

Species	Isolate	GenBank accession numbers		
		ITS	LSU	GPDH
Drechslera andersenii	**CBS 258.80**	AY004804		AY004835
D. andersenii	**CBS 967.87**	AY004805		
D. andersenii	**DAOM 229292**	JN943646	JN940084	
D. avenae	**CBS 189.29**	AY004795		AY004827
D. avenae	**CBS 279.31**	AY004796		AY004828
D. biseptata	**DAOM 208987**	AY004786		AY004817
D. biseptata	**CBS 308.69**	JN712464	JN712530	AY004819
D. biseptata	**CBS 599.7**	AY004787		AY004818
D. biseptata	**CBS 108940**	AY004788		
D. campanulata	**BRIP15927**	AF163058		
D. catenaria	**DAOM 63665A**	AY004802		AY004833
D. catenaria	**CBS 191.29**	AY004803		AY004834
D. dactylidis	**DAOM 92161**	AY004781		AY004812
D. dematioidea	**CBS 108963**	AY004789	JN712532	AY004820
D. dematioidea	**DAOM 229295**	JN943648	JN940094	
D. dematioidea	**CBS 108962**	JN712465	JN712531	
D.dematioidea	**CBS 108962**	AY004790	JN712531	AY004821
Drechslera dictyoides	**DAOM 63666**	AY004806	JN940080	AY004836
D. erythrospila	**CBS 108941**	AY004782		AY004813
D. erythrospila	**DAOM 55122**	AY004783		AY004814
D. fugax	**CBS 509.77**	AY004791		AY004822
D.nobleae	**CBS 259.80**	AY004792		AY004823
D. nobleae	**DAOM 229296**	JN943647	JN940095	
D. nobleae	**CBS 966.87**	AY004793		AY004824
D. nobleae	**CBS 316.69**	AY004794		AY004825
D. phlei	**CBS 315.69**	AY004807		AY004837
D. phlei	**DAOM 225627**	JN943656	JN940077	
D. poae	**DAOM 145373**	AY004801	JN940082	AY004832
D. poae	**DAOM 169240**	JN943651		
D. siccans	**DAOM 115701**	AY004797	JN940078	
D. siccans	**DAOM 115702**	AY004799		
***Drechslera* sp.**	**DAOM126766**	AY004800		AY004831
***Drechslera* sp.**	**DAOM126772**	AY004784		AY004815
***Drechslera* sp**	**CBS313.69**	AY004785		AY004816
D. triseptata	**NZ6120**	AF163059		
Pleospora herbarum	**CBS 191.86***	DQ491516	DQ247804	AY316969
Pyrenophora bromi	**DAOM 127414**	AY004809	JN940074	AY004839
P. chaetomioides	**DAOM 208989**	AF081445	JN940091	AF081371
P. dictyoides	**DAOM 75616**	JN943654	JN940079	
P. japonica	**DAOM 169286**	AF071347		AF081369
P. lolii	**CBS 318.69**	AY004798		AY004829
P. phaeocomes	**DAOM 222769**	JN943649	DQ499596	
P. semeniperda	**DAOM 213153**	AF081446	JN940089	AY004826
P. tetrarrhenae	**DAOM 171966**	JN943663	JN940090	
P. tritici-repentis	**DAOM 226213**	JN943670	AY544672	AF081370
P. tritici-repentis	**DAOM 208990**	AF071348	JN940071	AY004838
P. tritici-repentis	**DAOM 107224**	AY004808	DQ384097	
P. graminea	**11**	Y10748		
P. teres	**PM2**	Y08746		AY004830

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

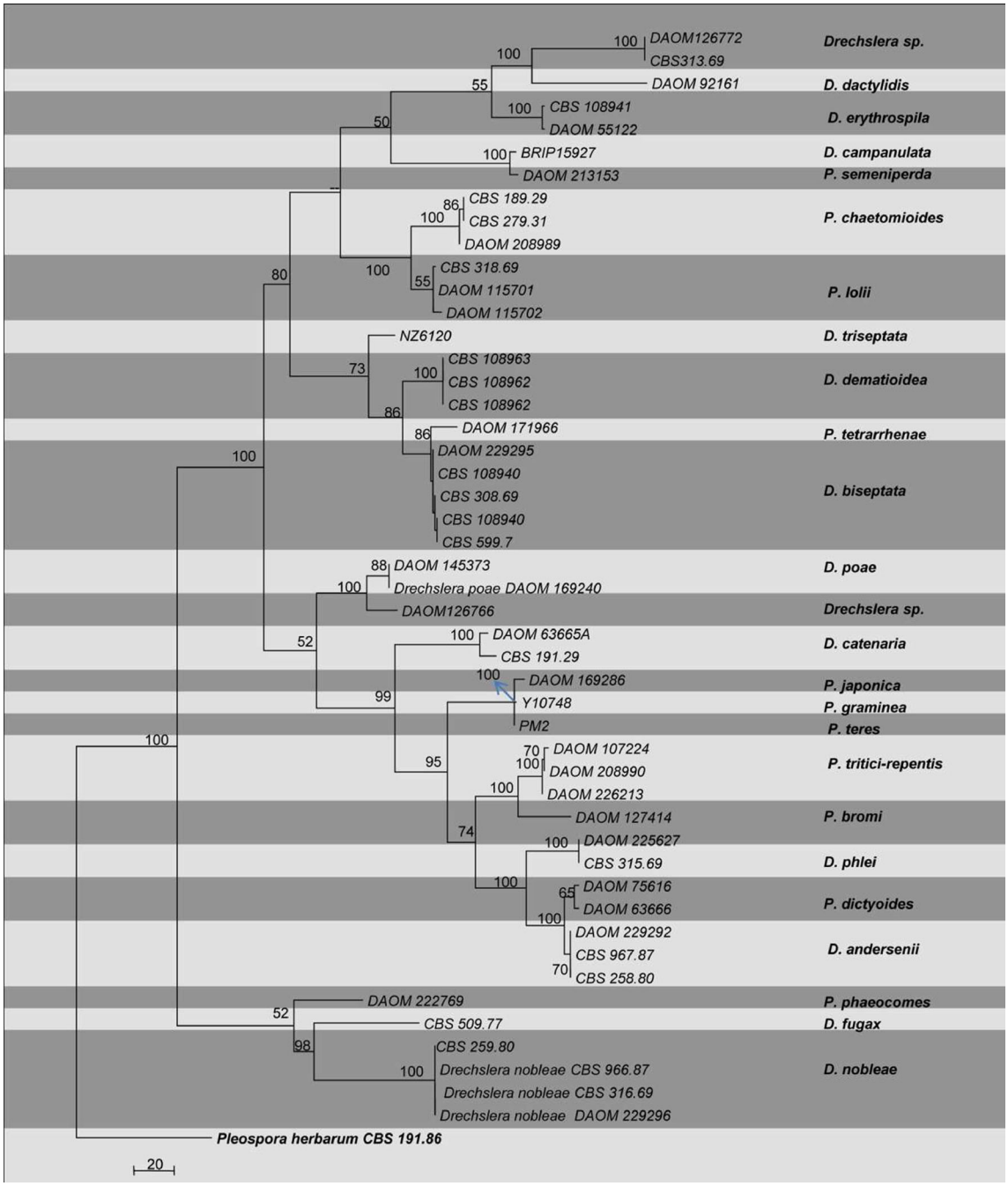


Fig. 22 Phylogram generated from parsimony analysis based on combined of ITS, *gdp* and LSU sequenced data of *Pyrenophora*. Parsimony bootstrap support values greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*. The tree is rooted with *Pleospora herbarum* CBS 276.37

was investigated as a biological warfare agent in the cold war (Line and Griffith 2001). It was the impetus for breeding wheat cultivars resistant to disease that started the Green Revolution, lead by 1970 Nobel Laureate, Norman Borlaug (Zeyen et al. 2014). Epidemics of stem rust of wheat caused by *P. graminis* remain a threat with the emergence of races such as Ug99 (Singh et al. 2011). Other species of *Puccinia* are also serious pathogens of grasses (*Poaceae*), including *P. coronata* and *P. striiformis* (Kirk et al. 2008). Rusts of *Asteraceae*, e.g., *P. helianthi*, and rusts of *Fabaceae* in the closely related genus *Uromyces*, e.g., *U. viciae-fabae*, *U. appendiculatus* and *U. ciceris-arietini*, are important pathogens of cultivated fodder and food crops.

Among the ca. 120 to 160 genera of rust fungi (Cummins and Hiratsuka 2003; Kirk et al. 2008), *Puccinia* is readily recognized by the two-celled teliospores and the shape of

the spermogonia (Cummins and Hiratsuka 2003). *Uromyces* with one-celled teliospores is typically differentiated from *Puccinia*, although some species of *Puccinia* have both one-celled (mesospores) and two-celled teliospores, e.g., *P. lagenophorae*. Teliospore morphology is homoplasious, and *Puccinia* and *Uromyces* were polyphyletic in systematic studies based on the LSU and SSU regions of nuclear ribosomal DNA (Maier et al. 2007; Aime 2006), and the two nuclear genes: elongation factor and β- tubulin (Van der Merwe et al. 2007). Some rust fungi have teliospores morphologically similar to *Puccinia*, but are not closely related or have an uncertain systematic position. For example, *Allodus podophylli* has two-celled teliospores convergent with *Puccinia*. A systematic analysis based on the nLSU and nSSU regions of rDNA determined *Allodus* and *Puccinia* were unrelated (Minnis et al. 2012). *Puccinia psidii*, which spread from South America to much of the Pacific region and South Africa, now infects 30 genera of Myrtaceae out of its natural host range (Pegg et al. 2013). It has two-celled teliospores, but its placement within the *Pucciniales* is unknown. Phylogenetic analyses of the nLSU and nSSU (Pegg et al. 2013) and the protein coding gene beta-tubulin (Van Der Merwe et al. 2008) indicated that *P. psidii* was sister to the *Pucciniaceae*. Several families and genera of rust fungi are polyphyletic, namely the *Raveneliaceae*, *Phakopsoraceae* and *Pucciniaceae*. These polyphyletic families and genera await resolution by molecular phylogenetic analyses.

Species identification and numbers

Rust fungi are usually considered host specific (Cummins and Hiratsuka 2003), although some, e.g., *Puccinia psidii* and *P. lagenophorae*, infect multiple host genera (McTaggart et al. 2014; Pegg et al. 2013). Some species of rust fungi are heteroecious, requiring two hosts in different families to complete their life cycle, e.g., *P. graminis* on *Triticum* (*Poaceae*) and *Berberis* (*Berberidaceae*).

Rust fungi have a complicated life cycle with up to five spore states (Cummins and Hiratsuka 2003). Consequently, up to three names have been proposed for the same taxon based on different life cycle stages. To add to the confusion, there are two systems of terminology that describe these spore states, one based on morphology (Laundon 1967), and the other on ontogeny (Arthur and Kern 1926; Cummins and Hiratsuka 2003; Hiratsuka 1973). These systems of terminology were summarised by Hennen and Hennen (2000).

Species of rust fungi are often identified on the basis of their host specificity, and monographs were organised by plant family (Sydow and Sydow 1904; McAlpine 1906; Cummins 1971, 1978). Morphological characters of the teliospores and urediniospores, such as size, apex shape and wall thickness, ornamentation, and germ pore position and number, are useful for species identification.

Molecular diagnostic tools have been developed for some species of *Puccinia* based on the ITS region of rDNA, e.g., *P. coronata* (Beirn et al. 2011; Pfunder et al. 2001), *P. kuehnii* (Glynn et al. 2010) and *P. psidii* (Langrell et al. 2008). The ITS region has successfully distinguished phylogenetic species in *Uromyces* (Barilli et al. 2011) and it was used in combination with TEF to resolve the taxonomy of *P. melampodii* (Seier et al. 2009). However, the ITS region was polymorphic in *Puccinia lagenophorae* (Littlefield et al. 2005; Scholler et al. 2011), and Morin et al. (2009) discovered a paralagous copy of the ITS region, which may have resulted from a hybridization event. A paralagous copy of the ITS region was also reported in *P. kuehnii* in the study by Virtudazo et al. (2001). Polymorphisms and paralogous copies are caveats for studies based on the ITS region in rust fungi.

Molecular phylogeny

Large-scale systematic studies of rust fungi have focused mainly on the SSU and LSU regions of rDNA (Aime 2006; Beenken et al. 2012; Dixon et al. 2010; Maier et al. 2003, 2007; Minnis et al. 2012; Wingfield et al. 2004; Yun et al. 2011) (Table 21). Protein coding genes such as beta-tubulin (Morin et al. 2009; Van der Merwe et al. 2007, 2008) and elongation factor (TEF) (Seier et al. 2009; Van der Merwe et al. 2007) were successfully used at the family, genus and species level in rust fungi, although beta-tubulin required cloning rather than direct sequencing of PCR product. Liu et al. (2013) included ITS, beta-tubulin, ribosomal polymerase subunit 2 (RPB2) and cytochrome c oxidase subunit 1 (COI) in a systematic study to resolve the *P. coronata* species complex. They discussed the difficulty of PCR amplification of older herbarium specimens, and that DNA repair was successful in some cases. Vialle et al. (2009) compared mitochondrial genes to rDNA markers in two genera of rusts, *Chrysomyxa* and *Melampsora*. They found rDNA had better species resolution than mitochondrial genes. Mitochondrial genes were since used in studies of the genera *Chrysomyxa* (Feau et al. 2011) and *Dasyspora* (Beenken et al. 2012), but have not yet been used for *Puccinia*.

Recommended genetic markers

- The large subunit of nrDNA (LSU)–is useful for genus and species level identification of all rust fungi
- The internal transcribed spacer (ITS)–is useful for species level identification, but may contain polymorphic sites and paralagous copies. Rust specific primers are recommended.

Rusts are obligate biotrophs and difficult to maintain in pure culture, which has posed a challenge for DNA extraction

Table 21 *Puccinia*. Details of the isolates used in the phylogenetic tree

Species	Isolate	Host	GenBank accession no.	
			LSU	SSU
Aecidium kalanchoe	BPI 843633	*Kalanchoe blossfeldiana*	AY463163	DQ354524
Allodus podophylli	BPI 842277	*Podophyllum peltatum*	DQ354543	DQ354544
Caeoma torreyae	ECS 553	*Torreya californica*	AF522183	AY123284
Cumminsiella mirabilissima	BPI 871101	*Mahonia aquifolium*	DQ354531	DQ354530
Helicobasidium purpureum	CBS324.47	Not provided	AY885168	D85648
Dietelia portoricensis	BPI 844288	*Mikania micrantha*	DQ354516	AY125414
Miyagia pseudosphaeria	BPI 842230	*Sonchus oleraceus*	DQ354517	AY125411
Pileolaria toxicodendri	BPI 871761	*Toxicodendron* sp.	DQ323924	AY123314
Prospodium lippiae	BPI 843901	*Aloysia plystachya*	DQ354555	DQ831024
P. tuberculatum	BRIP 57630	*Lantana camara*	KJ396195	KJ396196
Puccinia caricis	BPI 871515	*Grossularia* sp.	DQ354514	DQ354515
P. convolvuli	BPI 871465	*Calystegia sepium*	DQ354512	DQ354511
P. coronata		*Rhamnus cathartica*	DQ354526	DQ354525
P. dampierae	BRIP 57724	*Dampiera linearis*	KF690688	NA
P. gilgiana	BRIP 57719	*Lechenaultia linarioides*	KF690691	NA
P. graminis	NA	Not provided	AF522177[9]	NA
P. haemodori	BRIP 56965	*Anigozanthus* sp.	KF690692	NA
P. hemerocallidis	BPI 843967	*Hemerocallis* sp.	DQ354519	DQ354518
P. hordei	BPI 871109	*Poaceae*	DQ354527	DQ415278
P. lagenophorae	BRIP 57563	*Emilia sonchifolia*	KF690696	NA
P. menthae	BPI 871110	*Cunila origanoides*	DQ354513	AY123315
P. psidii	BRIP 57991	*Melaleuca leucadendra*	KF318443	KF318455
P. poarum	NA	*Tussilago* sp.	DQ831028	DQ831029
P. polysora	BPI 863756	*Zea mays*	GU058024	NA
P. saccardoi	BRIP 57725	*Scaevola spinescens*	KF690701	NA
P. smilacis	BPI 871784	*Smilax rotundifolia*	DQ354533	DQ354532
P. stylidii	BRIP 60107	*Stylidium armeria*	KJ622214	NA
P. ursiniae	BRIP 57993	*Ursinia anthemoides*	KF690705	NA
P. violae	BPI 842321	*Viola cucullata*	DQ354509	DQ354508
P. xanthosiae	BRIP 57729	*Xanthosia rotundifolia*	KF690706	NA
Pucciniosira solani	NA	*Solanum aphyodendron*	EU851137	NA
Uromyces appendiculatus	NA	*Phaseolus vulgaris*	AY745704	DQ354510
U. ari-triphylli	BPI 871111	*Arisaena triphyllum*	DQ354529	DQ354528
U. scaevolae	BRIP 60113	*Selliera radicans*	KJ622213	NA
U. viciae-fabae	NA	*Pisum* sp.	AY745695	NA

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

(Aime 2006). This is reflected by the relatively few species of *Puccinia* represented in GenBank, for example, there are ~110 species of *Puccinia* represented by the ITS and LSU regions of rDNA. This is less than 3 % of the estimated 4,000 species of *Puccinia* (Kirk et al. 2008). Reliance on molecular identification for some species of *Puccinia* is not recommended. For example, McTaggart et al. (2014) determined that several species of *Puccinia* on different plant families in Australia had near-identical ITS and LSU rDNA sequences (Fig. 23 *Puccinia*).

Rhizopus

Background

Rhizopus is a genus of cosmopolitan saprotrophic fungi, currently included in the family *Rhizopodaceae* within the *Mucorales* (former Zygomycota; Hoffmann et al. 2013). Many *Rhizopus* species are common postharvest pathogens, causing fruit rots, and spoilage of crops, vegetables and wide range of stored foods (Pitt and Hocking 2009; Ray and Ravi

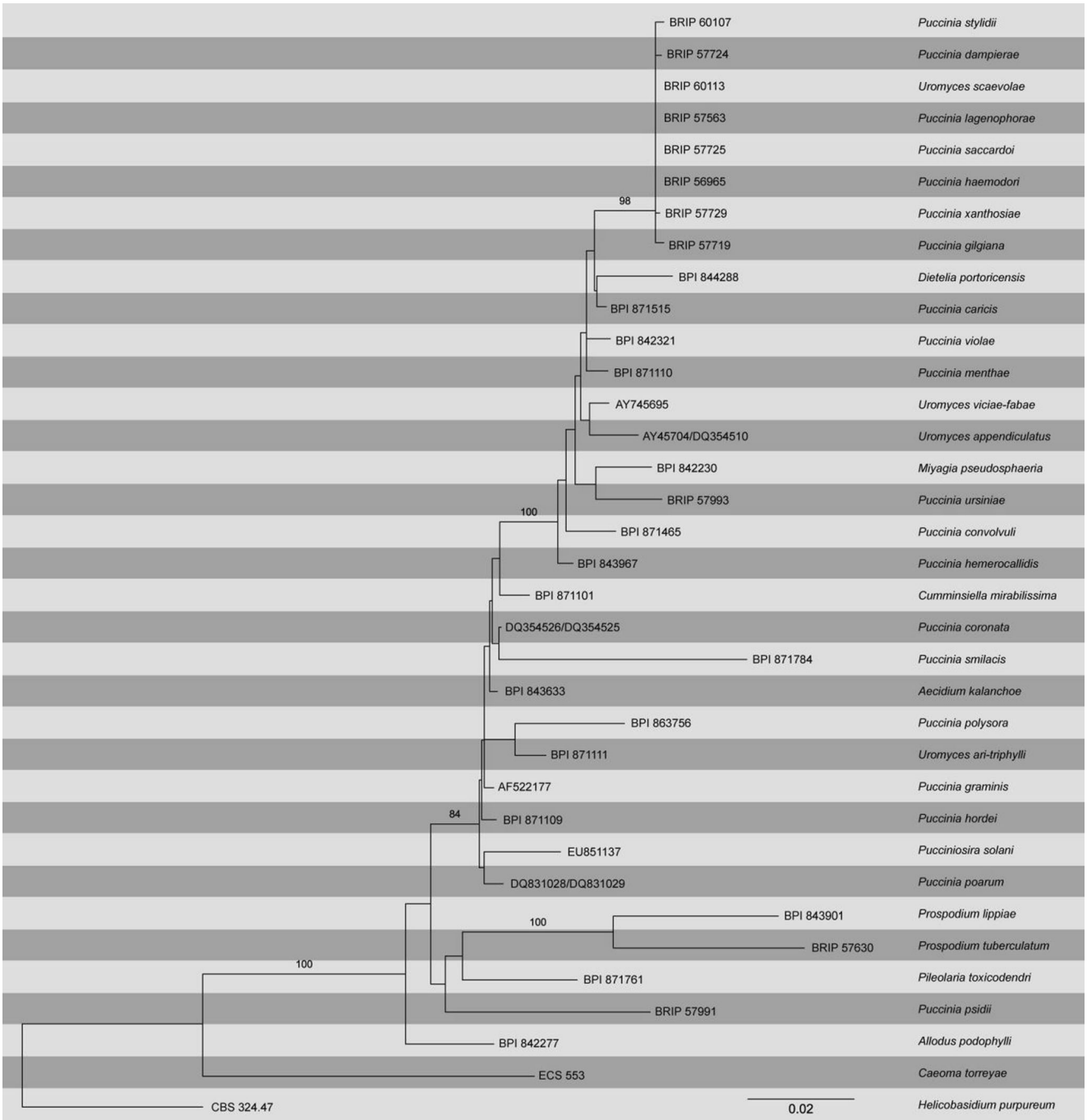


Fig. 23 *Puccinia*. Phylogram obtained from a ML search in RAxML with the SSU and LSU regions of nrDNA. Bootstrap values (≥70 %) from a ML search with 1,000 replicates above nodes; posterior probabilities (≥0.95) from Bayesian inference below nodes. *Puccinia* and *Uromyces* are polyphyletic, and genera such as *Cumminsiella*, *Dieteila*, *Miyagia* and *Pucciniosira* are paraphyletic. The LSU region is not sufficient to distinguish closely related taxa in Australia as seen in the *P. lagenophorae* clade

2005; Shtienberg 1997). Some species of this genus (e.g. *R. arrhizus, R. microsporus* and *R. stolonifer*) may also cause head rot disease in sunflowers (Yildirim et al. 2010). Among all *Rhizopus* species, *R. arrhizus* (syn. *R. oryzae*), and *R. stolonifer* are of particular importance, taking into account the frequency of isolation records (Farr and Rossman 2014). Extremely fast growth rates and abundant production of early maturing dry sporangiospores by *Rhizopus* species facilitate rapid spread of infection (Pitt and Hocking 2009). According to USDA Fungus-Host Database (Farr and Rossman 2014), *Rhizopus* species have been isolated from a wide range of plant taxa, both angiosperms and gymnosperms. Several members of the genus, among them *R. arrhizus* and *R. microsporus* are reported to cause human mucormycoses

(Pitt and Hocking 2009), mostly in immunocompromised patients (Roden et al. 2005; Pitt and Hocking 2009; Chakrabarti et al. 2010; Skiada et al. 2011). Nevertheless, *Rhizopus* species are used by humans. Fermentation process of several kinds of Asian food and beverage strongly depends on *Rhizopus* strains (Henkel 2005; Nout and Aidoo 2010).

Species identification and numbers

Identification of *Rhizopus* species was traditionally based on the complexity of rhizoids, the length of the sporangiophores and the size of the sporangia along with the ability to grow in certain temperatures. In their revision, Schipper and Stalpers (1984) recognized five species in three major complexes. Later several new species and varieties were described (e.g. Ellis 1985; Schipper and Samson 1994). Following a comprehensive morphological revision, Zheng et al. (2007) recognized ten species and seven varieties. Molecular analyses (Abe et al. 2006, 2010; Hoffmann et al. 2013; Walther et al. 2013) supported the three complexes defined by Schipper and Stalpers (1984), but revealed that *Rhizopus* is paraphyletic containing *Sporodiniella umbellata* and *Syzygites megalocarpus* (Hoffmann et al. 2013; Walther et al. 2013). Based on molecular phylogenetic analyses several species were recognized to represent synonyms: e.g. *Amylomyces rouxii* is now treated as synonymous with *R. arrhizus* (Abe et al. 2006), *R. reflexus* was recognized as a synonym of *R. lyococcus* (Liou et al. 2007), and *R. azygosporus* was revealed to be conspecific with *R. microsporus* (Abe et al. 2006). Dolatabadi et al. (2014b) showed that the morphologically defined varieties of *R. microsporus* are not recognized in multi-marker phylogenies and consequently they reduced the varieties to synonyms. Abe et al. (2007) revealed that strains of *R. arrhizus* (as *R. oryzae*) split into producers of lactic acid and producers of fumaric and malic acid and that these two groups were molecular phylogenetically distinct. As a consequence, the authors treated fumaric-malic acid producers as a separate species, *R. delemar*, formerly regarded as a variety by Zheng et al. (2007). Gryganskyi et al. (2010) supported this concept by molecular phylogenetic studies based on several markers including mating type genes. In agreement with the previous studies, Dolatabadi et al. (2014a) recognized two phylogenetic species. However, they treated them as varieties of a single biological species because of the formation of zygospores between strains of the *arrhizus*- and strains of the *delemar*-group, the lack of differences in morphology and ecology and the small genetic distance between the two groups compared to the remaining species in *Rhizopus*. Variety *tonkinensis*, a third variety besides var. *arrhizus* and var. *delemar,* was recognized morphologically (Zheng et al. 2007) and through the use of short tandem repeat motives of IGS rDNA sequences (Liu et al. 2008), but it has not come out as a separate lineage in molecular phylogenetic studies (Walther et al. 2013; Dolatabadi et al. 2014a) and is regarded as doubtful. Abe et al. (2010) consider *R. americanus* and *R. sexualis* as varieties of *R. stolonifer,* while other authors (e.g. Zheng et al. 2007) recognize them as separate species. However, the large genetic distances of the ITS region among these taxa (Walther et al. 2013) rather suggest separate species. In the ITS trees of Walther et al. (2013), the strains morphologically defined as *R. stolonifer* form two distinctly separated groups suggesting the existence of an undescribed species. Currently seven species are accepted in *Rhizopus*: *R. americanus*, *R. arrhizus* including var. *arrhizus* and var. *delemar*, R. *homothallicus*, R. *lyococcus*, *R. microsporus*, *R. sexualis*, and *R. stolonifer* (Table 22).

Molecular phylogeny

The marker of choice for species identification in the genus *Rhizopus* is the ITS region (Walther et al. 2013) that can also distinguish the two varieties of *R. arrhizus*: var. *arrhizus* and var. *delemar* (Fig. 24). For the three species *R. americanus*, *R. sexualis* and *R. stolonifer,* sequencing of the ITS is often hampered by extended poly-A- and poly-T-regions but the large subunit of the ribosomal DNA (LSU) can be sequenced for species identification in these cases because it can also resolve these species (Walther et al. 2013). In case of *R. americanus*, multiple different ITS sequences within one strain were found, which should be considered in molecular identification (Liu et al. 2007; Abe et al. 2010).

Several molecular markers have been applied for phylogenetic inference in this genus by using general fungal primers: actin (Abe et al. 2007, 2010; Dolatabadi et al. 2014a, b), ITS (Abe et al. 2006, 2007, 2010; Gryganskyi et al. 2010; Walther et al. 2013; Dolatabadi et al. 2014a, b), LSU (Abe et al. 2006; Liou et al. 2007; Walther et al. 2013; Dolatabadi et al. 2014a, b,), orotidine-5'-monophosphate decarboxylase gene (pyrG gene) (Liu et al. 2007), rpb1 (RNA polymerase II largest subunit gene) (Dolatabadi et al. 2014a), SSU (small subunit of the ribosomal DNA gene) (Abe et al. 2006), and tef (translation elongation factor gene) (Abe et al. 2007, 2010; Dolatabadi et al. 2014a, b). For *R. arrhizus* s.l., specific primers were designed for the rpb2 (RNA polymerase II second largest subunit gene) and the RNA helicase and the TP transporter gene of the mating locus by Gryganskyi et al. (2010) as well as for the lactate dehydrogenase B by Abe et al. (2007).

The tef marker cannot be recommended for phylogenetic studies because the gene is found in several different copies at least in *R. arrhizus;* these copies typically differ in the third base of numerous codons of this marker (Dolatabadi et al. 2014a). In the multi-marker study of Dolatabadi et al. (2014a), the rpb1 was the most variable gene.

Table 22 *Rhizopus*. Details of the isolates used in the phylogenetic tree

Species	Isolate	Host/source	GenBank accession no.
Rhizopus arrhizus	CBS111231	–	JN206338
R. arrhizus	CBS544.80	*Sorghum* malt	JN206337
R. arrhizus	CBS120.12	–	AB181318
R. arrhizus	IFO5438	–	DQ641276
R. arrhizus	CBS112.07	–	JN206323
R. arrhizus	CBS146.90	*Homo sapiens*	JN206324
R. arrhizus	**NRRL1469***	–	**DQ641279**
R. microsporus	CBS357.93	Tempeh	JN206343
R. microsporus	CBS631.82	Bread	JN206344
R. microsporus	CBS536.80	*Sorghum* malt	HM999971
R. microsporus	AS3.1145	–	DQ641305
R. microsporus	CBS337.62	–	JN206362
R. microsporus	**CBS699.68***	**Soil**	**HM999970**
R. homothallicus	**CBS336.62***	**Soil**	**HM999968**
R. homothallicus	CBS111232	–	JN206365
R. caespitosus	**CBS427.87***	–	**HM999965**
R. caespitosus	33515	–	AF115730
R. schipperae	**CBS138.95***	***Homo sapiens***	**HM999969**
Syzygites megalocarpus	CBS108947	*Amanita rubescens*	JN206370 JN206371
Sporodiniella umbellate	CBS195.77	*Umbonia*	JN206372
R. stolonifer	**CBS389.95***	–	**DQ641318**
Rhizopus sp. '*stolonifer*'	CBS442.74	Coffee-ground	JN206367
R. stolonifer	AFTOL-ID632	–	AY997085
R. sexualis	**CBS336.39***	***Fragaria***	**AB113017**
R. americanus	**CBS340.62***	**Air**	**HM999967**
R. lyococcus	CBS319.35	–	AB100449
R. lyococcus	CBS117.43	*Hordeum vulgare*	JN206375
R. lyococcus	**JCM5589***	–	**DQ641319**
Backusella sp.	CBS538.80	*Medicago sativa*	HM999964

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

Recommended genetic markers

- The internal transcribed spacer (ITS)–generic and species level
- The RNA polymerase II largest subunit gene (RPB1)–generic and species level
- The large and small subunits of nrDNA (LSU and SSU)–placement within the *Mucorales* order, higher-level phylogeny
- The partial actin gene (ACT)–higher-level phylogeny

Stagonosporopsis

Background

Stagonosporopsis is a coelomycetous genus in *Didymellaceae* (de Gruyter et al. 2009), accommodating several important phytopathogenic species, some of which have well-described sexual forms in *Didymella* (Diedicke 1912; Aveskamp et al. 2010). Many *Stagonosporopsis* species are considered serious quarantine organisms in many parts of the world. Some species have a global distribution. *Stagonosporopsis andigena*, the cause of black blight of potato (Turkensteen 1978), and *S. crystalliniformis*, a destructive pathogen of tomato and potato (Loerakker et al. 1986; Noordeloos et al. 1993), have only been reported in the Andes region, and thus listed as A1 quarantine organisms (EPPO 2014). *Stagonosporopsis chrysanthemi* and *S. inoxydabilis* are the cause of ray (flower) blight of *Asteraceae* (Stevens 1907; Van der Aa et al. 1990; Vaghefi et al. 2012), and A2 quarantine organisms (EPPO 2014) (listed as *Didymella ligulicola*). In Australia, *S. tanaceti* is known as the causal agent of ray blight of pyrethrum, capable of causing complete yield loss (Pethybridge et al. 2008). *Stagonosporopsis cucurbitacearum* (sexual state *Didymella bryoniae*) is a destructive seed-borne pathogen of *Cucurbitaceae* worldwide, causing gummy stem blight and black fruit rot (Punithalingam and Holliday 1972; Lee et al. 1984; Zitter and Kyle 1992). *Stagonosporopsis* species have also been reported from other plant families including *Amaranthaceae, Campanulaceae, Caryophyllaceae, Fabaceae, Lamiaceae, Ranunculaceae,* and *Valerianaceae*. The only species not isolated from a plant substrate is *S. oculo-hominis*, which was reported from human corneal ulcer in the USA (Punithalingam 1976).

Species identification and numbers

Stagonosporopsis was originally separated from *Ascochyta* on the basis of occasional formation of multi-septate (*Stagonospora*-like) conidia (Diedicke 1912). No type material was specified by Diedicke (1912) such that the first species combination described, *S. actaeae*, was interpreted as the generic type by some authors (Boerema et al. 1997, 2004). However, *S. boltshauseri*, currently known as *S. hortensis* (Boerema and Verhoeven 1979), was designated as the lectotype by Clements and Shear (1931).

In vitro, *S. hortensis* predominantly produces non-septate *Phoma*-like conidia, resembling those of *Boeremia exigua* var. *exigua*, while a few larger septate conidia can occasionally be found. *In vivo*, however, *S. hortensis* can be distinguished from *B. exigua* by predominance of one-septate (*Ascochyta*-like) conidia and occasional occurrence of two- or multi-septate (*Stagonospora*-like) spores. It is thus not a typical *Ascochyta* or *Stagonospora*, both of which produce septate

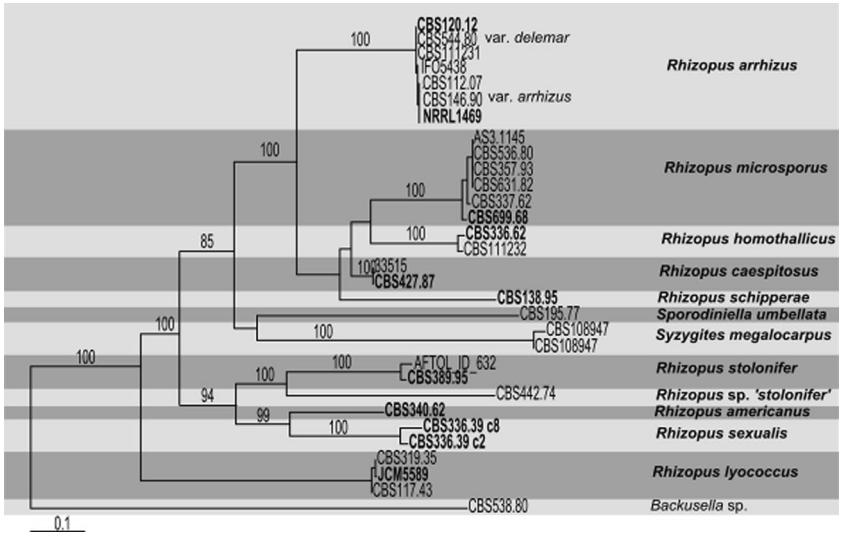


Fig. 24 Phylogram generated from Maximum likelihood analysis based on ITS sequenced data of *Rhizopus*. Bootstrap support values greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*

conidia both *in vivo* and *in vitro*, and was classified under the genus *Stagonosporopsis* (Boerema and Verhoeven 1979).

Boerema et al. (1997, 1999) described multiple *Stagonosporopsis* spp. to be synanamorphs for several *Phoma* species in section *Heterospora*. The characteristic of section *Heterospora* is the *in vivo* production of distinctly large conidia (ascochytoid /stagonosporoid) in addition to relatively small (phomoid) conidia. The large conidial phenotypes may be dominant *in vivo*, hence described as *Stagonosporopsis* synanamorphs (Boerema et al. 1997, 1999, 2004).

Recent phylogenetic delineation of *Phoma* and allied genera placed the presumed *Stagonosporopsis* types in the family *Didymellaceae* (de Gruyter et al. 2009), and an emended description of the genus was proposed (Aveskamp et al. 2010). Some of the heterosporous *Phoma* species with known *Stagonosporopsis* synanamorphs were retrieved outside the *Stagonosporopsis* clade. On the other hand, many species from sections *Heterospora*, *Phoma* and *Phyllostictoides*, for which no records of a *Stagonosporopsis* synanamorph had been made, clustered with *Stagonosporopsis* spp. This indicated that the connection of *Stagonosporopsis* with heterosporous *Phoma* species was not justified. It also suggested that presence of *Stagonospora*-like spores is not a reliable criterion for identification of *Stagonosporopsis* species. *Stagonosporopsis dorenboschiae*, *S. loticola,* and *S. ajacis* lack the *Stagonospora*-like spores and any further features than a plain, globose pycnidium, and aseptate, hyaline conidia (Aveskamp et al. 2010). Due to unreliability of morphological characters, phylogenetic species recognition is essential for identification of *Stagonosporopsis* species.

Stagonosporopsis in its original description by Diedicke (1912) accommodated seven species, and currently more than 40 species are linked to this genus (data from MycoBank and Index Fungorum). However, only 21 *Stagonosporopsis* species have thus far been recognised based on multi-gene phylogenies (Table 23) (Aveskamp et al. 2010; Vaghefi et al. 2012). The phylogenetic reassessment of *Didymellaceae* (Aveskamp et al. 2010) included only those *Stagonosporopsis* species that had been designated as *Phoma* synanmorphs by Boerema *et al.* (1997, 1999). Molecular data for multiple other *Stagonosporopsis* species are still lacking and, therefore, the taxonomy of the genus *Stagonosporopsis* remains to be comprehensively reviewed.

Molecular phylogeny

Few phylogenetic analyses of *Stagonosporopsis* species are available (Pethybridge et al. 2004; Aveskamp et al. 2010; de Gruyter et al. 2012; Vaghefi et al. 2012, 2014), with the most comprehensive analysis being the three-marker phylogeny performed by Aveskamp et al. (2010). The phylogeny of combined sequences of large subunit nrDNA (LSU), the internal transcribed spacers and the 5.8 S nrRNA (ITS), and β-tubulin regions resulted in the recognition of 19 species (Aveskamp et al. 2010). Phylogenies based on the partial actin (ACT) sequence were later found to be congruent with the LSU- ITS- β- tubulin phylogeny (de Gruyter et al. 2012; Vaghefi et al. 2012). A four-marker phylogeny of the *Stagonosporopsis* spp. for which these DNA sequence data are available is shown (Fig. 25).

Recommended genetic markers

- The internal transcribed spacer (ITS)–family/generic level
- β- tubulin and ACT–inter-specific delineation

A high level of infra-specific variation has been recorded for calmodulin (CAL) in *Phoma*-like species, however, it may be difficult to amplify in some *Stagonospsosopsis* species, and

Table 23 *Stagonosporopsis*. Details of the isolates used in the phylogenetic tree

Species name	Strain no.	Host	GenBank accession number					
			LSU	SSU	ITS	β- tubulin	ACT	CAL
Stagonosporopsis actaeae*	CBS 106.96; PD 94/1318	*Actaea spicata*	GU238166	QBank	GU237734	GU237671	JN251974	–
S. ajacis*	CBS 177.93; PD 90/115	*Delphinium* sp.	GU238168	QBank	GU237791	GU237673	JN251962	QBank
S. andigena	CBS 101.80; PD 75/909; IMI 386090	*Solanum* sp.	GU238169	GU238233	GU237714	GU237674	JN251958	QBank
S. artemisiicola	CBS 102636; PD 73/1409	*Artemisia dracunculus*	GU238171	QBank	GU237728	GU237676	JN251971	QBank
S. astragali	CBS 178.25; MUCL 9915	*Astragalus* sp.	GU238172	QBank	GU237792	GU237677	JN251963	QBank
S. caricae	CBS 248.90	*Carica papaya*	GU238175	QBank	GU237807	GU237680	JN251969	QBank
S. chrysanthemi	CBS 500.63; MUCL 8090	*Chrysanthemum indicum*	GU238190	QBank	GU237871	GU237695	JN251973	QBank
S. crystalliniformis*	CBS 713.85; ATCC 76027; PD 83/826	*Lycopersicon esculentum*	GU238178	QBank	GU237903	GU237683	JN251960	QBank
S. cucurbitacearum	CBS 133.96; PD 79/127	*Cucurbita* sp.	GU238181	GU238234	GU237780	GU237686	JN251968	QBank
S. dennisii	CBS 631.68; PD 68/147	*Solidago floribunda*	GU238182	GU238235	GU237899	GU237687	QBank	QBank
S. dorenboschii*	CBS 426.90; IMI 386093; PD 86/551	*Physostegia virginiana*	GU238185	QBank	GU237862	GU237690	JN251980	QBank
S. heliopsidis	CBS 109182; PD 74/231	*Heliopsis patula*	GU238186	QBank	GU237747	GU237691	QBank	QBank
S. hortensis	CBS 104.42	Unknown	GU238198	QBank	GU237730	GU237703	QBank	QBank
S. inoxydabilis*	CBS 425.90; PD 81/520	*Chrysanthemum parthenii*	GU238188	QBank	GU237861	GU237693	JN251972	QBank
S. loticola*	CBS 562.81; ICMP 6884	*Lotus pedunculatus*	GU238192	QBank	GU237890	GU237697	JN251978	QBank
S. lupini	CBS 101494; PD 98/5247	*Lupinus albus*	GU238194	QBank	GU237724	GU237699	QBank	QBank
S. oculo-hominis*	CBS 634.92; IMI 193307	*Homo sapiens*	GU238196	QBank	GU237901	GU237701	JN251976	QBank
S. rudbeckiae	CBS 109180; PD 79/175	*Rudbeckia bicolor*	GU238197	QBank	GU237745	GU237702	QBank	QBank
S. tanaceti*	CBS 131484; TAS 1	*Tanacetum cinerariifolium*	JQ897461	–	JQ897481	JQ897496	JQ897512	–
S. trachelii	CBS 379.91; PD 77/675	*Campanula isophylla*	GU238173	QBank	GU237850	GU237678	JN251977	QBank
S. valerianellae	CBS 329.67; PD 66/302	*Valerianella locusta* var. *oleracea*	GU238201	QBank	GU237832	GU237706	JN251965	QBank

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

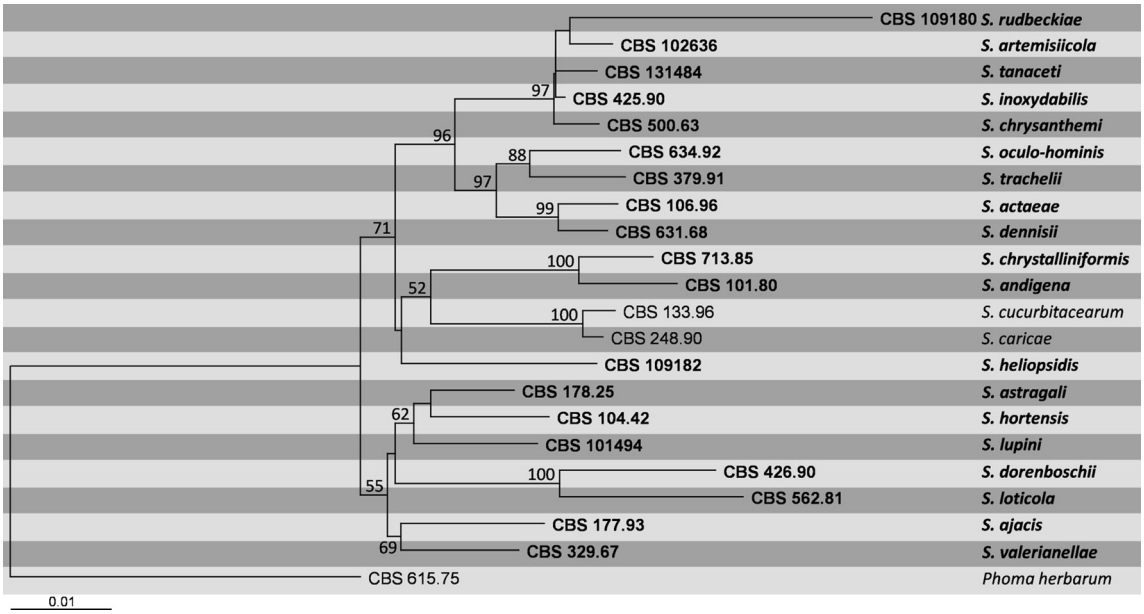


Fig. 25 Phylogram generated from Maximum likelihood analysis based on combined LSU, ITS, β- tubulin and ACT sequenced data of *Stagonosporopsis*. Bootstrap support values greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*. The tree is rooted with *Phoma herbarum* CBS 615.75

requires optimization using different degenerate primers (Aveskamp et al. 2009, 2010; Vaghefi et al. 2012). Thus use of β- tubulin and ACT is suggested as they will give sufficient distinction between species, and are easier to amplify.

Ustilago

Background

Ustilago is the largest genus of the *Ustilaginaceae* in the order of smut fungi, *Ustilaginales*, with about 200 currently accepted species (Vánky 2013). *Ustilago* and related genera contain many important plant pathogens that destroy the inflorescence or culms of grasses (*Poaceae*) (Vánky 2011). Some agriculturally important pathogens of grain and edible crops are *U. tritici* on wheat (*Triticum*), *U. hordei* on barley (*Hordeum*) and *U. maydis* on corn (*Zea mays*). Species of *Ustilago* have been used as model organisms for the study of plant disease pathways and mating types (Andrews et al. 2000; Bakkeren et al. 2008; Kellner et al. 2011), as well as for studies in the co-evolution of pathogens with their hosts (Begerow et al. 2004). The genomes of *U. maydis* and *U. hordei* were released in 2003 and 2012, respectively (Kamper et al. 2006; Laurie et al. 2012).

Ustilago was until recently a catch-all genus for smut fungi on a diversity of host families, including the *Carophyllaceae, Cyperaceae, Poaceae, Polygonaceae, Restionaceae,* and *Tilliaceae* (McTaggart et al. 2012b). Closely related genera were not easily distinguished from *Ustilago* by morphology, and formed a complex (Stoll et al. 2003, 2005). Subsequent systematic studies reserved *Ustilago s. lat.* for species that infected *Poaceae*, with *Ustilago s. str.* restricted to the tribe Pooideae (McTaggart et al. 2012a; Stoll et al. 2005). Soral morphology and host range were later found to be synapomorphic character states for the smut genera *Anthracocystis*, *Langdonia*, *Sporisorium*, *Stollia* and *Triodiomyces*, which were differentiated from *Ustilago* (McTaggart et al. 2012c). *Melanopsichium* is closely related to *Ustilago*, and appears to have jumped hosts from *Poaceae* to *Polygonaceae* (Begerow et al. 2004; Stoll et al. 2005).

Species identification and numbers

The diversity of smuts in the *Ustilaginaceae* on *Poaceae* encompasses over 530 species (Vánky 2011). Cryptic species are certain to be revealed when species complexes, e.g., *Macalpinomyces eriachnes*, are investigated. Vánky (2011) recognised approximately 170 species of *Ustilago*, which were delimited by host and spore morphology. It is likely the species number of *Ustilago* will decrease when generic concepts are resolved in the *Ustilaginaceae*. Species currently recognized as *Ustilago* will be transferred to new or other genera delimited by sorus morphology and host range. For example, *U. maydis* does not fit the concept of *Ustilago s. str.* and warrants transfer to the earliest valid genus, *Mycosarcoma*, when these closely related genera are resolved (McTaggart et al. 2012a; Stoll et al. 2005; Vánky and Lutz 2011; Piepenbring et al. 2002) (Table 24).

Table 24 *Ustilago*. Details of the isolates used in the phylogenetic tree

Species	Isolate	Host	Marker/GenBank accession no.	
			ITS	LSU
Anomalomyces panici	BRIP 46421	*Panicum trachyrachis*	DQ459348	DQ459347
Anthracocystis destruens	Ust. Exs. 472	*Panicum miliaceum*	AY344976	AY747077
Langdonia aristidae	BRIP 52755	*Aristida hygrometrica*	HQ013096	NA
Macalpinomyces eriachnes	56573 (M)	*Eriachne aristidea*	AY740037	AY740090
M. mackinlayi	BRIP 52549	*Eulalia mackinlayi*	GU014817	HQ013131
M. neglectus	RB 2056 (TUB)	*Setaria pumila*	AY740056	AY740109
M. simplex	56577 (M)	*Loudetia simplex*	AY740152	NA
M. spermophorus	HUV 13634	*Eragrostis ferruginea*	AY740171	NA
	BRIP 51858	*Sporobolus australasicus*	NA	HQ013130
M. viridans	BRIP 49133	*Sporobolus actinocladus*	HQ013089	HQ013125
Melanopsichium pennsylvanicum	HUV 17548	*Polygonum glabrum*	AY740040	AY740093
Moesziomyces bullatus	Ust. Exs. 833	*Paspalum distichum*	AY740153	AY740153
Sporisorium aegyptiacum	Ust. Exs. 756	*Schismus arabicus*	AY344970	AY740129
S. sorghi	MP 2036a (USJ)	*Sorgum bicolor*	AY740021	AF009872
S. spinulosum	HMAS 193085	*Capillipedium parviflorum*	GU139172	GU139171
Stollia ewartii	BRIP 51818	*Sarga timorense*	HQ013087	HQ013127
Triodiomyces altilis	Ust. Exs. 418	*Triodia pungens*	AY740166	NA
	BRIP 52543	*Triodia* sp.	NA	HQ013136
T. triodiae	HUV 17662	*Triodia microstachya*	AY740074	AY740126
Tubisorus pachycarpus	HUV 21891	*Mnesithea rottboellioides*	JN871718	JN871717
Ustilago affinis	MP 692	*Stenotaphrum secundatum*	AY344995	AF133581
U. austro-africana	56516 (M)	*Enneapogon cenchroides*	AY740061	AY740115
U. avenae	DB 559 (TUB)	*Avena barbata*	AY344997	AF453933
U. bouriqueti	56517 (M)	*Stenotaphrum dimidiatum*	AY740167	NA
U. bromivora	HUV 19322	*Bromus catharticus*	AY740064	AY740118
U. bullata	MP 2363 (TUB)	*Bromus diandrus*	AY344998	AF453935
U. calamagrostidis	56518 (M)	*Calamagrostis epigeios*	AY740065	AY740119
U. crameri	Ust. Exs. 995	*Setaria italica*	AY344999	AY740143
U. curta	Ust. Exs. 1090	*Tripogon loliiformis*	AY740165	HQ013123
U. cynodontis	MP 1838	*Cynodon dactylon*	AY345000	AF009881
U. davisii	HUV 19252	*Glyceria multiflora*	AY740169	NA
U. drakensbergiana	56523 (M)	*Digitaria tricholaenoides*	AY740170	
U. echinata	Ust. Exs. 540	*Phalaris arundinacea*	AY345001	AY740144
U. esculenta	Ust. Exs. 590	*Zizania latifolia*	AY345002	AF453937
U. filiformis	RB 3011 (TUB)	*Glyceria fluitans*	AY740066	AY740120
U. hordei	Ust. Exs. 784	*Hordeum vulgare*	AY345003	AF453943
U. ixophori	MP 2194	*Ixophorus unisetus*	AY740067	AY740121
U. maydis	RB 3093	*Zea mays*	AY345004	NA
	NA	*Zea mays*	NA	AF453938
U. nuda	HUV 17782	*Hordeum leporinum*	AY740069	AJ236139
U. pamirica	Ust. Exs. 789	*Bromus gracillimus*	AY345005	AY740145
U. schmidtiae	BRIP 51848	*Enneapogon* sp.	HQ013121	HQ013129
U. schroeteriana	Ust. Exs. 887	*Paspalum paniculatum*	AY345006	AY740146
U. sparsa	Ust. Exs. 892	*Dactyloctenium radulans*	AY345008	NA
U. sporoboli-indici	BRIP 39706	*Sporobolous pyramidalis*	AY772736	NA
U. striiformis	HUV 18286	*Alopecurus pratensis*	AY740172	DQ875375
U. syntherismae	Ust. Exs. 998	*Digitaria ternata*	AY740071	AY740123

Table 24 (continued)

Species	Isolate	Host	Marker/GenBank accession no.	
			ITS	LSU
U. tragana	56562 (M)	*Tragus berteronianus*	AY740072[3]	AY740124[3]
U. tritici	NA	*Triticum aestivum*	AF135424[11]	NA
U. trichophora	56564 (M)	*Echinochloa colona*	AY345009[3]	AY740148[3]
U. turcomanica	HUV 23	*Eremopyrum distans*	AY345011[3]	AF453936[3]
U. vetiveriae	HUV 17954	*Vetiveria zizanioides*	AY345011[3]	AF453937[3]
U. xerochloae	Ust. Exs. 1000	*Xerochloa imberbis*	AY345012[3]	AF453938[3]

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

Molecular phylogeny

Relationships between *Ustilago* and closely related genera are still unresolved, and *Ustilago* is polyphyletic (Fig. 26 *Ustilago*). Systematic studies based on the nLSU or ITS regions of rDNA have assigned taxa within these closely related genera (Shivas et al. 2013a; Vánky and Lutz 2011; McTaggart et al. 2012c). Nuclear genes (EF1α, GPDH, RPB1 and RPB2), another ribosomal gene (SSU) and mating loci were explored as markers for the evolution of smut fungi in the *Ustilaginaceae* (Kellner et al. 2011; McTaggart et al. 2012a; Munkacsi et al. 2007). At this stage, these markers are not as widely used as ITS and LSU, which are recommended for species identification and generic placement, respectively.

Recommended genetic markers

- The large subunit (LSU) of nrDNA–generic level
- The internal transcribed spacer (ITS) of nrDNA–species level

Verticillium

Background

Verticillium belongs in the family *Plectosphaerellaceae* of the Ascomycota. *Verticillium* species are soilborne, vascular, fungal plant pathogens that cause Verticillium wilt disease in many important agricultural crops throughout the world (Pegg and Brady 2002). Based on susceptibility, 410 plant species that include nearly 80 plant genera have been recorded as being infected by *Verticillium* species (Pegg and Brady 2002). Correct species identification is important for determining the ecological roles of *Verticillium* species and for diagnosing disease. Sexual stages have not been identified for *Verticillium* species although mating type idiomorphs MAT1-1 and MAT1-2 have been identified in separate isolates of *V. dahliae*, *V. albo-atrum*, *V. longisporum*, *V. alfalfa* and *V. nonalfalfae,* indicating that these species are potentially heterothallic (Inderbitzin et al. 2011a, b; Usami et al. 2009).

Species identification and numbers

The genus *Verticillium sensu stricto* refers to a monophyletic group of plant pathogens comprising *V. dahliae* as the type of *Verticillium* (Gams et al. 2005). The genus can be identified based on its distinct 'verticillate conidiophores' with flask-shaped conidiophores arranged in whorls attached along a main axis that comprise the spore forming cells (Pegg and Brady 2002). The genus *Verticillium* has a long taxonomic history and approximately 190 species were originally classified by Zare et al. (2004). Recently Inderbitzin et al. (2011a) used four-marker phylogenetic analysis to identify ten *Verticillium* species.

Earlier studies identified *Verticillium* species primarily on the basis of morphology and sub-specific groups by virulence and aggressiveness on various hosts (Rowe 1995). Variation in conidial morphology of *Verticillium* species is minor and thus cannot be used to separate species (Rowe 1995). Resting structure morphology has been the major morphological character used to differentiate species of *Verticillium*.

Verticillium albo-atrum and *V. dahliae* are the most important plant pathogenic species. *Verticillium albo-atrum* was first described in Germany, 1879, by Reinke and Berthold as the causal agent of potato wilt. The resting structures identified from the diseased plant tissue were brown-pigmented hyphae which were described as 'Dauermycelien'. Later this pigmented hyphae was termed dark 'resting mycelium' which had only transverse walls and no lateral budding (Isaac 1949). No microsclerotia were produced by *V. albo-atrum*.

Verticillium dahliae was first isolated by Klebahn in 1913 from wilting Dahlia. The isolate produces smaller and oval to elongate microsclerotia as a resting structure from budding hyphae, but not dark resting mycelium (Smith 1965). *Verticillium tricorpus* forms large and irregular microsclerotia with melanised hyphae and chlamydospores (hence the prefix "tri"). Moreover, *V. tricorpus* often produces yellow colonies

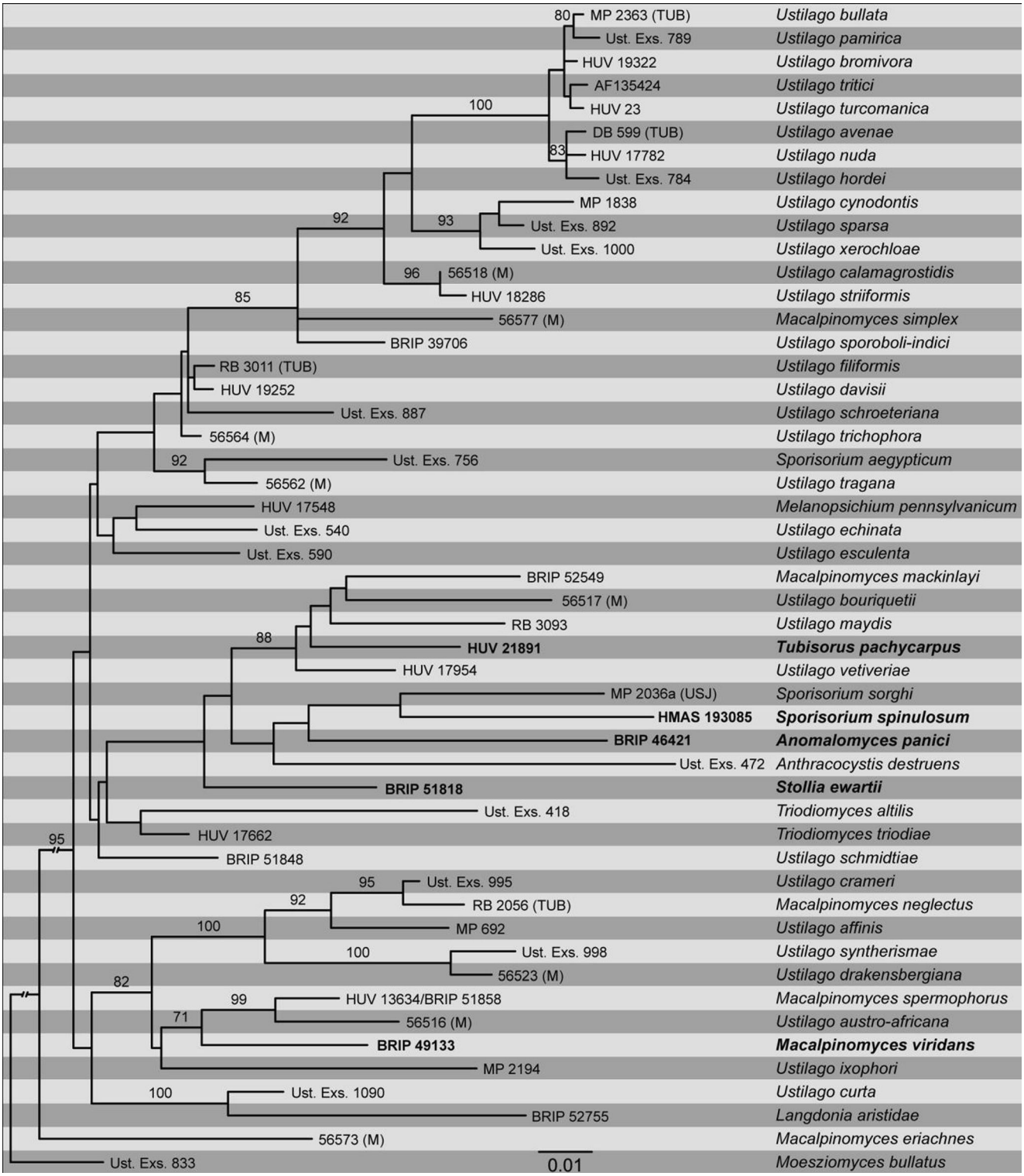


Fig. 26 Phylogram generated from ML search in RA × ML based on combined ITS and LSU sequenced data of *Ustilago*. Bootstrap support values greater than 70 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*

on PDA upon first isolation (Goud et al. 2003). *Verticillium nubilum* produces only rounded to elongate chlamydospores, individually or in chains (Inderbitzin et al. 2011a). *Verticillium longisporum* refers to the species proposed by Karapapa et al. (1997) that infected hosts in the family *Brassicaceae*. Isolates of this species produce microsclerotia which are rounded to elongate with relatively long conidia, and nearly double the nuclear DNA content (Inderbitzin et al. 2011a).

Molecular techniques have been used in the characterisation and identification of *Verticillium* species for both species identification and phylogenetic comparisons (Collins et al. 2003; Collado-Romero et al. 2008). Using restriction fragment length polymorphism (RFLP) analysis, Typas et al. (1992) reported that mitochondrial DNA of *Verticillium* species were distinctive and easily differentiated *V. albo-atrum* (from alfalfa) from other *V. albo-atrum* isolates. Carder and Barbara (1991) used RFLP analysis to differentiate *V. dahliae* from all isolates of *V. albo-atrum* and found intraspecific variation within *V. dahliae* isolates. Subsequently, Okoli et al. (1993) probed Southern blots derived from 17 isolates of *V. dahliae* with 71 random genomic clones from *V. dahliae* and found that 15 isolates fitted clearly into two RFLP groups designated A and B. Although these groups correlated with isozyme patterns they did not show any correlation with host plant or geographic origin. Random amplified polymorphic DNA (RAPD) markers clearly differentiated 15 *V. albo-atrum* potato isolates from 20 alfalfa *V. albo-atrum* isolates and found that these two groups were genetically distinct (Barasubiye et al. 1995). Komatsu et al. (2001) used repetitive extragenic palindromic polymerase chain reaction (REP-PCR) and RAPD markers to show that *V. dahliae* isolates from potato were similar in genetic background, regardless of geographic origin.

In North America, characterization of vegetative compatibility groups (VCGs have the ability to undergo hyphal anastomosis with other isolates) using molecular markers confirmed that VCG 4A isolates of *V. dahliae* were more highly virulent than VCG 4B isolates (Dobinson et al. 2000). Molecular characterization of VCGs has been determined in many other crops (Collado-Romero et al. 2006, 2009; Dobinson et al. 1998).

Molecular phylogeny

Nazar et al. (1991) found only five nucleotide differences between *V. dahliae* and *V. albo-atrum* on the basis of the non-conserved ITS region (ITS 1 and ITS 2) of rDNA. Robb et al. (1993) reported 17 nucleotide differences between *V. dahliae* and *V. tricorpus* and 12 between *V. albo-atrum* and *V. tricorpus* (Moukhamedov et al. 1994). Phylogenetic analysis of the complete intergenic spacer (IGS) region of the nuclear ribosomal RNA (rDNA) and the β-tubulin gene showed distinct groups comprising isolates of *V. albo-atrum*, *V. tricorpus*, and *V. dahliae* from cruciferous and noncruciferous hosts (Qin et al. 2006).

Fahleson et al. (2004) studied three different markers (mitochondrial cytochrome *b* gene (*cob*), the mitochondrial small subunit rRNA gene (*rns*) and the nuclear ITS2 region) sequences from five plant pathogenic isolates of *Verticillium* and found five monophyletic groups corresponding to the *Verticillium* species. In addition, *V. tricorpus* displayed a closer relationship to *V. albo-atrum*, *V. dahliae* and *V. longisporum*. But *V. nigrescens* was distantly related to the other species. Based on nuclear large subunit ribosomal DNA (LSU) and ITS sequences, Zare et al. (2007) proposed *Gibellulopsis* as a genus to accommodate *V. nigrescens*.

Recent molecular phylogenetic studies by Inderbitzin et al. (2011a) using four gene sequences viz actin, elongation factor 1-alpha, glyceraldehyde-3-phosphate dehydrogenase and tryptophan synthase, divided *Verticillium* into two separate groups, corresponding to the production of yellow pigment in culture (clade Flavexudans), or the lack of yellow pigment (clade Flavnonexudans). The species *Verticillium albo-atrum*, *V. tricorpus*, *V. zaregamsianum*, *V. isaacii* and *V. klebahnii* were placed in the Flavexudans clade of which the latter two species were morphologically indistinguishable from *V. tricorpus*. The species *Verticillium dahliae*, *V. nubilum*, *V. longisporum*, *V. alfalfae* and *V. nonalfalfae* were placed in the clade Flavnonexudans (Inderbitzin et al. 2011a). Interestingly, *V. longisporum* which is a diploid hybrid had alleles in different clades including the *V. dahliae* clade thus reflecting the ancestral origin of the hybrid. According to Inderbitzin et al. (2011b), each *V. longisporum* isolate contained two alleles at each locus with allele A1 being present in all isolates in addition to alleles D1, D2 or D3. Therefore, according to Inderbitzin et al. (2011a), *V. longisporum* should remain a polyphyletic species.

The phylogenetic tree of the ten species adopted by Inderbitzin et al. (2011a) did not include the ribosomal internal transcribed spacer region ITS, because *V. longisporum* isolates only had one ITS allele consistent with all other *Verticillium* species and hence this gene sequence could not retrace the evolution of the species (Inderbitzin et al. 2011b). Nevertheless, neither the four gene phylogenetic analysis nor the single ITS phylogenetic tree were able to differentiate *V. longisporum* alleles D2 and D3 from *V. dahliae* (Inderbitzin et al. 2011b).

In contrast to the above results, a four gene phylogenetic tree composed of only the type isolates (Fig. 27) failed to differentiate *V. isaacii* from *V. klebahnii*; while *V. alfalfa* was identical to *V. nonalfalfae*; and *V. dahliae* was identical to *V. longisporum* allele D2. Nevertheless, the phylogenetic tree based only on ITS (Fig. 28) provided better discrimination to differentiate *V. isaacii* from *V. klebahnii*, and *V. alfalfa* from *V. nonalfalfae,* albeit with weak bootstrap supports.

Another anomaly with the four gene phylogenetic tree based on only type isolates was that *V. nubilum* cladded with the yellow pigment forming Flavexudans species whereas in the tree by Inderbitzin et al. (2011a), *V. nubilum* cladded with the Flavnonexudans species. Nevertheless, the phylogenetic tree based only

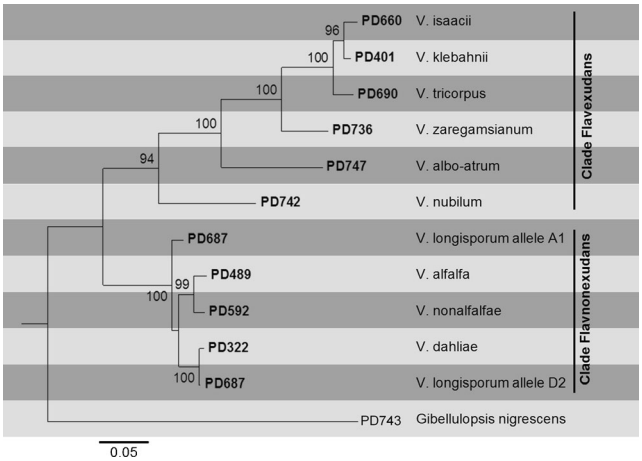


Fig. 27 Phylogram generated from parsimony analysis based on combined ACT, TEF, GPD and TS sequenced data of *Verticillium*. Parsimony bootstrap support values greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*. The tree is rooted with *Gibellulopsis nigrescens*

on ITS (Fig. 28) placed *V. nubilum* in the Flavnonexudans species group. In fact *V. nubilum* does not produce yellow pigment in culture, such that it is better placed in the Flavnonexudans species group.

Recommended genetic markers

Most of the ten *Verticillium* species can be identified using the ITS sequences of the type isolates (Table 25, Fig. 28) however, strong bootstrap support is provided for most clades using four gene sequences (Table 25, Fig. 27).

- Internal transcribed spacer (ITS)–species level
- Actin (ACT)–generic/species level

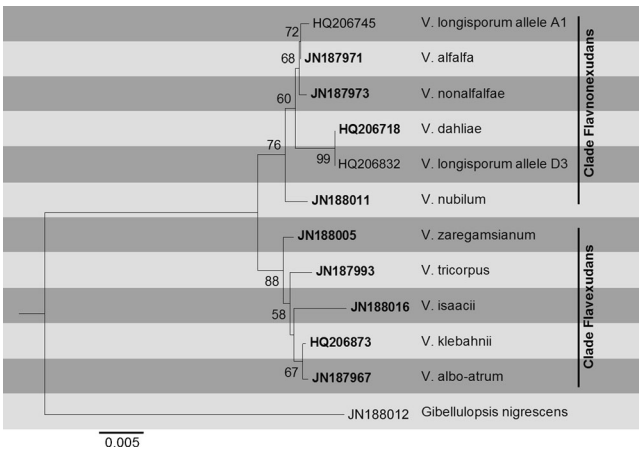


Fig. 28 Phylogram generated from parsimony analysis based on ITS sequenced data of *Verticillium*. Parsimony bootstrap support values greater than 50 % are indicated above the nodes. The ex-type (ex-epitype) and voucher strains are in *bold*. The tree is rooted with *Gibellulopsis nigrescens*

- Elongation factor 1-alpha (EF)–generic/ species level
- Glyceraldehyde-3-phosphate dehydrogenase (GPD)–generic/ species level
- Tryptophan synthase (TS)–generic/ species level

Discussion

The present effort is far from exhaustive, and the selection of fungal lineages reflects the backgrounds of the authors rather than degree of pathogenicity or economic impact of the underlying fungi. Indeed, several of the groups covered are pathogens on plants that are used neither in agriculture nor forestry. Furthermore, the fact that a group is addressed in the present study should not be taken to mean that no further discoveries or insights in the group are likely to emerge; the opposite is certain to be true for all of the groups studied here. Knowledge of phytopathogenic fungi accumulates at a high pace, and we hope that the readers will use this study as a starting point in their pursuit. Towards that end, we aim to maintain rich, updated backbone trees of as many groups of plant pathogenic fungi as we can. These will be published as a joint paper on an annual or biennial basis as new data are produced. Researchers who can cover any group not presently covered–or improve on any of the groups that are covered already–are warmly invited to take part in this effort by contacting the corresponding author.

As one of the pursuits of this effort, we have attempted to address the question of which genes and genetic markers that will provide the highest phylogenetic/taxonomic resolution in various groups of plant pathogenic fungi. These differ markedly among groups. At the same time, for someone examining a sample of an unknown phytopathology-related fungus, the choice of initial genetic markers is easy. The ITS region–the formal fungal barcode–is the most commonly sequenced marker in mycology, such that a rich array of reference sequences is available. Although the ITS region will not always provide resolution at the species level, it will nearly always provide enough resolution to support assignment of the species to at least the level of subgenus/species complex. This information is likely to be enough for many applications; for others, it makes it much easier to make an informed choice of what genes to sequence next. However, researchers sometimes recover fungal ITS sequences that are not easily fitted into the corpus of reference ITS sequences. The next most sequenced marker in mycology is the nuclear ribosomal large subunit (nLSU; Begerow et al. 2010), which is significantly more conserved than the ITS region and offers resolution at the genus to order level. The nLSU is something of the mainstay of large-scale phylogenetic inference in fungi (Blackwell et al. 2006), and nearly all fungal nLSU sequences can be assigned to at least the ordinal level. For unknown samples, we thus advice researchers to sequence the ITS and nLSU regions as a first step.

Table 25 *Verticillium*. Details of the isolates used in the phylogenetic tree

Species	Isolate	Host	GenBank accession number				
			ITS	ACT	EF	GPD	TS
V. dahliae	**PD322***	Lettuce	HQ206718	HQ206718	HQ414624	HQ414719	HQ414909
V. alfalfae	**PD489***	Alfalfae	JN187971	JN188097	JN188225	JN188161	JN188033
V. nubilum	**PD742***	Soil	JN188011	JN188139	JN188267	JN188203	JN188075
V. isaacii	**PD660***	Lettuce	HQ206873	HQ206985	HQ414688	HQ414783	HQ414973
V. nonalfalfae	**PD592***	Irish Potato	JN187973	JN188099	JN188227	JN188163	JN188035
V. albo-atrum	**PD747***	Potato Soil	JN188016	JN188144	JN188272	JN188208	JN188080
V. zaregamsianum	**PD736***	Lettuce	JN188005	JN188133	JN188261	JN188197	JN188069
V. tricorpus	**PD690***	Garden Tomato	JN187993	JN188121	JN188249	JN188185	JN188057
V. klebahnii	**PD401***	Lettuce	JN187967	JN188093	JN188221	JN188157	JN188029
V. longisporum	**PD687*** Allele D2	Horseradish		HQ206994	HQ414697	HQ414792	HQ414982
V. longisporum	**PD687*** Allele A1	Horseradish		HQ206993	HQ414696	HQ414791	HQ414981

Ex-type (ex-epitype) strains are bolded and marked with an * and voucher stains are bolded

Fungal plant pathogens attract the attention of numerous scientific and applied fields, including mycology, botany, agriculture, horticulture, silviculture, and medicine. In many cases this attention will centre on establishing, or ruling out, a pathogenic nature of specific fungal samples; and in many cases, such efforts will be based on molecular data. Molecular identification of fungi–DNA barcoding–has a long and rich history but was only recently formalized (Bruns et al. 1990; Schoch et al. 2012). Indeed, many parts of its realization still loom on the horizon. For instance, central barcoding resources and databases of wide acceptance in the mycological community are largely lacking. Most researchers, when processing newly generated fungal sequences, turn to GenBank (Benson et al. 2014) for sequence identification. Many entries in GenBank suffer from technical complications or low-resolution annotations, but efforts to standardize and improve on the data and level of metadata given are under way (Nilsson et al. 2014; Schoch et al. 2014). The largest database focusing on the formal fungal barcoding region–ITS–is UNITE (Kõljalg et al. 2013). Sharing data with GenBank, UNITE serves as the provider of reference fungal ITS datasets for a long range of applications and downstream uses. The results of the present effort–in particular, the sequences from type material–are being implemented in UNITE for all its diverse uses and for subsequent distribution to GenBank. We hope that this will lead to increased scientific resolution for researchers recovering any of the fungal lineages treated in this study.

The heterogeneous user base of data pertaining to phytopathogenic fungi suggests that many users of data pertaining to phytopathogenic fungi will not be–and cannot expected to be–up to date on recent developments in mycology, systematics, or the use of molecular data in biology. It is thus largely up to mycologists to provide the scientific community with as accurate and easily interpreted information on fungi and phytopathological fungal species as possible. The mycological community lives up to that expectation with various degrees of success. Improvement is particularly needed in the public sequence databases, where many researchers routinely submit phytopathologically relevant fungal sequences without any notion of taxonomic affiliation, host association, or country of collection (notably "Uncultured fungus"). Such sequences will be excluded from, or treated only superficially in, most research efforts and sequence comparisons, leading to reduced scientific resolution and explanatory power. We urge mycologists with a phytopathological inclination–indeed, with any inclination–to set good examples in this regard by providing rich, reliable annotations for their sequences. Guidelines on how to establish the integrity and improve the wide usefulness of fungal sequence data are readily available for consideration (Nilsson et al. 2012; Hyde et al. 2013a, b; Schoch et al. 2014). We similarly hope that all mycologists, when describing new species, will make it a habit to bundle at least one DNA sequence–starting with the ITS region–with the description (cf. Seifert and Rossman 2010). This will help others to interpret the name and will go a long way to make it available to the general scientific audience. Enclosing molecular data with species descriptions is not required by the current nomenclatural code governing fungi (McNeill et al. 2012), but we feel that this is a good opportunity for mycology to show its progressive nature. In a time where mycology finds it increasingly hard to compete for funding with disciplines deemed more cutting-edge, mycologists should make every effort to propagate their results and findings to the widest audience possible.

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