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A class-wide phylogenetic assessment of *Dothideomycetes*

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Abstract: We present a comprehensive phylogeny derived from 5 genes, nucSSU, nucLSU rDNA, *TEF1*, *RPB1* and *RPB2*, for 356 isolates and 41 families (six newly described in this volume) in *Dothideomycetes*. All currently accepted orders in the class are represented for the first time in addition to numerous previously unplaced lineages. Subclass *Pleosporomycetidae* is expanded to include the aquatic order *Jahnulales.* An ancestral reconstruction of basic nutritional modes supports numerous transitions from saprobic life histories to plant associated and lichenised modes and a transition from terrestrial to aquatic habitats are confirmed. Finally, a genomic comparison of 6 dothideomycete genomes with other fungi finds a high level of unique protein associated with the class, supporting its delineation as a separate taxon.

Key words: *Ascomycota*, *Pezizomycotina*, Dothideomyceta, fungal evolution, lichens, multigene phylogeny, phylogenomics, plant pathogens, saprobes, Tree of Life.

INTRODUCTION

Multi laboratory collaborative research in various biological disciplines is providing a high level of interaction amongst researchers with diverse interests and backgrounds. For the mycological community, the "Assembling the Fungal Tree of Life" project (AFTOL) provided the first DNA-based comprehensive multigene phylogenetic view of the fungal Kingdom (Lutzoni *et al.* 2004, James *et al.* 2006). This has also made it possible to revise the classification of the fungi above the ordinal level (Hibbett *et al.* 2007). Subsequent work is focused on elucidating poorly resolved nodes that were highlighted in the initial DNA-based phylogeny (McLaughlin *et al.* 2009).

At the other end of the scale from the tree of life projects, taxon sampling with relatively small numbers of sequence characters are also progressing in various barcoding projects (Seifert *et al.* 2007, Chase *et al.* 2009, Seifert 2009). It remains important to link these two ends of the spectrum by also sampling intensively at foci of interest between barcoding and the tree of life. With this in mind it is the aim of this paper and subsequent ones in this volume to provide a broadly sampled phylogeny at class level and below for *Dothideomycetes.* This result is combined efforts and data from a diverse group of researchers to focus on systematic sampling, therefore developing a more robust fungal class wide phylogeny of *Dothideomycetes*. This is especially important as a framework

for comprehending how fungi have evolved as they shift ecological habitats and adapt to new environments and nutritional modes.

It is apparent that the assemblage of fungi, now defined as *Dothideomycetes,* exemplifies a dynamic evolutionary history. This is by far the largest and arguably most phylogenetically diverse class within the largest fungal phylum, *Ascomycota* (Kirk *et al.* 2008). It contains a heterogeneous group of fungi that subsist in the majority of the niches where fungi can be found. The best-known members of the group are plant pathogens that cause serious crop losses. Species in the genera *Cochliobolus*, *Didymella, Phaeosphaeria, Pyrenophora, Venturia, Mycosphaerella* and *Leptosphaeria,* or their anamorphs, are major pathogens of corn, melons, wheat, barley, apples, bananas and brassicas respectively, in most areas of the world where they are cultivated. Other species are important pathogens in forestry *e.g.* species in the genera *Botryosphaeria* and *Mycosphaerella* and their anamorphs that attack economically important tree species.

Despite a large body of work containing taxonomic, phytopathological, genetic and genomic research, the majority of fungi hypothesised to be members of *Dothideomycetes* remain under-sampled within a systematic framework. Several studies performed during the course of the last four years have advanced our understanding of these fungi, but phylogenetic relationships of the saprobes, aquatic, asexual and lichenised species remain particularly poorly studied. Indeed, their conspicuous absence in phylogenetic analyses frustrates a broader understanding of dothideomycete evolution.

Dothideomycetes share a number of morphological characters with other fungal classes. It was recently formally described (Eriksson & Winka 1997) replacing in part the long-recognised loculoascomycetes (Luttrell 1955). This redefinition of the loculoascomycetes was mainly prompted by DNA sequencing comparisons of ribosomal RNA genes (Berbee & Taylor 1992, Spatafora *et al.* 1995) that was subsequently expanded and confirmed (Berbee 1996, Silva-Hanlin & Hanlin 1999, Lindemuth *et al.* 2001, Lumbsch & Lindemuth 2001). These early phylogenetic studies demonstrated that loculoascomycetes, as it was defined, is not monophyletic, although contrary views exist (Liu & Hall 2004). Nevertheless the majority of analyses have shown that some loculoascomycete taxa, such as the "black yeasts" in *Chaetothyriales* as well as the lichenised *Verrucariales*, reside within *Eurotiomycetes* as subclass *Chaetothyriomycetidae* (Spatafora *et al.* 1995, Winka *et al.* 1998, Geiser *et al.* 2006, Gueidan *et al.* 2008). The majority of the remaining loculoascomycete species are now placed in *Dothideomycetes*. Although finer morphological distinctions between the distantly related members of loculoascomycetes can be made, their synapomorphies remain elusive (Lumbsch & Huhndorf 2007). These findings all point to the fact that a number of loculoascomycete morphological characters are either retained ancestral traits or that they exhibit convergence due to similar selection pressures.

Traditionally the most important morphological characters used to define major groups in *Ascomycota* were the type of ascus, septation of ascospores, the morphology and development of the ascoma, as well as the structure and organisation of the centrum. *Dothideomycetes* (and previously, loculoascomycetes) have fissitunicate (or functionally bitunicate) asci, that emerge from ascolocular development in preformed locules within vegetative tissue, that represents the ascoma. The reproductive structures in ascolocular development are derived from cells before fusion of opposing mating types occurs and can contain one or several locules. This form of ascolocular development is in contrast to the ascohymenial development found in most other fungal classes. During ascohymenial development asci are generated in a hymenium and the reproductive structure is derived from cells after fusion of opposing mating types. The fissitunicate ascus has been described for more than a century, but the importance of ascolocular development was first emphasised in 1932 (Nannfeldt 1932). Importantly Nannfeldt's concepts were also the basis for the Santesson's integration of lichens into the fungal classification (Santesson 1952). In fissitunicate asci, generally, the ascospores are dispersed by the rupture of the thick outer layers (ectotunica) at its apex, allowing the thinner inner layer (endotunica) to elongate similar to a "jack in a box". The elongated endotunica ruptures apically and releases the ascospores forcefully through the ascoma opening. The spores are then released in the air, or in aquatic species, under water. Building on this work and that of others (Miller 1949), Luttrell proposed Loculoascomycetes, synonymous to Nannfeldt's "Ascoloculares" (Luttrell 1955). Importantly, he proposed a correlation between fissitunicate asci and ascolocular development, also emphasising the importance of ascus morphology and dehiscence as well as the development of surrounding elements within the ascoma.

Although the concept of a group of fungi (including the *Dothideomycetes*) with fissitunicate asci and ascolocular development has been accepted by several authors, much less agreement could be found on ordinal definitions in the era before molecular characters. This ranged from proposing a single order (von Arx & Müller 1975) to three (Müller & von Arx 1962), five (Luttrell 1951, 1955) six (Barr 1979), or seven (Barr 1987). Luttrell initially described a number of important development types centered on descriptions of all tissues inside the ascoma (the centrum concept) and combined this with ascoma structure to define his five orders (Luttrell 1951, 1955). Of Luttrell's initial centrum concepts three are applicable to the *Dothideomycetes* as they are presently defined. Thus, the *Pleospora* type, the *Dothidea* type and the *Elsinoë* type centra correspond to the dothideomycete orders *Pleosporales*, *Dothideales* and *Myriangiales*, respectively. An important refinement to Luttrell's ideas was introduced with the concept of the hamathecium by Eriksson (Eriksson 1981). This is defined as a neutral term for sterile hyphae or other tissues between the asci in the ascoma (Kirk *et al.* 2008). For example, hamathecial types can include the presence or absence of pseudoparaphyses, which are sterile cells that extend down from the upper portion of the ascomatal cavity. They become attached at both ends, although the upper part may become free at maturity. Other important concepts introduced by Müller and von Arx (Müller & von Arx 1962) focused on the morphology of the ascoma opening and ascus shape. The *Dothidea* type centrum in the type species of *Dothidea*, *D. sambuci* illustrates several typical dothideomycete morphologies (Fig. 1). These include the thick-walled fissitunicate asci produced within a multilocular stroma.

The most recent dothideomycete class-wide morphological assessments were carried out by Barr (Barr 1979, 1987). Her subclasses were determined based on characters in the centrum, including the absence, presence and types of hamathecial tissues. Consistent with several earlier authors, Barr's ordinal classifications were based on ascomatal shape (perithecioid or apothecioid) and manner in which nutrients are obtained by the fungus (Barr 1987). In addition to these characters she emphasised the importance of finer distinctions in the hamathecium such as the shape and structure of the pseudoparaphyses (Barr 1979, 1987).

The introduction of molecular phylogenies for *Dothideomycetes* (Berbee 1996) provided an opportunity to verify the significance

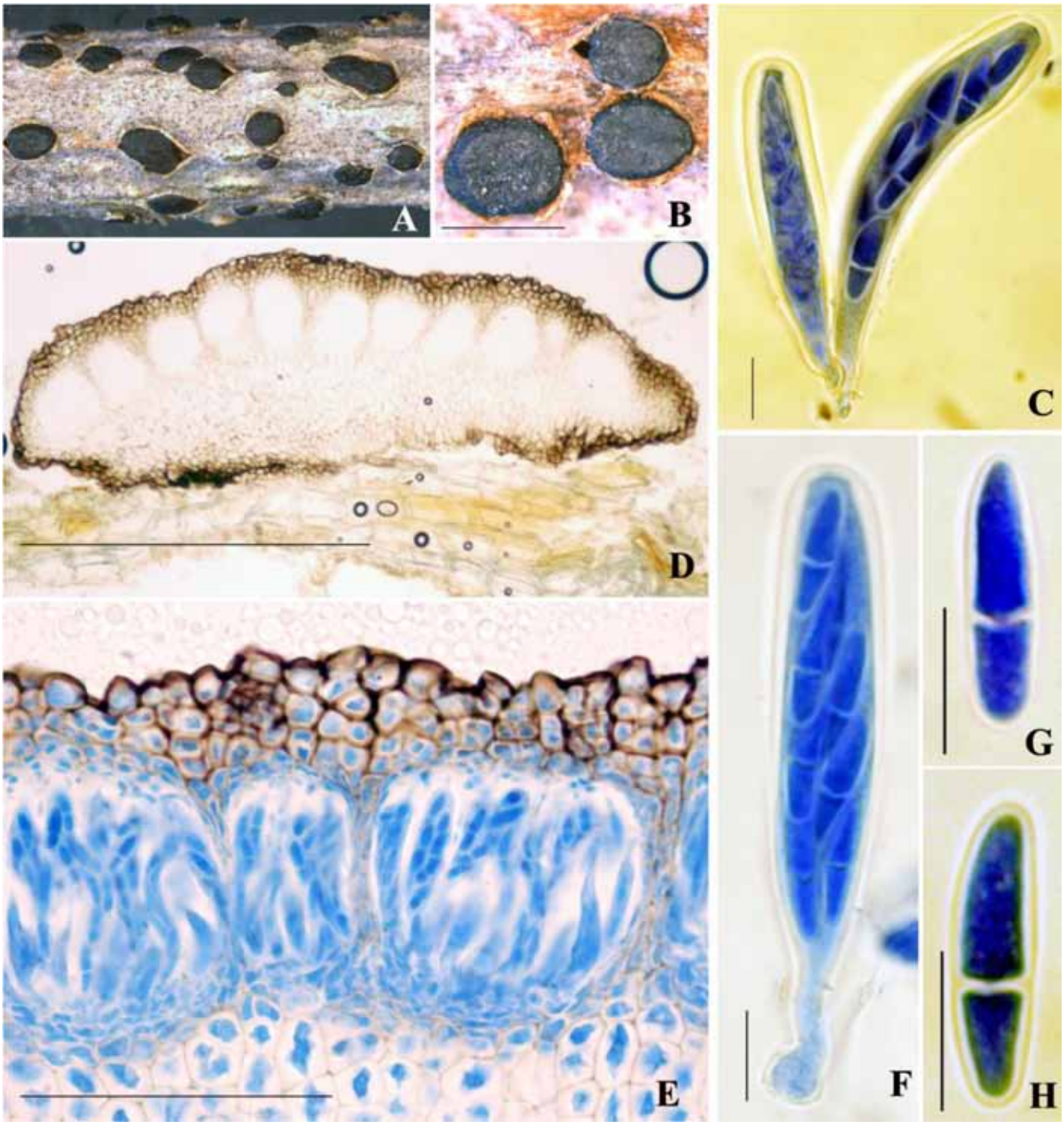

Fig. 1. *Dothidea sambuci.* A–B. Appearance of ascomata on the host surface. C, F. Asci in cotton blue reagent. D. Vertical section through ascomata illustrating the mutilocule at the upper layer. E. Vertical section through ascomata in cotton blue reagent illustrating the locule. G–H. Ascospores in cotton blue reagent. Scale bars: B = 1000 µm; C = 500 µm; E = 100 µm; F–H = 10 µm.

of various morphological characters used in the aforementioned classifications. The clearest correlation with a DNA sequence-based phylogeny was for the presence or absence of pseudoparaphyses, largely agreeing with the first orders proposed by Luttrell (Liew *et al.* 2000, Lumbsch & Lindemuth 2001). Barr's concept of applying the shape of the pseudoparaphyses to define orders was rejected by molecular phylogenies (Liew *et al.* 2000). This set the stage for more comprehensive analyses incorporating protein data, and resulted in the definition of two subclasses, *Pleosporomycetidae* (pseudoparaphyses present) and the *Dothideomycetidae* (pseudoparaphyses absent; Schoch *et al.* 2006). Numerous orders and other taxa remained unresolved outside of these two subclasses.

The most recent class level phylogenetic analyses combining sequences from protein coding genes with ribosomal RNA sequences fortified the view that *Dothideomycetes* is a monophyletic group (Schoch *et al.* 2009a, b). Furthermore, strong support was found for a sister relationship between *Dothideomycetes* and the lichenised class *Arthoniomycetes* (Lumbsch *et al.* 2005, Spatafora *et al.* 2006, Schoch *et al.* 2009a). This clade was recently defined as a rankless taxon "Dothideomyceta" (Schoch *et al.* 2009a, b). The *Arthoniomycetes* consists of a single order (*Arthoniales*) of lichens and lichenicolous fungi (Ertz *et al.* 2009) that produce bitunicate asci in ascohymenial apothecia and was proposed as an intermediate group or "Zwischengruppe" (Henssen & Thor 1994). This placement raises intriguing questions regarding the origins of

ascolocular development and further illustrates the importance of including lichen-forming fungi in dothideomycete phylogenies.

While considerable progress has been made in defining these fungi the placement of *Dothideomycetes* in relation to the majority of other *Ascomycota* classes remains unresolved. Here, greater clarity would likely require a huge increase of characters from genome projects. In this regard, the first phylogenomic studies have shown low resolution for this relationship (Fitzpatrick *et al.* 2006, Kuramae *et al.* 2006, Robbertse *et al.* 2006). This could indicate a rapid radiation event, but more likely suggests taxon sampling bias. This latter view is supported by the fact that none of these studies has included lichenised species that represent about 25 % of the number of species in *Ascomycota*.

The authors of this volume have focused on two primary goals. These are to considerably expand the taxon sampling of existing orders by including saprobes, asexual species and other poorly sampled groups. Secondly we aim to sample widely within specific environmental niches and present a multigene phylogeny that exposes the highly diverse nature of *Dothideomycetes*.

MATERIAL AND METHODS

DNA extraction, amplification and sequencing

The majority of fungal cultures were obtained from the CBS culture collection and additional sources mentioned in other papers of this volume. DNA was also provided by authors of several papers presented in this volume and the reader is referred to Boehm *et al*. (2009a), Crous *et al*. (2009a), Suetrong *et al*. (2009) and Zhang *et al*. (2009). For additional details see Table 1 - see online Supplementary Information. Fungal genomic DNA was obtained by scraping mycelium from PDA plates. Samples were subsequently pulverised and the DNA was extracted using the FastDNA® kit and the FastPrep® instrument from MPI Biochemicals (Irvine, CA, U.S.A.). DNA amplifications were completed using *Taq* polymerase (GenScript, Piscataway, NJ, U.S.A.), with FailSafe™ PCR 2× PreMix E (Epicentre, San Diego, CA, U.S.A.). Primers were used as noted in the Assembling the Fungal Tree of Life project (AFTOL; Schoch *et al.* 2009a). This resulted in DNA sequence data obtained from the small and large subunits of the nuclear ribosomal RNA genes (SSU, LSU) and three protein coding genes, namely the translation elongation factor-1 alpha (*TEF1*) and the largest and second largest subunits of RNA polymerase II (*RPB1, RPB2*). Primer sets used for these genes were as follows: SSU: NS1/NS4; LSU: LR0R/LR5; *TEF1* 983/2218R (initially obtained from S. Rehner: ocid.nacse.org/research/deephyphae/EF1primer.pdf); *RPB2*: fRPB2-SF/fRPB2-7cR; *RPB1*: RPB1-Ac/RPB1-Cr (obtained from V. Hofstetter). Primer sequences are available at the WASABI database at the AFTOL website (aftol.org). PCRs for these genes were performed in various laboratories of the coauthors mentioned but the majority of reactions were run under conditions described previously (Lutzoni *et al.* 2004, Schoch *et al.* 2009a). Two duplicate sets of sequences were inadvertently included in the analysis (indicated in Table 1).

Sequence alignment and phylogenetic analyses

Sequences were obtained from WASABI (Kauff *et al.* 2007) as well as from previous publications (*e.g.* Lutzoni *et al*. 2004, Schoch *et al*. 2009a). Introns were removed and an initial core set of 171 taxa were aligned by using default options for a simultaneous method of estimating alignments and tree phylogenies, SATé (Liu *et al.* 2009). In order to consider codons without the insertion of unwanted gaps, protein coding fragments were translated in BioEdit v. 7.0.1 (Hall 2004) and aligned within SATé as amino acids. These were then realigned with their respective DNA sequences using the RevTrans 1.4 Server (Wernersson & Pedersen 2003). After the removal of intron sequences the alignment was examined manually in BioEdit with a shade threshold of 40 % and regions with high amounts of gap characters were excluded. This resulted in a reduction of 99 columns in the LSU data set, 118 in *RPB1* and 162 in *RPB2*, for a total of 379. Nothing was removed for *TEF1*. In order to allow for the extension of our alignment as newly generated sequences became available from other studies in this volume, these were subsequently added to this core alignment with MAFFT v. 6.713 (Katoh *et al.* 2009). The E-INS-i setting, focused on high accuracy with a high percentage of unalignable regions such as introns, was applied and the SATé alignment was used as a seed. This resulted in a supermatrix of five genes (LSU, SSU *TEF1*, *RPB1*, *RPB2*) consisting of 52 % gaps and undetermined characters out of a total of 6 582 characters. GenBank accession numbers are shown in Table 1.

Conflict tests

Conflict tests on the initial core set of 204 taxa were conducted by selecting single gene data sets and doing comparisons on a gene by gene basis. This was done using the "bootstopping" criterion in RAxML v. 7.0.4 (Stamatakis *et al*. 2008) under the CIPRES v. 2.1 webportal to produce trees of comparative gene sets where all taxa have the gene present. Comparisons between all potential sets of gene trees with no missing taxa were done using a script (Kauff & Lutzoni 2002) obtained through the Lutzoni lab website and to detect present or absent taxa within clades with a cut-off bootstrap value of 70 %. This is described in more detail elsewhere (Miadlikowska *et al.* 2006, Schoch *et al.* 2009a).

Phylogeny

A phylogenetic analysis was performed using RAxML v. 7.0.4 (Stamatakis 2006) applying unique model parameters for each gene and codon. The dataset was divided in 11 partitions as previously described in Schoch *et al.* (2009a). A general time reversible model (GTR) was applied with a discrete gamma distribution and four rate classes following procedures laid out in Schoch *et al*. (2009). Ten thorough maximum likelihood (ML) tree searches were done in RAxML v. 7.0.4 under the same model, each one starting from a randomised tree. Bootstrap pseudo replicates were performed 2000 times using the fast bootstrapping option and the best scoring tree form 10 separate runs were selected. The resulting trees were printed with TreeDyn v. 198.3 (Chevenet *et al.* 2006). All alignments are deposited in TreeBASE. Additionally, the data sets were analyzed in GARLI v. 0.96 (Zwickl 2006) using the GTR-gamma-invariant model. In this case 200 bootstraps were run under default conditions.

Fig. 2A–C. (Page 5–7). Best scoring ML tree with RAxML and GARLI bootstrap values respectively above (green) and below (red) the nodes. Values below 50 % were removed and branches with more than 90 % bootstrap for both methods are thickened without values. Environmental sources relevant to the papers in this volume are indicated in the key (R-Rock; M-Marine; F-Freshwater; D-Dung; B-Bamboo). Nutritional characters are indicated by colour as per the key.

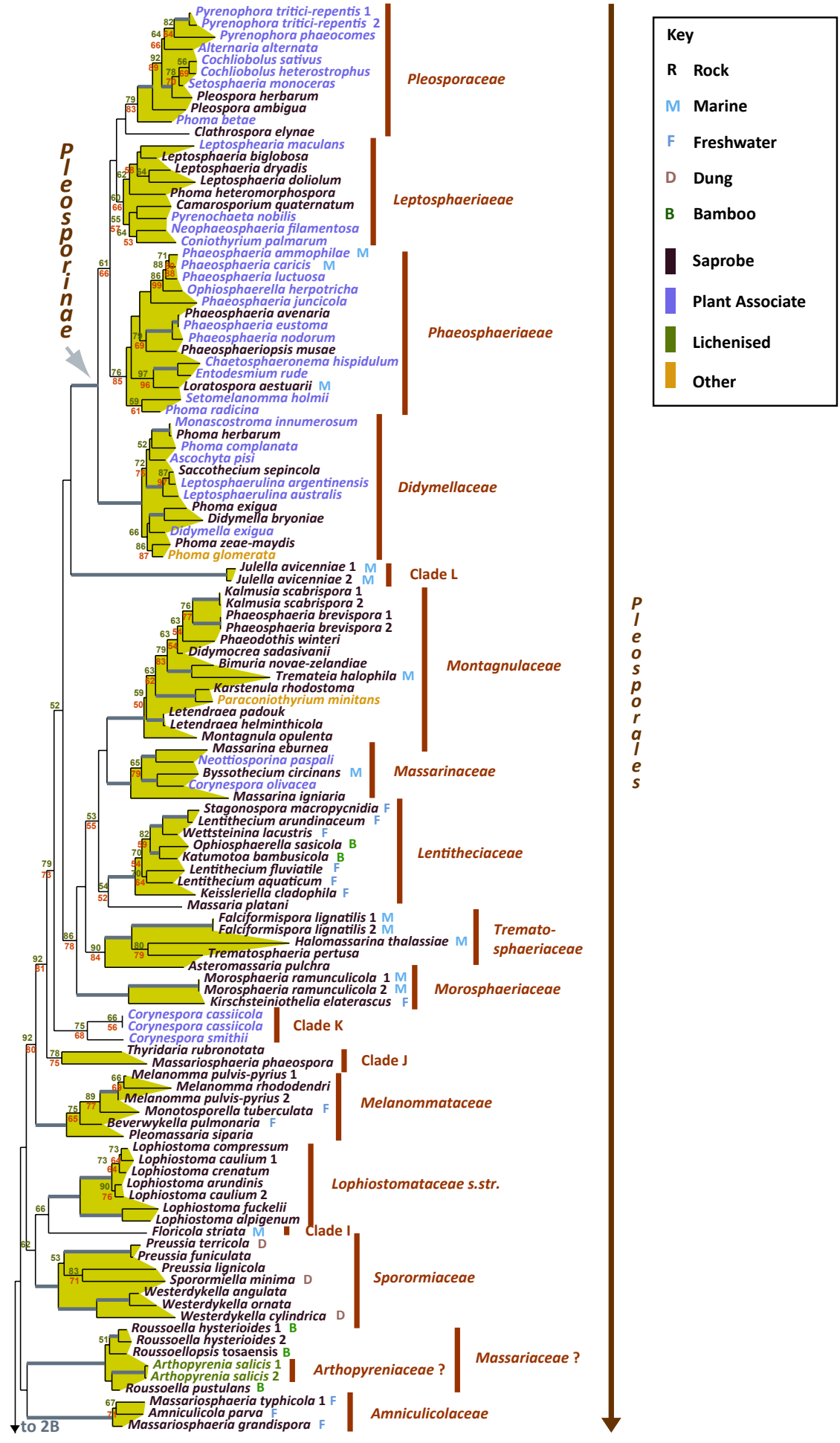
Pyrenophora tritici-repentis 1
Pyrenophora tritici-repentis 2
Pyrenophora phaeocomes
Alternaria alternata
Cochliobolus sativus
Cochliobolus heterostrophus
Setosphaeria monoceras
Pleospora herbarum
Pleospora ambigua
Phoma betae
Clathrospora elynae
Pleosporaceae
Leptosphearia maculans
Leptosphaeria biglobosa
Leptosphaeria dryadis
Leptosphaeria doliolum
Phoma heteromorphospora
Camarosporium quaternatum
Pyrenochaeta nobilis
Neophaeosphaeria filamentosa
Coniothyrium palmarum
Leptosphaeriaeae
Phaeosphaeria ammophilae M
Phaeosphaeria caricis M
Phaeosphaeria luctuosa
Ophiosphaerella herpotricha
Phaeosphaeria juncicola
Phaeosphaeria avenaria
Phaeosphaeria eustoma
Phaeosphaeria nodorum
Phaeosphaeriopsis musae
Chaetosphaeronema hispidulum
Entodesmium rude
Loratospora aestuarii M
Setomelanomma holmii
Phoma radicina
Phaeosphaeriaeae
Monascostroma innumerosum
Phoma herbarum
Phoma complanata
Ascochyta pisi
Saccothecium sepincola
Leptosphaerulina argentinensis
Leptosphaerulina australis
Phoma exigua
Didymella bryoniae
Didymella exigua
Phoma zeae-maydis
Phoma glomerata
Didymellaceae
Julella avicenniae 1 M
Julella avicenniae 2 M
Clade L
Kalmusia scabrispora 1
Kalmusia scabrispora 2
Phaeosphaeria brevispora 1
Phaeosphaeria brevispora 2
Phaeodothis winteri
Didymocrea sadasivanii
Bimuria novae-zelandiae
Trematheia halophila M
Karstenula rhodostoma
Paraconiothyrium minitans
Letendraea padouk
Letendraea helminthicola
Montagnula opulenta
Montagnulaceae
Massarina eburnea
Neottiosporina paspali
Byssothecium circinans M
Corynespora olivacea
Massarina igniaria
Massarinaceae
Stagonospora macropycnidia F
Lentithecium arundinaceum F
Wettsteinina lacustris F
Ophiosphaerella sasicola B
Katumotoa bambusicola B
Lentithecium fluviatile F
Lentithecium aquaticum F
Keissleriella cladophila F
Massaria platani
Lentitheciaceae
Falciformispora lignatilis 1 M
Falciformispora lignatilis 2 M
Halomassarina thalassiae M
Trematosphaeria pertusa
Asteromassaria pulchra
Trematosphaeriaceae
Morosphaeria ramunculicola 1 M
Morosphaeria ramunculicola 2 M
Kirschsteiniothelia elaterascus F
Morosphaeriaceae
Corynespora cassiicola
Corynespora cassiicola
Corynespora smithii
Clade K
Thyridaria rubronotata
Massariosphaeria phaeospora
Clade J
Melanomma pulvis-pyrius 1
Melanomma rhododendri
Melanomma pulvis-pyrius 2
Monotosporella tuberculata F
Beverwykella pulmonaria F
Pleomassaria siparia
Melanommataceae
Lophiostoma compressum
Lophiostoma caulium 1
Lophiostoma crenatum
Lophiostoma arundinis
Lophiostoma caulium 2
Lophiostoma fuckelii
Lophiostoma alpigenum
Lophiostomataceae s.str.
Floricola striata M
Clade I
Preussia terricola D
Preussia funiculata
Preussia lignicola
Sporormiella minima D
Westerdykella angulata
Westerdykella ornata
Westerdykella cylindrica D
Sporormiaceae
Roussoella hysterioides 1 B
Roussoella hysterioides 2
Roussoellopsis tosaensis B
Arthopyrenia salicis 1
Arthopyrenia salicis 2
Arthopyreniaceae ?
Roussoella pustulans B
Massariaceae ?
Massariosphaeria typhicola 1 F
Amniculicola parva F
Massariosphaeria grandispora F
Amniculicolaceae
to 2B
Pleosporinae
Pleosporales
Key
R Rock
M Marine
F Freshwater
D Dung
B Bamboo
Saprobe
Plant Associate
Lichenised
Other

Fig. 2A.

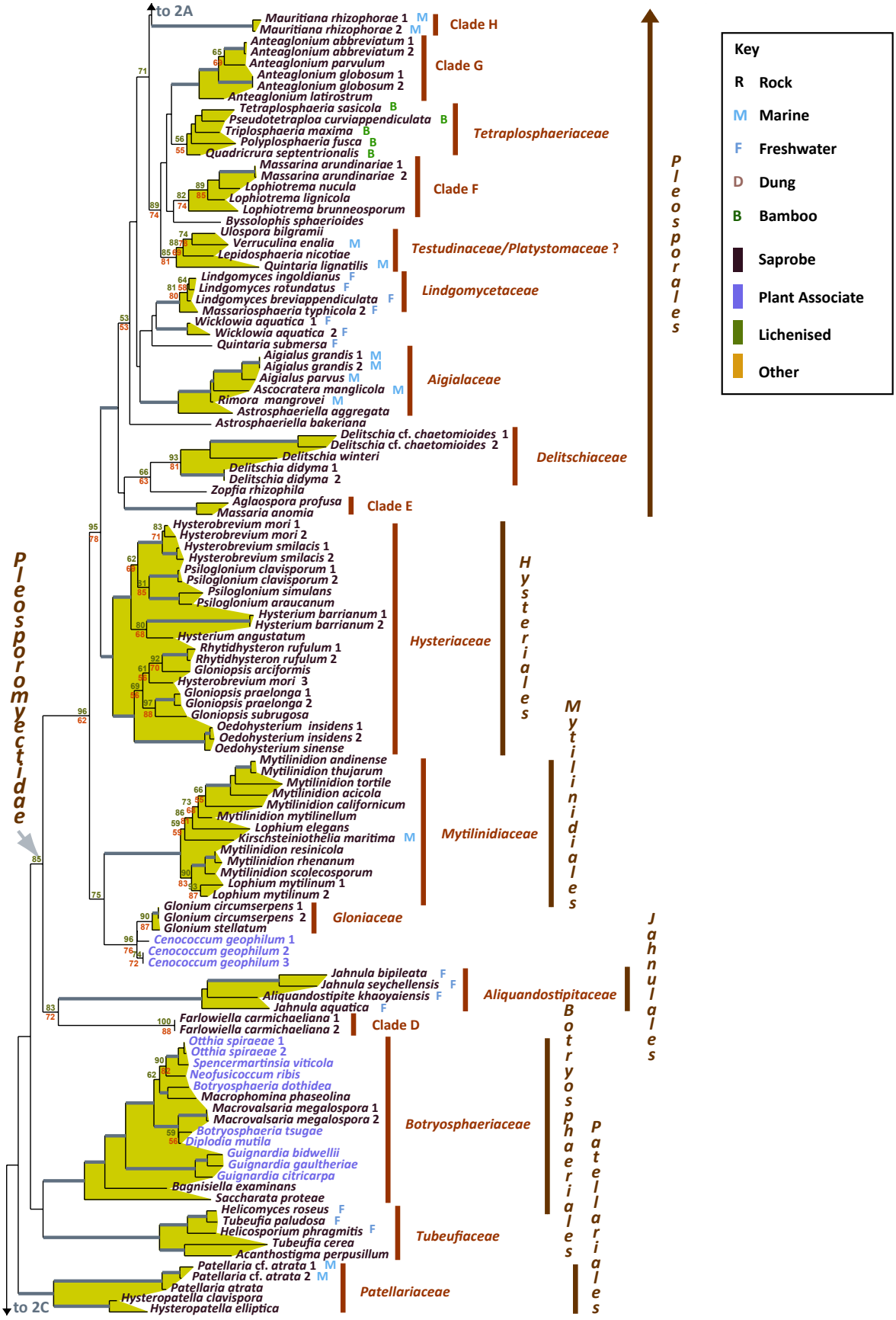
to 2A
Mauritiana rhizophorae 1 M
Mauritiana rhizophorae 2 M
Clade H
Anteaglonium abbreviatum 1
Anteaglonium abbreviatum 2
Anteaglonium parvulum
Anteaglonium globosum 1
Anteaglonium globosum 2
Anteaglonium latirostrum
Clade G
Tetraplosphaeria sasicola B
Pseudotetraploa curviappendiculata B
Triplosphaeria maxima B
Polyplosphaeria fusca B
Quadricrura septentrionalis B
Tetraplosphaeriaceae
Massarina arundinariae 1
Massarina arundinariae 2
Lophiotrema nucula
Lophiotrema lignicola
Lophiotrema brunneosporum
Clade F
Byssolophis sphaerioides
Ulospora bilgramii
Verruculina enalia M
Lepidosphaeria nicotiae
Quintaria lignatilis M
Testudinaceae/Platystomaceae ?
Lindgomyces ingoldianus F
Lindgomyces rotundatus F
Lindgomyces breviappendiculata F
Massariosphaeria typhicola 2 F
Lindgomycetaceae
Wicklowia aquatica 1 F
Wicklowia aquatica 2 F
Quintaria submersa F
Aigialus grandis 1 M
Aigialus grandis 2 M
Aigialus parvus M
Ascocratera manglicola M
Rimora mangrovei M
Astrosphaeriella aggregata
Aigialaceae
Astrosphaeriella bakeriana
Delitschia cf. chaetomioides 1
Delitschia cf. chaetomioides 2
Delitschia winteri
Delitschia didyma 1
Delitschia didyma 2
Delitschiaceae
Zopfia rhizophila
Aglaospora profusa
Massaria anomia
Clade E
Pleosporales
Pleosporomycetidae
Hysterobrevium mori 1
Hysterobrevium mori 2
Hysterobrevium smilacis 1
Hysterobrevium smilacis 2
Psiloglonium clavisporum 1
Psiloglonium clavisporum 2
Psiloglonium simulans
Psiloglonium araucanum
Hysterium barrianum 1
Hysterium barrianum 2
Hysterium angustatum
Rhytidhysteron rufulum 1
Rhytidhysteron rufulum 2
Gloniopsis arciformis
Hysterobrevium mori 3
Gloniopsis praelonga 1
Gloniopsis praelonga 2
Gloniopsis subrugosa
Oedohysterium insidens 1
Oedohysterium insidens 2
Oedohysterium sinense
Hysteriaceae
Hysteriales
Mytilinidion andinense
Mytilinidion thujarum
Mytilinidion tortile
Mytilinidion acicola
Mytilinidion californicum
Mytilinidion mytilinellum
Lophium elegans
Kirschsteiniothelia maritima M
Mytilinidion resinicola
Mytilinidion rhenanum
Mytilinidion scolecosporum
Lophium mytilinum 1
Lophium mytilinum 2
Mytilinidiaceae
Mytilinidiales
Glonium circumserpens 1
Glonium circumserpens 2
Glonium stellatum
Gloniaceae
Cenococcum geophilum 1
Cenococcum geophilum 2
Cenococcum geophilum 3
Jahnula bipileata F
Jahnula seychellensis F
Aliquandostipite khaoyaiensis F
Jahnula aquatica F
Aliquandostipitaceae
Jahnulales
Farlowiella carmichaeliana 1
Farlowiella carmichaeliana 2
Clade D
Otthia spiraeae 1
Otthia spiraeae 2
Spencermartinsia viticola
Neofusicoccum ribis
Botryosphaeria dothidea
Macrophomina phaseolina
Macrovalsaria megalospora 1
Macrovalsaria megalospora 2
Botryosphaeria tsugae
Diplodia mutila
Guignardia bidwellii
Guignardia gaultheriae
Guignardia citricarpa
Bagnisiella examinans
Saccharata proteae
Botryosphaeriaceae
Helicomyces roseus F
Tubeufia paludosa F
Helicosporium phragmitis F
Tubeufia cerea
Acanthostigma perpusillum
Tubeufiaceae
Botryosphaeriales
Patellaria cf. atrata 1 M
Patellaria cf. atrata 2 M
Patellaria atrata
Hysteropatella clavispora
Hysteropatella elliptica
Patellariaceae
Patellariales
to 2C
Key
R Rock
M Marine
F Freshwater
D Dung
B Bamboo
Saprobe
Plant Associate
Lichenised
Other

Fig. 2B.

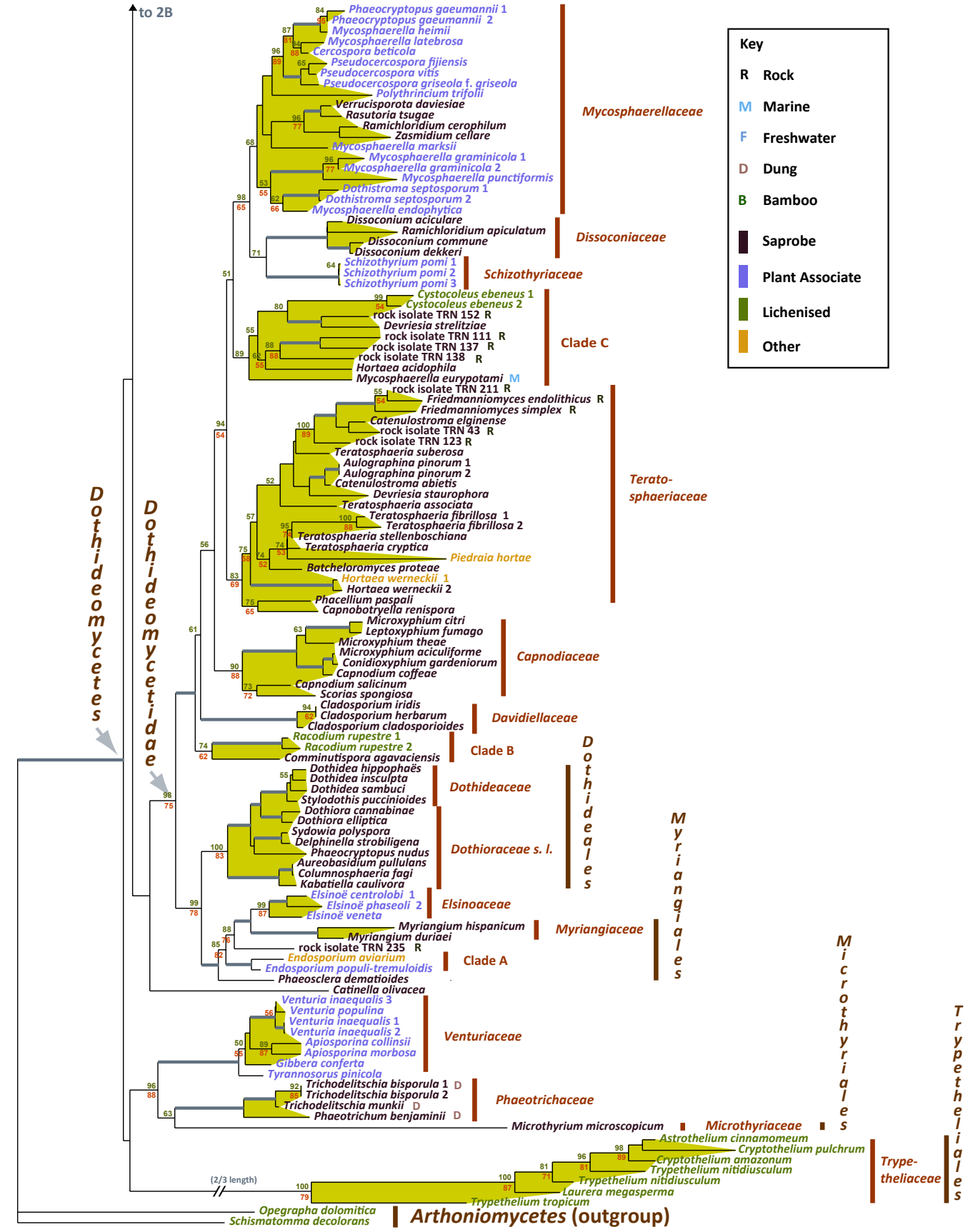
to 2B
Key
R Rock
M Marine
F Freshwater
D Dung
B Bamboo
Saprobe
Plant Associate
Lichenised
Other
Dothideomycetes
Dothideomycetidae
Mycosphaerellaceae
Dissoconiaceae
Schizothyriaceae
Clade C
Teratosphaeriaceae
Capnodiaceae
Davidiellaceae
Clade B
Dothideaceae
Dothioraceae s. l.
Dothideales
Elsinoaceae
Myriangiaceae
Myriangiales
Clade A
Venturiaceae
Phaeotrichaceae
Microthyriaceae
Microthyriales
Trypetheliaceae
Trypetheliales
(2/3 length)
Opegrapha dolomitica
Schismatomma decolorans
Arthoniomycetes (outgroup)

Fig. 2C.

Ancestral reconstruction

Ancestral reconstructions were performed in Mesquite v. 2.6 with character states traced over 2000 bootstrapped trees obtained with RAxML-MPI v. 7.0.4 (Stamatakis 2006). Following the phylogeny presented (Fig. 2) this reconstruction was performed with a maximum-likelihood criterion using the single parameter Mk1 model. Ancestral states were assigned to a node if the raw likelihood was higher by at least 2 log units than the likelihood value of the other ancestral state(s) according to default settings. Character states were also mapped using TreeDyn v. 198.3 (Chevenet *et al.* 2006), shown in Fig. 3. This is presented as a clockwise circular tree, starting with outgroup taxa. Only clades with more than two taxa of the same state are shown and bootstrap recovery was not considered in assigning character states. In applying the character states of saprobes (including rock heterotrophs), plant associated fungi (including pathogens, endophytes and mycorrhizae) and lichenised fungi the broad concepts presented were followed as laid out in Schoch *et al.* (2009a). Some character assessments were taken from Zhang *et al*. (2009; this volume). Ecological characters of sampling sources, terrestrial, fresh water and marine were assessed based on papers elsewhere in this volume (Suetrong *et al*. 2009*,* Shearer *et al*. 2009*)*.

Genome analyses

A MCL (Markov Cluster Algorithm) protein analysis of 52 fungi and one metazoan (*Drosophila melanogaster*) (Table 2 - see online Supplementary Information) and the phylogenetic placement of these species was used to characterise the phylogenetic profile of each cluster. *Chytridiomycota* and *Mucoromycotina* each were represented by one and two species, respectively. In *Dikarya*, *Basidiomycota* and *Ascomycota* were represented by 8 and 40 species respectively. The *Pezizomycotina* (filamentous ascomycetes) was presented by 26 species in four classes [*Sordariomycetes* (12), *Leotiomycetes* (2), *Dothideomycetes* (6) and *Eurotiomycetes* (6)].

RESULTS AND DISCUSSION

Taxon sampling

The phylogram presented in Fig. 2 represents the largest ever phylogenetic assessment of *Dothideomycetes* to date. Here the focus has been on expanding taxon diversity in the class while specifically avoiding a small number of taxa that other analyses suggest reside on long unstable branches. This still allowed for an extensive sweep of dothideomycete taxon diversity; in doing so we followed the premise of allowing for missing data in our supermatrix (Wiens 2006). An effort was made to intersperse taxa with poor character sampling amongst those having better sampling throughout the tree, but the inclusion of missing characters could still have unanticipated effects on phylogenetic assessments (Lemmon *et al.* 2009). While recognising this caveat, a recent expansive data set covering all of *Ascomycota* noted very little changes in major nodes even after the removal of taxa with high proportions of missing characters (Schoch *et al.* 2009a). The phylogeny presented here agrees well with broad phylogenies in this volume and elsewhere (Schoch *et al.* 2006, Crous *et al.* 2007a, Zhang *et al.* 2008, Crous *et al.* 2009b). After all introns and 379 ambiguous character positions were removed, the matrix consisted of 52 % missing and indeterminate characters. This maximum-likelihood analysis had 5 069 distinct alignment patterns and produced a best known likely tree with a log likelihood of -207247.761117.

Evolution of nutritional modes

The ancestral reconstructions in Fig. 3 indicate that phytopathogenicity can be confined to a number of terminal clades throughout the tree and that these always reside within saprobic lineages. A maximum of seven transitions likely occurred in several lineages of the orders *Pleosporales, Capnodiales* and singular lineages in *Myriangiales*, *Botryosphaeriales* and *Venturiaceae* (also see in this volume; Crous *et al.* 2009a, Zhang *et al.* 2009). Several transitions to lichenisation have also occurred, although phylogenetic uncertainty may limit this to a minimum of two. Due to the use of lichenised *Arthoniomycetes* as outgroup a broader assessment is required to determine whether the *Dothideomycetes* evolved from a lichenised ancestor. Previous studies suggested that the saprobic habit is an ancestral trait but only with marginal support (Schoch *et al.* 2009a). Similar conclusions can be reached for the aquatic ecological characters – the majority of fresh water and marine clades reside within terrestrial clades as has been shown previously *e.g.* (Spatafora *et al.* 1998, Vijaykrishna *et al.* 2006). Transitions from a terrestrial life style to fresh water likely occurred at least three times and transitions to marine environments up to six times. Phylogenetic uncertainty for the placement of some marine clades can limit this to a minimum of four times (Fig. 2). Reversions from aquatic to terrestrial environments are rare, with one possible exception in the *Lentitheciaceae* where bambusicolous saprobes reside, nested within several fungi occurring in freshwater habitats (for additional details see Zhang *et al.* 2009; this volume). Phylogenetic resolution will have to improve to test this further.

An analysis of recently released genomes was compared to consider whether genome composition reinforces phylogenetic support for *Dothideomycetes* (Fig. 4). Relative to a clustering analysis of proteins from 52 sequenced fungi and *Drosophila melanogaster*, about 5 515 protein coding genes from *Dothideomycetes* shared protein clusters with proteins from other dothideomycete fungi only. This comprises roughly 8–11 % of the protein coding genes in each of six sequenced *Dothideomycetes*. The species profile of each protein cluster was used to assign a phylogenetically informed designation. The profiles most frequently seen were those of the most conserved proteins, namely clusters designated as having a shared Ophistokont phylogenetic profile. Among the more derived nodes of the *Dothideomycetes*, protein clusters were observed that had a species composition that could reflect the result of selection pressure on more distantly related fungi that share the same niche.

A phylogenomic profile (Fig. 4) of the proteins from six *Dothideomycetes* from the two largest orders seen in Fig. 1 is presented (*Mycosphaerella graminicola, Mycosphaerella fijiensis, Phaeosphaeria nodorum, Alternaria brassicicola, Pyrenophora tritici-repentis, Cochliobolus heterostrophus*). The highest percentage of proteins (excluding species specific proteins) were conserved outside kingdom *Fungi* (Ophistokont node, 23 %), followed by proteins specific for the *Dikarya* (14 %) and the *Pezizomycotina* (13 %). This breakdown was also prevalent within other *Pezizomycotina* classes. Approximately 8 % of the proteins from the six *Dothideomycetes* were conserved across and within derived nodes in this class. Relative to this analysis 28 % of the proteins were specific to the *Dothideomycetes* (including species specific proteins). The other class containing loculoascomyetes, *Eurotiomycetes,* had 19.5 % proteins characterised as class specific. This means the percentage dothideomycete specific proteins were about 8.5 % more. *Eurotiomycetes* in the analysis were mostly human pathogens, with most having no known sexual state whereas the *Dothideomycetes* in the analysis were all plant

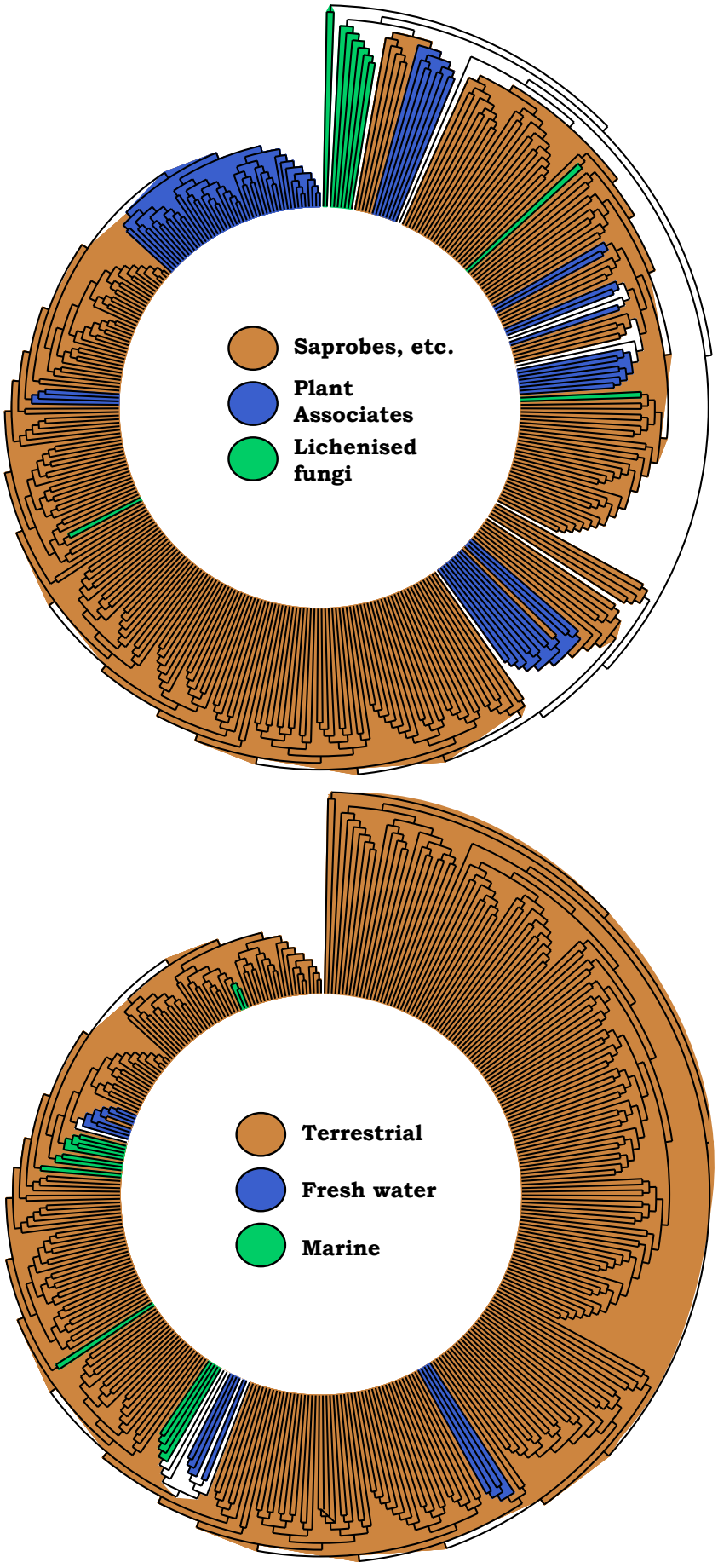

Fig. 3. Simplified ancestral state reconstructions, showing potential transitions between character states. The same phylogeny as in Fig. 2A–C is shown, with the outgroups positioned at twelve o' clock and subsequent clades arranged in a clockwise manner. Characters were traced over 2 000 bootstrap trees and those that were recovered in the majority are coloured on the nodes. In the case of equivocal construction no colour was used (white). To simplify the figure, only clades with two or more neighbouring character states are shown.

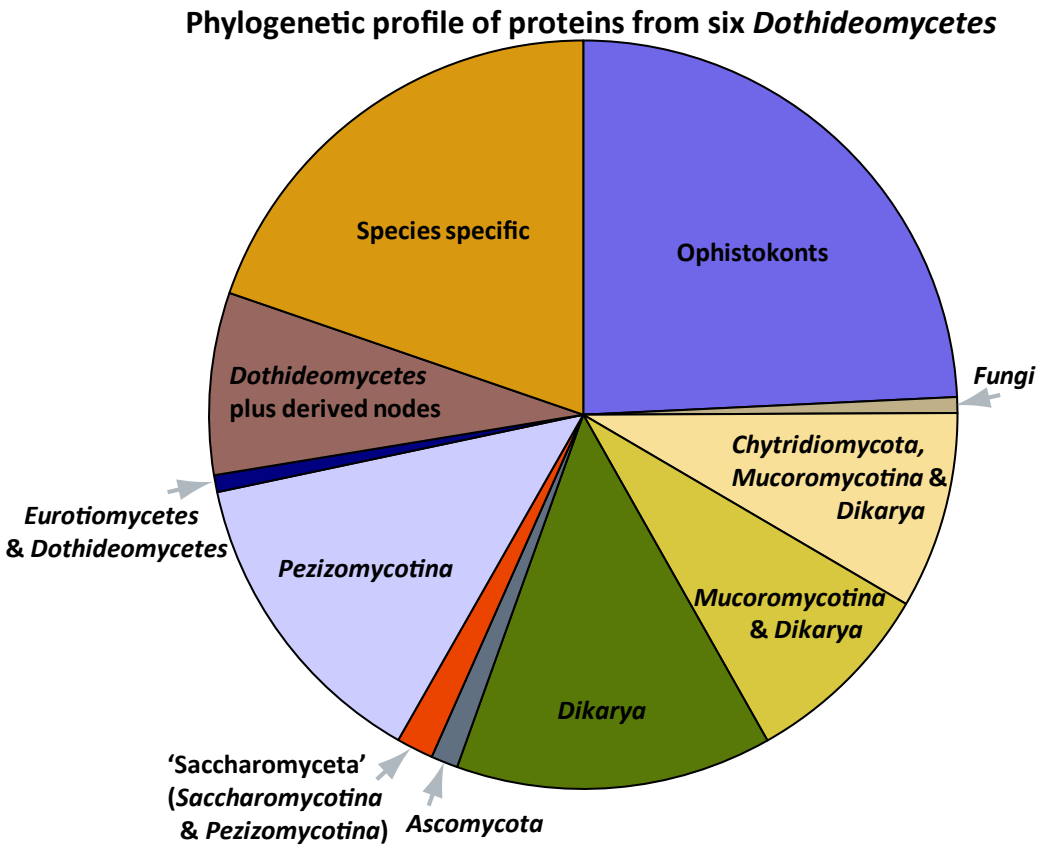

Fig. 4. Pie chart showing relative numbers of unique proteins per genome according to taxonomic classification.

pathogens and mostly with known sexual states. This breakdown of nutritional modes, although not comprehensive for these two classes, is somewhat representative. In *Eurotiomycetes* human pathogens are more diverse and plant pathogens uncommon, with the converse being true for *Dothideomycetes*. Both classes contain melanised species with similar morphologies and more comprehensive comparative studies need to expand sampling to incorporate species from the different nutritional modes for both classes.

Phylogenetic relationships

In the phylogram presented (Fig. 2) the two dothideomycete subclasses previously described based on presence or absence of pseudoparaphyses (Schoch *et al.* 2006) could be recovered with varying levels of bootstrap representation. Subclass *Pleosporomycetidae* previously included *Pleosporales* plus a single species, representing *Mytilinidiaceae*, namely *Lophium mytilinum* (Schoch *et al.* 2006). Taxon sampling for the *Mytilinidiaceae* was considerably expanded by Boehm *et al*. (2009b), with the addition of a number of new taxa, leading to the establishment of the *Mytilinidiales*. Likewise, extensive taxon sampling for the family *Hysteriaceae* led to a newly redefined *Hysteriales* also included in this subclass (Boehm *et al.* 2009a; this volume). It appears that persistent, hysteriaceous carbonaceous ascomata that dehisce via a longitudinal slit (*e.g.*, hysterothecia) have evolved multiple times within *Pleosporomycetidae* (Mugambi & Huhndorf 2009). *Pleosporomycetidae* can be expanded to tentatively include *Jahnulales* (Fig. 2B) based on strong bootstrap support from RAxML analyses and morphology. Perithecioid ascomata and a hamathecium of wide cellular pseudoparaphyses are characteristic of *Jahnulales* (Inderbitzin *et al.* 2001, Pang *et al.* 2002; Shearer *et al.* 2009; this volume) and agree with diagnostic features for *Pleosporomycetidae*. We also recommend that the definition of the subclass be reassessed with more inclusive character sets. Also, *Leptosphaerulina* species characterised by the absence of pseudoparaphyses reside within the pseudoparaphysate *Pleosporales* (Fig. 2C; Silva-Hanlin & Hanlin 1999, Kodsueb *et al.* 2006), indicating that pseudoparaphyses could have been lost multiple times. It should be noted that the maturity of ascomata may play an important role in these assessments. Immature specimens may contain pseudoparaphyses that dehisce when mature and these characteristics need to be evaluated with more complete sampling of the numerous aparaphysate taxa still listed as *incertae sedis*. The second subclass, *Dothideomycetidae,* previously circumscribed based on the absence of pseudoparaphyses remains well supported (Fig. 2C).

The results of this study provided continued support for ten orders within class *Dothideomycetes*, namely *Pleosporales*, *Hysteriales*, *Mytilinidiales*, *Patellariales*, *Botryosphaeriales*, *Jahnulales*, *Dothideales*, *Capnodiales, Myriangiales* and *Trypetheliales*. The latter order was recently proposed (Aptroot *et al.* 2008) and represents the largest lichen forming clade in *Dothideomycetes*. Another recently proposed order, *Botryosphaeriales* includes only the single family, *Botryosphaeriaceae*. The analysis (Fig. 2B), however, shows strong support for a narrower interpretation of the *Botryosphaeriaceae,* typified by *Botryosphaeria dothidea* and related genera, excluding a separate clade of species residing in *Guignardia* (with *Phyllosticta* anamorphs). *Bagnisiella examinens* and *Saccharata protea* did not reside in either of the above clades, placed on early diverging branches. A more extensive taxon sampling is required to address the diversity in this order, which most likely will validate the separation of additional families. Another currently accepted order, *Microthyriales*, consisting of

species occurring as saprobes or epiphytes on stems and leaves is represented in this study by only a single sample, *Microthyrium microscopicum* (Fig. 2C). Members of this order are poorly represented in culture and have unusual thyrothecial ascomata that have a scutate covering comprising a thin layer of radiating cells. This structure is generally lacking a basal layer and is quite unlike any morphologies in other orders. This positioning adjacent to the plant parasitic *Venturiaceae* and coprophilic *Phaeotrichaceae*, is unexpected but since the single representative of the *Microthyriales* is on a long branch this is a relationship that will require more intensive taxon sampling.

Additional families that could not be placed in an order are *Tubeufiaceae* and *Gloniaceae* (Fig. 2B). Species in *Tubeufiaceae* have superficial clustered ascomata and characteristic bitunicate asci with relatively long ascospores, often with helicosporous anamorphs (Kodsueb *et al.* 2008). Members of *Tubeufiaceae*, which frequently occur in freshwater habitats include anamorph genera, such as *Helicoon* and *Helicodendron,* and are ecologically classified as aeroaquatic species. A few teleomorph taxa such as *Tubeufia asiana* occur on submerged wood (Tsui *et al*. 2007), and *Tubeufia paludosa* occur on herbaceous substrates in wet habitats (Webster 1951). The *Gloniaceae* are saprobic, have dichotomously branched, laterally anastomosed pseudothecia that form radiating pseudo-stellate composites and dehisce by an inconspicuous, longitudinal, but evaginated slit. They reside sister to the saprobic *Mytilinidiales* but due to conspicuous morphological differences and moderate statistical support they are placed in *Pleosporomycetidae incertae sedis* (Boehm *et al.* 2009a, this volume).

Several other well supported clades representing families were evident in this study (Fig. 2). These include several families in *Pleosporales,* treated elsewhere (Zhang *et al.* 2009; this volume). Other clades have lower levels of support. For example *Leptosphaeriaceae* (Fig. 2A) have moderate bootstrap support and it is treated in the very broad sense here. There was also support for several newly described families treated in different papers within this volume. In *Pleosporales* these include *Amniculicolaceae* and *Lentitheciaceae* (Zhang *et al.* 2009; this volume). The *Lindgomycetaceae* (Shearer *et al.* 2009; this volume, Hirayama *et al.* 2010) encompassing a majority of species isolated from fresh water habitats. Two other novel families, *Aigialaceae* and *Morosphaeriaceae* include mainly marine species (Suetrong *et al.* 2009; this volume). In addition to these, the sampling of a wide diversity of fungi on bamboo yielded the description of *Tetraplosphaeriaceae* (Tanaka *et al.* 2009; this volume). Another novel family, *Dissoconiaceae,* is proposed by Crous *et al.* 2009 (this volume) for foliicolous commensalists on *Eucalyptus* leaves, some of which are putative hyper parasites and reside in *Capnodiales.*

Results of this study suggest that sampling within existing families also requires continued expansion as familial definitions in *Dothideomycetes* remains problematic. A paper focused on two families, with poor representation in molecular data sets, *Melanommataceae* and *Lophiostomataceae* addresses this in more detail (Mugambi & Huhndorf 2009; this volume). Numerous other clades in our tree remain without familial placement. This includes a diverse group in *Capnodiales* (Fig. 2C, clade C) a newly described group of hysteriaceous fungi in *Pleosporales* (Fig. 2A, clade G) and additional marine lineages (clades H, L, Fig. 2A). An interesting clade tentatively circumdescribed by Zhang *et al*. (2009; this volume) as *Massariaceae* contains bambusicolous fungi and appears related to the lichenised *Arthopyreniaceae* (Fig. 2A).

Finally, a clade including *Corynespora* anamorphs (clade K, Fig. 2A) is placed for the first time, but without clear relationship to any other currently defined families. The genus *Corynespora* includes anamorphic fungi with tretic, percurrent, and acropetal conidiogenesis. The melanised, pseudoseptate conidia have a pronounced hilum from which the conidial germ tube emerges and are borne apically from solitary, melanised conidiophores. Though nearly 100 species are described based on differences in morphology, considerable phenotypic plasticity within individual isolates complicates species recognition, and molecular analyses that may result in taxonomic clarification have not been done. *Corynespora* species fill a diversity of roles as saprobes, pathogens, and endophytes on and in woody and herbaceous plants, other fungi, nematodes, and human skin (Dixon *et al.* 2009). One of the species represented here, *C. cassiicola* is an important pathogen of rubber. The teleomorphic fungi *Pleomassaria swidae* (*Pleomassariaceae*; Tanaka *et al.* 2005) and *Corynesporasca caryotae* (*Corynesporascaceae*; Sivanesan 1996) have unnamed *Corynespora* species as anamorphs. In this study, species currently placed in *Corynespora* are not monophyletic and are positioned in at least two families: *Massarinaceae* and Clade K (Fig. 2A).

Anamorph taxa

The previously mentioned *Dissoconiaceae* relies on taxonomic descriptions based on anamorph characters. This is a theme that is expected to continue for mitosporic taxa in *Dothideomycetes* as molecular data accelerates their integration. The artificial nature of the "higher" taxa of anamorphs *e.g.*, deuteromycetes (Kirk *et al.* 2001) is now well recognised, but the integration of anamorphs into the phylogenetic classification of teleomorphs remains a significant challenge in fungal systematics (Shenoy *et al.* 2007). The correlation of teleomorphs and anamorphs (Seifert *et al.* 2000) is not always predictive but it has been applied in some genera within *Dothideomycetes*, *e.g. Botryosphaeria* and *Mycosphaerella* (Crous *et al.* 2006, 2009b). However, numerous examples underscoring anamorph convergence can be found throughout the class *e.g. Dictyosporium* (Tsui *et al.* 2006, Kodsueb *et al.* 2008), *Sporidesmium* (Shenoy *et al.* 2006), *Cladosporium* (Crous *et al.* 2007b) and *Phoma* (Fig. 2A; Aveskamp *et al.* 2009, de Gruyter *et al.* 2009, Woudenberg *et al.* 2009) as well as *Fusicoccum* and *Diplodia* (Crous *et al.* 2006, Phillips *et al.* 2008). The use of large multigene phylogenies will be essential to bring taxonomic order to cryptic anamorph lineages.

Ecological diversity

Besides the unclassified diversity found in anamorphic genera, numerous ecological niches contain diverse lineages of fungi lacking systematically sampled molecular characters. Several examples of this knowledge gap can be found in papers in this volume. In this regard, the rock inhabiting fungi are amongst the least understood. These fungi exist ubiquitously as melanised, slow growing colonies and that usually do not produce generative structures. They subsist on bare rock surfaces and are consequently highly tolerant of the environmental stresses induced by lack of nutrients, water and extremes in radiation and temperature (Palmer *et al.* 1990, Sterflinger 1998, Ruibal 2004, Gorbushina *et al.* 2008). Members of this ecological guild are diverse and occur in two classes – *Eurotiomycetes* and *Dothideomycetes*. Ruibal *et al.* 2009 (this volume) present the results of an expanded sampling of rock-inhabiting fungi that include lineages residing within *Dothideomycetes* and sister class *Arthoniomycetes*. These rock inhabiting fungi can be placed in

Capnodiales, *Pleosporales*, *Dothideales* and *Myriangiales*, as well as some unclassified lineages of *Dothideomycetes*. Interestingly, some associated lineages were without clear placement within either *Arthoniomycetes* or *Dothideomycetes*. The rock isolates included in Fig. 2C illustrate a subsection of genetic diversity seen in these extremophiles, in particular for the *Capnodiales*, with two rock isolates-rich lineages *Teratosphaeriaceae* and Clade C (Fig. 2C). A more detailed analysis (Ruibal *et al.* 2009; this volume) allows for the presentation of hypotheses related to evolution of pathogenicity and lichenisation because these modes of nutrition are often found in close proximity of rock inhabiting fungal lineages.

The lichenised fungi allied with the *Dothideomycetes* represent another poorly sampled group of fungi. Several lichenised species remain enigmatically placed after they were confirmed as members of *Dothideomycetes* based on DNA sequence data (Lumbsch *et al.* 2005, Del Prado *et al.* 2006). Although the number of species is comparatively small, their placement can play an important link in determining how transitions to and from lichenisation influenced dothideomycete evolution. *Trypetheliaceae* known for its anastomosing, branched pseudoparaphyses was until very recently still placed within *Pyrenulales*, an ascohymenial order in *Eurotiomycetes*, based on bitunicate asci and lense-shaped lumina in the ascospores (Del Prado *et al.* 2006). Attempts to resolve members of this family remain challenging as they tend to occur on long, rapidly evolving branches in our phylogenetic analyses, which often lead to artifacts. Nelsen *et al.* 2009 (this volume) demonstrate the occurrence of two additional lichen-forming lineages within *Dothideomycetes* representing the families *Strigulaceae* and *Monoblastiaceae*. The delineation of lichenised family *Arthopyreniaceae* should continue to be assessed given their placement with a clade containing bambusicolous fungi (Tanaka *et al.* 2009; this volume) and their non monophyly is also confirmed elsewhere (Nelsen *et al.* 2009; this volume). The relationship between the lichenised groups and bambusicolous genera *Roussoella* and *Roussoellopsis* (*Didymosphaeriaceae;* Ju *et al.* 1996, Lumbsch & Huhndorf 2007) is strongly supported, but their affinity is not fully understood due to their considerable morphological differences.

The fungi collected from marine and freshwater habitats contain yet more varied species that have not been assessed well within a molecular based framework. Their diversity is supported by the fact that whole orders (*Jahnulales*) and several families, already mentioned, almost exclusively consist of species collected from these environments. A recent assessment of marine fungi tallied a number of more than 500 species with more than a fifth of these suggested to reside in *Dothideomycetes* (Jones *et al.* 2009). The number for fungi from fresh water habitats is somewhat lower (about 170 taxa).

Despite similarities in their preferred medium for spore dispersal (water) an examination of phylogenetic diversity within *Dothideomycetes* indicates that these groups of fungi tend to reside in divergent parts of the tree (Figs 2, 3). However, some exceptions may occur: For example, members of *Aigialaceae* are weakly supported to share ancestry with members of freshwater clade *Lindgomycetaceae* (Raja *et al.* 2010). The *Jahnulales* represents another recently delineated aquatic lineage with an interesting mixture of fresh water and marine taxa. It was delineated based on molecular and morphological data (Inderbitzin *et al.* 2001, Pang *et al.* 2002) and now contains four genera and several species (Campbell *et al.* 2007). Previously, two anamorphic species in the *Jahnulales, Xylomyces rhizophorae* (described from mangrove wood of *Rhizophora)* and *X. chlamydosporus* have been reported from mangroves and thus saline habitats (Kohlmeyer & Volkmann-Kohlmeyer 1998). It has further been documented that *X. chlamydosporus* is the anamorph of *Jahnula aquatica,* a freshwater species (Sivichai, pers. comm.).

Marine *Dothideomycetes* generally exist in association with algae and plants in marine and brackish environments, usually with intertidal or secondary marine plants (*e.g.*, mangroves). The majority of these fungi have been classified in families and genera that comprise mostly terrestrial species (*e.g.*, *Pleospora*) and no definitive clades of marine *Dothideomycetes* have been identified. Here we find support for diverse aquatic lineages similar to the situation in *Sordariomycetes*. Papers by Suetrong *et al.* 2009 (this volume) and Shearer *et al.* 2009 (this volume) continue to address this disparity by using multigene phylogenies to describe several lineages within a class wide context. In contrast, many marine members of the *Dothideomycetes* await interrogation at the DNA sequence level, especially the genera *Belizeana, Thalassoascus, Lautospora* and *Loratospora,* all exclusively marine taxa.

The final environmentally defined group sampled in this volume is the bambusicolous fungi. More than 1 100 fungal species have been described or recorded worldwide from bamboo (Hyde *et al.* 2002). Furthermore, their ecological specialisation as pathogens, saprophytes, and endophytes has been relatively well documented (*e.g.* Hino 1961). However, relatively few studies based on DNA sequence comparisons have been undertaken for many bambusicolous fungi. Several unique lineages, *e.g.* the *Katumotoa bambusicola-Ophiosphaerella sasicola* clade in a freshwater lineage (*Lentitheciaceae*) and the *Roussoella-Roussoellopsis* clade close to lichen-forming families could be found (Fig. 2). Particularly, a new family *Tetraplosphaeriaceae* including five new genera characterised by a *Tetraploa* anamorph *s. l.* is introduced as a lineage of fungi with bamboo habitat (Tanaka *et al.* 2009; this volume). It is clear that much additional diversity within this group of fungi remains to be sampled using DNA sequence data

A number of other niches remain poorly discussed in this volume. Coprophilous fungi occur in three families *Delitschiaceae*, *Phaeotrichaceae*, and *Sporormiaceae* (Figs 2A, C). These families are not closely related and it is clear that the fimicolous life style has arisen more than once in the *Dothideomycetes*. Also, many species from these groups are not strictly dung-inhabiting, but can be found on other substrates like soil, wood, and plant-debris. Interestingly, some are human pathogens, plant endophytes and lichenicolous fungi. As is true throughout the *Ascomycota,* a change in substrate is apparently not a substantial evolutionary step in these taxa (Kruys & Wedin 2009).

Additional observations

Several orders *e.g. Dothideales*, *Myriangiales* and *Microthyriales* have not been treated using the extensive systematic sampling that is true for studies treated in this volume. However, individual smaller studies continue to provide interesting and surprising results. One such example is the first described meristematic and endoconidial species residing in *Myriangiales* (Fig. 2C) reported by Tsuneda *et al.* (2008). These *Endosporium* species were isolated from very different substrates such as: poplar twigs and a dead bird. They also have a close relationship to a single lineage of rock inhabiting fungi. The nutritional shifts represented by these closely related species correlate well with scenarios described by Ruibal *et al.* (2009; this volume) for rock inhabiting fungi. Another melanised meristematic fungus, *Sarcinomyces crustaceus*, isolated from pine trees appears in a similar position in a phylogeny presented in the aforementioned paper (Ruibal *et al.* 2009; this volume).

Another unusual species, *Catinella olivacea* is included in Fig. 2C, but without any clearly resolved position, diverging early to *Dothideomycetidae*. This species was initially placed in *Leotiomycetes,* due to their flattened apothecia, found on the underside of moist, well-decayed logs of hardwood. Asci are unitunicate but they appear to form after ascolocular development. As in the previous analysis, it was not possible to identify relationships between this species and any known order, although there are indications of a close relationship with the *Dothideomycetidae* (Greif *et al.* 2007).

The placement of the single asexual mycorrhizal lineage representing *Cenococcum geophilum* in the *Dothideomycetes* (LoBuglio *et al.* 1996), allied to members of the saprobic *Gloniaceae* is intriguing (Fig. 2B; Boehm *et al.* 2009a; this volume). No resolved placement for this species in *Dothideomycetes* has been possible in the past. The results of this study were also unexpected because no biological data suggest a connection to the family. *Cenococcum* is a fungus that is intensively used in environmental studies and this could suggest a very interesting biology for members of the ostensibly saprobic *Gloniaceae*. Results of this study advocate a more expansive sampling of *Cenococcum* in order to confirm this intriguing result.

CONCLUSIONS

One of the major obstacles in dothideomycete systematics remains the lack of a clear understanding of what species are members of the class based on morphology alone. Throughout most of the 20th Century, comparative morphological studies have been the only character on which to base phylogenetic relationships. The advent of large DNA-sequence data sets should allow for a substantially improved interpretation of morphological characters for this class of fungi. Studies in this volume and elsewhere have provided a clear understanding that many of the characters classically used in taxonomy and systematics of the group are homoplastic and not helpful for reconstructing phylogenetic relationships. Dothideomycete taxonomy also needs to keep pace with the rapid advances being made in phylogenetics, genomics and related fields. The important principle here is that our classification should communicate diversity accurately and allow dothideomycete biologists from disparate fields to have access to an agreed upon set of taxonomic names to aid communication. In addition, it should allow for a focus on under-sampled groups and clades (i.e. poorly sampled saprobes and others). A major task ahead will be to add asexual genera to present phylogenetic schemes, and integrate these into the existing familial and ordinal classification. As most of these asexual genera are in fact poly- and paraphyletic, their type species will need to be recollected to clarify their phylogenetic position. In addition to this, it appears that even some concepts of teleomorphic taxa will require extensive reconsideration. Finally, we should attempt to incorporate valuable biological information from past workers, such as the three mycologists to which this volume is dedicated, by reliably assessing culture and sequence identity. It is hoped that the papers in this volume will make a meaningful contribution towards these goals.

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SUPPLEMENTARY INFORMATION

Table 1. Isolates of *Dothideomycetes* included in this study. Newly deposited sequences are shown in bold.

Taxon	voucher/culture[1]	SSU	LSU	*RPB1*	*RPB2*	*TEF1*
Acanthostigma perpusillum	UAMH	AY856937	AY856892			
Aglaospora profusa	CBS 123109	**GU296130**	**GU301792**			**GU349062**
Aigialus grandis 1	2Q	**GU296132**	**GU301794**			**GU349063**
Aigialus grandis 2	JK 5244A	**GU296131**	**GU301793**		**GU371762**	
Aigialus parvus	A6	**GU296133**	**GU301795**		**GU371771**	**GU349064**
Aliquandostipite khaoyaiensis	CBS 118232	AF201453	**GU301796**		FJ238360	**GU349048**
Alternaria alternata	CBS 916.96	DQ678031	DQ678082		DQ677980	DQ677927
Amniculicola parva	CBS 123092	**GU296134**	FJ795497			**GU349065**
Anteaglonium abbreviatum 1	ANM 925.1		GQ221877			GQ221924
Anteaglonium abbreviatum 2	GKM 1029		GQ221878			GQ221915
Anteaglonium globosum 1	SMH 5283		GQ221911			GQ221919
Anteaglonium globosum 2	ANM 925.2		GQ221879			GQ221925
Anteaglonium latirostrum	L100N 2		GQ221876			GQ221938
Anteaglonium parvulum	SMH 5210		GQ221907			GQ221917
Apiosporina collinsii	CBS 118973	**GU296135**	**GU301798**	**GU357778**		**GU349057**
Apiosporina morbosa	dimosp		EF114694			
Arthopyrenia salicis 1	1994 Coppins		AY607730	AY607742		
Arthopyrenia salicis 2	CBS 368.94	AY538333	AY538339	**GU371814**		
Ascochyta pisi	CBS 126.54	DQ678018	DQ678070		DQ677967	DQ677913
Ascocratera manglicola	JK 5262C	**GU296136**	**GU301799**		**GU371763**	
Asteromassaria pulchra	CBS 124082	**GU296137**	**GU301800**		**GU371772**	**GU349066**
Astrosphaeriella aggregata	MAFF 239486	AB524450	AB524591		AB539105	AB539092
Astrosphaeriella bakeriana	CBS 115556		**GU301801**	**GU357752**		**GU349015**
Astrothelium cinnamomeum	DUKE 0000007		AY584652			DQ782896
Aulographina pinorum 1	CBS 302.71				**GU371766**	
Aulographina pinorum 2	CBS 174.90	**GU296138**	**GU301802**	**GU357763**	**GU371737**	**GU349046**
Aureobasidium pullulans	CBS 584.75	DQ471004	DQ470956	DQ471148	DQ470906	DQ471075
Bagnisiella examinans	CBS 551.66	**GU296139**	**GU301803**	**GU357776**	**GU371746**	**GU349056**
Batcheloromyces proteae	CBS 110696	AY251102	EU019247			
Beverwykella pulmonaria	CBS 283.53		**GU301804**		**GU371768**	
Bimuria novae-zelandiae	CBS 107.79	AY016338	AY016356	DQ471159	DQ470917	DQ471087
Botryosphaeria dothidea	CBS 115476	DQ677998	DQ678051	**GU357802**	DQ677944	DQ767637
Botryosphaeria tsugae	CBS 418.64	AF271127	DQ767655		DQ767644	DQ677914
Byssolophis sphaerioides	IFRDCC2053	**GU296140**	**GU301805**		GU456348	GU456263
Byssothecium circinans	CBS 675.92	AY016339	AY016357		DQ767646	**GU349061**
Camarosporium quaternatum	CBS 483.95	**GU296141**	**GU301806**	**GU357761**		**GU349044**
Capnobotryella renispora	CBS 215.90	AY220613	GQ852582			
Capnodium coffeae	CBS 147.52	DQ247808	DQ247800	DQ471162	DQ247788	DQ471089
Capnodium salicinum	CBS 131.34	DQ677997	DQ678050			DQ677889
Catenulostroma abietis (as *Trimmatostroma abietis*)	CBS 459.93	DQ678040	DQ678092	**GU357797**		DQ677933
Catenulostroma elginense	CBS 111030	GU214517	EU019252			
Catinella olivacea	UAMH 10679	DQ915484	EF622212			
Cenococcum geophilum 1	HUNT A1	L76616				
Cenococcum geophilum 2	CGMONT	L76617				
Cenococcum geophilum 3	10	L76618				

Table 1. (Continued).

Taxon	voucher/culture[1]	SSU	LSU	*RPB1*	*RPB2*	*TEF1*
Cercospora beticola	CBS 116456	DQ678039	DQ678091			DQ677932
Chaetosphaeronema hispidulum	CBS 216.75	EU754045	EU754144	**GU357808**	**GU371777**	
Cladosporium cladosporioides	CBS 170.54	DQ678004	DQ678057	**GU357790**	DQ677952	DQ677898
Cladosporium iridis (teleomorph *Davidiella macrospora*)	CBS 138.40		DQ008148			
Clathrospora elynae	CBS 196.54	**GU296142**	**GU323214**			
Cochliobolus heterostrophus	CBS 134.39	AY544727	AY544645		DQ247790	DQ497603
Cochliobolus sativus	DAOM 226212	DQ677995	DQ678045		DQ677939	
Columnosphaeria fagi	CBS 171.93	AY016342	AY016359		DQ677966	
Comminutispora agavaciensis	CBS 619 95	Y18699	EU981286			
Conidioxyphium gardeniorum	CPC 14327	**GU296143**	**GU301807**	**GU357774**	**GU371743**	**GU349054**
Coniothyrium palmarum	CBS 400.71	DQ678008	DQ767653		DQ677956	DQ677903
Corynespora cassiicola 1	CBS 100822	**GU296144**	**GU301808**	**GU357772**	**GU371742**	**GU349052**
Corynespora cassiicola 2	CCP	**GU296145**				
Corynespora olivacea	CBS 114450		**GU301809**			**GU349014**
Corynespora smithii	CABI 5649b		**GU323201**	**GU371804**	**GU371783**	**GU349018**
Cryptothelium amazonum	47		GU327713			GU327731
Cryptothelium pulchrum	63C		GU327714			
Cystocoleus ebeneus 1	L348	EU048573	EU048580			
Cystocoleus ebeneus 2	L315	EU048572				
Davidiella tassiana	CBS 399.80	DQ678022	DQ678074	**GU357793**	DQ677971	DQ677918
Delitschia cf. *chaetomioides* 1	GKM 3253.2		**GU390656**			
Delitschia cf. *chaetomioides* 2	GKM 1283		**GU385172**			
Delitschia didyma 1 (duplicate)	UME 31411		**DQ384090**			
Delitschia didyma 2	UME 31411	AF242264	DQ384090			
Delitschia winteri	CBS 225.62	DQ678026	DQ678077		DQ677975	DQ677922
Delphinella strobiligena	CBS 735.71		DQ470977	DQ471175	DQ677951	DQ471100
Devriesia staurophora	CBS 375.81	EF137359	DQ008151			
Devriesia strelitziae	CBS 122379	**GU296146**	**GU301810**		**GU371738**	**GU349049**
Didymella bryoniae (as *Phoma cucurbitacearum)*	CBS 133.96		**GU301863**		**GU371767**	
Didymella exigua	CBS 183.55	**GU296147**		**GU357800**	**GU371764**	
Didymocrea sadasivanii	CBS 438 65	DQ384066	DQ384103			
Diplodia mutila (teleomorph *Botryosphaeria stevensii*)	CBS 431.82	DQ678012	DQ678064		DQ677960	DQ677907
Dissoconium aciculare	CBS 204.89	GU214523	GQ852587			
Dissoconium commune (teleomorph *Mycosphaerella communis*)	CBS 110747	GU214525	GQ852589			
Dissoconium dekkeri (teleomorph *Mycosphaerella lateralis*)	CBS 111282	GU214531	GU214425			
Dothidea hippophaës	CBS 188.58	U42475	DQ678048	**GU357801**	DQ677942	DQ677887
Dothidea insculpta	CBS 189.58	DQ247810	DQ247802	DQ471154	AF107800	DQ471081
Dothidea sambuci	DAOM 231303	AY544722	AY544681		DQ522854	DQ497606
Dothiora cannabinae	CBS 737.71	DQ479933	DQ470984	DQ471182	DQ470936	DQ471107
Dothiora elliptica	CBS 736.71		**GU301811**			**GU349013**
Dothistroma septosporum 1 (teleomorph *Mycosphaerella pini*)	CBS 543 74		**GU301853**		**GU371730**	
Dothistroma septosporum 2	CBS 112498	GU214533	GQ852597			
Elsinoë centrolobi	CBS 222.50	DQ678041	DQ678094	**GU357798**		DQ677934
Elsinoë phaseoli	CBS 165.31	DQ678042	DQ678095	**GU357799**		DQ677935
Elsinoë veneta	CBS 150.27	DQ767651	DQ767658			DQ767641
Endosporium aviarium	UAMH 10530	EU304349	EU304351			

Table 1. (Continued).

Taxon	voucher/culture[1]	SSU	LSU	*RPB1*	*RPB2*	*TEF1*
Endosporium populi-tremuloidis	UAMH 10529	EU304346_	EU304348			
Entodesmium rude	CBS 650.86		**GU301812**			**GU349012**
Falciformispora lignatilis 1	BCC 21118	**GU371835**	**GU371827**			**GU371820**
Falciformispora lignatilis 2	BCC 21117	**GU371834**	**GU371826**			**GU371819**
Farlowiella carmichaeliana 2	CBS 179.73	**GU296148**				
Farlowiella carmichealiana 1 (as anamorph *Acrogenospora sphaerocephala*)	CBS 164.76	**GU296129**	**GU301791**	**GU357780**	**GU371748**	**GU349059**
Floricola striata	JK 5678I	**GU296149**	**GU301813**		**GU371758**	
Friedmanniomyces endolithicus	CCFEE 522	DQ066715				
Friedmanniomyces simplex	CBS 116775	DQ066716				
Gibbera conferta	CBS 191.53	**GU296150**	**GU301814**	**GU357758**		**GU349041**
Gloniopsis arciformis	GKM L166A	**GU323180**	**GU323211**			
Gloniopsis praelonga 1	CBS 112415	FJ161134	FJ161173		FJ161113	FJ161090
Gloniopsis praelonga 2	CBS 123337	FJ161154	FJ161195	FJ161103		FJ161103
Gloniopsis subrugosa	CBS 123346	FJ161170	FJ161210	**GU371808**	FJ161131	
Glonium circumserpens 1	CBS 123342	FJ161168	FJ161208			
Glonium circumserpens 2	CBS 123343	FJ161160	FJ161200	**GU371806**	FJ161126	FJ161108
Glonium stellatum	CBS 207.34	FJ161140	FJ161179			FJ161095
Guignardia bidwellii	CBS 237.48	DQ678034	DQ678085	**GU357794**	DQ677983	
Guignardia citricarpa	CBS 102374	**GU296151**	**GU301815**	**GU357773**		**GU349053**
Guignardia gaultheriae	CBS 447.70		DQ678089	**GU357796**	DQ677987	
Halomassarina ramunculicola 1 (as *Massarina ramunculicola*)	BCC 18404	GQ925838	GQ925853			
Halomassarina ramunculicola 2 (as *Massarina ramunculicola*)	BCC 18405	GQ925839	GQ925854			
Halomassarina thalassiae (as *Massarina thalassia*)	JK 5262D		**GU301816**			**GU349011**
Helicomyces roseus	CBS 283.51	DQ678032	DQ678083		DQ677981	DQ677928
Hortaea acidophila	CBS 113389		**GU323202**	**GU357768**		
Hortaea werneckii	CBS 708.76	**GU296153**	**GU301818**	**GU357779**	**GU371747**	**GU349058**
Hortaea werneckii	CBS 100496	**GU296152**	**GU301817**		**GU371739**	**GU349050**
Hysterium angustatum	CBS 123334	FJ161167	FJ161207		FJ161129	FJ161111
Hysterium barrianum 1	ANM 1495	**GU323182**	GQ221885			
Hysterium barrianum 2	ANM 1442	**GU323181**	GQ221884			
Hysterobrevium mori 1	CBS 123336	FJ161164	FJ161204			
Hysterobrevium mori 2	SMH 5273		**GU301820**			GQ221936
Hysterobrevium mori 3	GKM 1013		**GU301819**			**GU397338**
Hysterobrevium smilacis 1	CBS 114601	FJ161135	FJ161174	**GU357806**	FJ161114	FJ161091
Hysterobrevium smilacis 2	SMH 5280	**GU323183**	GQ221912	**GU371810**	**GU371784**	
Hysteropatella clavispora	CBS 247.34	DQ678006	AY541493		DQ677955	DQ677901
Hysteropatella elliptica	CBS 935.97	EF495114	DQ767657		DQ767647	DQ767640
Jahnula aquatica	R68-1	EF175633	EF175655			
Jahnula bipileata	F49-1	EF175635	EF175657			
Jahnula seychellensis	SS2113.1	EF175644	EF175665			
Julella avicenniae 1	BCC 18422	**GU371831**	**GU371823**		**GU371787**	**GU371816**
Julella avicenniae 2	BCC 20173	**GU371830**	**GU371822**		**GU371786**	**GU371815**
Kabatiella caulivora	CBS 242.64	EU167576	EU167576	**GU357765**		
Kalmusia scabrispora 1	MAFF 239517	AB524452	AB524593		AB539093	AB539106
Kalmusia scabrispora 2	NBRC 106237	AB524453	AB524594		AB539094	AB539107

Table 1. (Continued).

Taxon	voucher/culture[1]	SSU	LSU	*RPB1*	*RPB2*	*TEF1*
Karstenula rhodostoma	CBS 690.94	**GU296154**	**GU301821**		**GU371788**	**GU349067**
Katumotoa bambusicola	MAFF 239641	AB524454	AB524595		AB539095	AB539108
Keissleriella cladophila	CBS 104.55	**GU296155**	**GU301822**		**GU371735**	**GU349043**
Kirschsteiniothelia elaterascus	A22-5A / HKUCC7769	AF053727	AY787934			
Kirschsteiniothelia maritima	CBS 221.60		**GU323203**			**GU349001**
Laurera megasperma	AFTOL 2094		FJ267702			
Lentithecium aquaticum	CBS 123099	**GU296156**	**GU301823**		**GU371789**	**GU349068**
Lentithecium arundinaceum	CBS 619.86	**GU296157**	**GU301824**		FJ795473	
Lentithecium fluviatile	CBS 122367	**GU296158**	**GU301825**			**GU349074**
Lepidosphaeria nicotiae	CBS 101341		DQ678067		DQ677963	DQ677910
Leptosphaeria biglobosa	CBS 303.51		**GU301826**			**GU349010**
Leptosphaeria doliolum	CBS 505.75	**GU296159**	**GU301827**			**GU349069**
Leptosphaeria dryadis	CBS 643.86		**GU301828**		**GU371733**	**GU349009**
Leptosphaerulina argentinensis	CBS 569.94		**GU301829**	**GU357759**		**GU349008**
Leptosphaerulina australis	CBS 317.83	**GU296160**	**GU301830**		**GU371790**	**GU349070**
Leptosphearia maculans	DAOM 229267	DQ470993	DQ470946	DQ471136	DQ470894	DQ471062
Leptoxyphium fumago	CBS 123.26	**GU296161**	**GU301831**	**GU357771**	**GU371741**	**GU349051**
Letendraea helminthicola	CBS 884.85	AY016345	AY016362			
Letendraea padouk	CBS 485.70	**GU296162**	AY849951			
Lindgomyces breviappendiculata	HHUF 28193	AB521733	AB521748			
Lindgomyces ingoldianus	ATCC_200398	AB521719	AB521736			
Lindgomyces rotundatus	HHUF_27999	AB521723	AB521740			
Lophiostoma alpigenum	GKM 1091b		**GU385193**			
Lophiostoma arundinis	CBS 621.86	DQ782383	DQ782384		DQ782386	DQ782387
Lophiostoma caulium 1	CBS 623.86	**GU296163**	**GU301833**		**GU371791**	
Lophiostoma caulium 2	CBS 624.86		**GU301832**			**GU349007**
Lophiostoma compressum	IFRD 2014	**GU296164**	**GU301834**		FJ795457	
Lophiostoma crenatum	CBS 629.86	DQ678017	DQ678069		DQ677965	DQ677912
Lophiostoma fuckelii	GKM 1063		**GU385192**			
Lophiotrema brunneosporum	CBS 123095	**GU296165**	**GU301835**			**GU349071**
Lophiotrema lignicola	CBS 122364	**GU296166**	**GU301836**			**GU349072**
Lophiotrema nucula	CBS 627.86	**GU296167**	**GU301837**		**GU371792**	**GU349073**
Lophium elegans	EB 0366	**GU323184**	**GU323210**			
Lophium mytilinum 1	CBS 114111	EF596819	EF596819			
Lophium mytilinum 2	CBS 269.34	DQ678030	DQ678081		DQ677979	DQ677926
Loratospora aestuarii	JK 5535B	**GU296168**	**GU301838**		**GU371760**	
Macrophomina phaseolina	CBS 227.33	DQ678037	DQ678088		DQ677986	DQ677929
Macrovalsaria megalospora 1	178150	FJ215707	FJ215701			
Macrovalsaria megalospora 2	178149	FJ215706	FJ215700			
Massaria anomia	CBS 591.78	**GU296169**	**GU301839**		**GU371769**	
Massaria platani	CBS 221.37	DQ678013	DQ678065		DQ677961	DQ677908
Massarina arundinariae 1	MAFF 239461	AB524455	AB524596		AB539096	AB524817
Massarina arundinariae 2	NBRC 106238	AB524456	AB524597		AB539097	AB524818
Massarina eburnea	CBS 473.64	**GU296170**	**GU301840**	**GU357755**	**GU371732**	**GU349040**
Massarina igniaria	CBS 845.96	**GU296171**	**GU301841**		**GU371793**	
Massariosphaeria grandispora	CBS 613 86	**GU296172**	**GU301842**	**GU357747**	**GU371725**	**GU349036**

Table 1. (Continued).

Taxon	voucher/culture[1]	SSU	LSU	*RPB1*	*RPB2*	*TEF1*
Massariosphaeria phaeospora	CBS 611.86	**GU296173**	**GU301843**		**GU371794**	
Massariosphaeria typhicola 1	CBS 123126	**GU296174**	**GU301844**		**GU371795**	
Massariosphaeria typhicola 2	KT 797	AB521730	AB521747			
Mauritiana rhizophorae 1	BCC 28866	**GU371832**	**GU371824**		**GU371796**	**GU371817**
Mauritiana rhizophorae 2	BCC 28867	**GU371833**	**GU371825**		**GU371797**	**GU371818**
Melanomma pulvis-pyrius 1	SMH 3291		**GU385197**			
Melanomma pulvis-pyrius 2	CBS 371.75		**GU301845**		**GU371798**	**GU349019**
Melanomma rhododendri	ANM 73		**GU385198**			
Microthyrium microscopicum	CBS 115976	**GU296175**	**GU301846**		**GU371734**	**GU349042**
Microxyphium aciculiforme	CBS 892.73	**GU296176**	**GU301847**	**GU357762**	**GU371736**	**GU349045**
Microxyphium citri	CBS 451.66	**GU296177**	**GU301848**	**GU357750**	**GU371727**	**GU349039**
Microxyphium theae	CBS 202.30	**GU296178**	**GU301849**	**GU357781**		**GU349060**
Monascostroma innumerosum	CBS 345.50	**GU296179**	**GU301850**			**GU349033**
Monotosporella tuberculata	CBS 256.84		**GU301851**			**GU349006**
Montagnula opulenta	CBS 168.34	AF164370	DQ678086		DQ677984	
Mycosphaerella endophytica	CBS 114662	GU214538	DQ246255			
Mycosphaerella eurypotami	JK 5586J		**GU301852**		**GU371722**	
Mycosphaerella graminicola 1	CBS 292.38	DQ678033	DQ678084		DQ677982	
Mycosphaerella graminicola 2	CBS 115943	GU214540	GU214436			
Mycosphaerella heimii	CBS 110682	GU214541	GQ852604			
Mycosphaerella latebrosa	CBS 687.94	DQ848331	GU214444			
Mycosphaerella marksii	CBS 110942	GU214549	GQ852612			
Mycosphaerella punctiformis (anamorph *Ramularia endophylla*)	CBS 113265	DQ471017	DQ470968	DQ471165	DQ470920	DQ471092
Myriangium duriaei	CBS 260.36	AY016347	DQ678059		DQ677954	DQ677900
Myriangium hispanicum	CBS 247.33	**GU296180**	**GU301854**	**GU357775**	**GU371744**	**GU349055**
Mytilinidion acicola	EB 0349	**GU323185**	**GU323209**		**GU371757**	
Mytilinidion andinense	CBS 123562	FJ161159	FJ161199		FJ161125	FJ161107
Mytilinidion californicum	EB 0385	**GU323186**	**GU323208**			
Mytilinidion mytilinellum	CBS 303.34	FJ161144	FJ161184	**GU357810**	FJ161119	FJ161100
Mytilinidion resinicola	CBS 304.34	FJ161145	FJ161185	FJ161101	FJ161101	FJ161120
Mytilinidion rhenanum	EB 0341	**GU323187**	**GU323207**			
Mytilinidion scolecosporum	CBS 305.34	FJ161146	FJ161186	**GU357811**	FJ161121	FJ161102
Mytilinidion thujarum	EB 0268	**GU323188**	**GU323206**			
Mytilinidion tortile	EB 0377	**GU323189**	**GU323205**			
Neofusicoccum ribis (teleomorph *Botryosphaeria ribis*)	CBS 115475	DQ678000	DQ678053	**GU357789**	DQ677947	DQ677893
Neophaeosphaeria filamentosa	CBS 102202	GQ387516	GQ387577	**GU357803**	**GU371773**	**GU349084**
Neottiosporina paspali	CBS 331.37	EU754073	EU754172	**GU357812**	**GU371779**	**GU349079**
Oedohysterium insidens 1	CBS 238.34	FJ161142	FJ161182		FJ161118	FJ161097
Oedohysterium insidens 2	ANM 1443	**GU323190**	GQ221882	**GU371811**	**GU371785**	
Oedohysterium sinense	CBS 123345	FJ161169	FJ161209	**GU371807**	FJ161130	
Opegrapha dolomitica	DUKE 0047528	DQ883706		DQ883717	DQ883714	DQ883732
Ophiosphaerella herpotricha	CBS 620.86	DQ678010	DQ678062		DQ677958	DQ677905
Ophiosphaerella sasicola	MAFF 239644	AB524458	AB524599		AB539098	AB539111
Otthia spiraeae 1	CBS 114124	EF204515	EF204498			
Otthia spiraeae 2	CBS 113091	EF204516	EF204499	**GU357777**		
Paraconiothyrium minitans	CBS 122788	EU754074	EU754173	**GU357807**	**GU371776**	**GU349083**

Table 1. (Continued).

Taxon	voucher/culture[1]	SSU	LSU	*RPB1*	*RPB2*	*TEF1*
Patellaria atrata	CBS 958.97	**GU296181**	**GU301855**	**GU357749**	**GU371726**	**GU349038**
Patellaria cf. *atrata* 1	BCC 28876	**GU371836**	**GU371828**			
Patellaria cf. *atrata* 2	BCC 28877	**GU371837**	**GU371829**			
Phacellium paspali	CBS 113093	GU214669	GQ852627			
Phaeocryptopus gaeumannii 1	CBS 244.38			**GU357766**	**GU371740**	
Phaeocryptopus gaeumannii 2	CBS 267.37	EF114722	EF114698	**GU357770**		
Phaeocryptopus nudus	CBS 268.37	**GU296182**	**GU301856**	**GU357745**		**GU349034**
Phaeodothis winteri	CBS 182.58	**GU296183**	**GU301857**			**DQ677917**
Phaeosclera dematioides	CBS 157.81	**GU296184**	**GU301858**	**GU357764**		**GU349047**
Phaeosphaeria ammophilae	CBS 114595	**GU296185**	**GU301859**	**GU357746**	**GU371724**	**GU349035**
Phaeosphaeria avenaria	DAOM 226215	AY544725	AY544684		DQ677941	DQ677885
Phaeosphaeria brevispora 1	NBRC 106240	AB524460	AB524601		AB539100	AB539113
Phaeosphaeria brevispora 2	MAFF 239276	AB524459	AB524600		AB539099	AB539112
Phaeosphaeria caricis	CBS 120249		**GU301860**			**GU349005**
Phaeosphaeria eustoma	CBS 573.86	DQ678011	DQ678063		DQ677959	DQ677906
Phaeosphaeria juncicola	CBS 595.86					**GU349016**
Phaeosphaeria luctuosa	CBS 308.79		**GU301861**			**GU349004**
Phaeosphaeria nodorum	Broad	Genome	Genome	Genome	Genome	Genome
Phaeosphaeriopsis musae	CBS 120026	**GU296186**	**GU301862**	**GU357748**		**GU349037**
Phaeotrichum benjaminii	CBS 541.72	AY016348	AY004340	**GU357788**	DQ677946	DQ677892
Phoma betae	CBS 109410	EU754079	EU754178	**GU357804**	**GU371774**	**GU349075**
Phoma complanata	CBS 268.92	EU754081	EU754180	**GU357809**	**GU371778**	**GU349078**
Phoma exigua	CBS 431.74	EU754084	EU754183	**GU357813**	**GU371780**	**GU349080**
Phoma glomerata	CBS 528.66	EU754085	EU754184		**GU371781**	**GU349081**
Phoma herbarum	CBS 276.37	DQ678014	DQ678066	**GU357792**	DQ677962	DQ677909
Phoma heteromorphospora	CBS 115.96	EU754089	EU754188		**GU371775**	**GU349077**
Phoma radicina	CBS 111.79	EU754092	EU754191	**GU357805**		**GU349076**
Phoma zeae-maydis	CBS 588.69	EU754093	EU754192	**GU357814**	**GU371782**	**GU349082**
Piedraia hortae	CBS 480.64	AY016349	AY016366		DQ677990	
Pleomassaria siparia	CBS 279.74	DQ678027	DQ678078		DQ677976	DQ677923
Pleospora ambigua	CBS 113979		AY787937	**GU357760**		
Pleospora herbarum	CBS 191.86	DQ247812	DQ247804	DQ471163	DQ247794	DQ471090
Polyplosphaeria fusca	MAFF 239685	AB524463	AB524604			
Polythrincium trifolii (as *Cymadothea trifolii*)	133	EU167612	EU167612			
Preussia funiculata	CBS 659.74	**GU296187**	**GU301864**		**GU371799**	**GU349032**
Preussia lignicola (as *Sporormia lignincola*)	CBS 264.69	**GU296197**	**GU301872**		**GU371765**	**GU349027**
Preussia terricola	DAOM 230091	AY544726	AY544686	DQ471137	DQ470895	DQ471063
Pseudocercospora fijiensis (teleomorph *Mycosphaerella fijiensis*)	OSC 100622	DQ767652	DQ678098		DQ677993	
Pseudocercospora griseola f. *griseola*	CPC 10461	**GU323191**	**GU348997**			
Pseudocercospora vitis	CPC 11595	DQ289864	GU214483			
Pseudotetraploa curviappendiculata	MAFF 239495	AB524467	AB524608			
Psiloglonium araucanum	CBS 112412	FJ161133	FJ161172	**GU357743**	FJ161112	FJ161089
Psiloglonium clavisporum 1	CBS 123338	FJ161156	FJ161197		FJ161123	
Psiloglonium clavisporum 2	GKM L172A	**GU323192**	**GU323204**			
Psiloglonium simulans	CBS 206.34	FJ161139	FJ161178		FJ161116	FJ161094
Pyrenochaeta nobilis	CBS 407.76		DQ678096		DQ677991	DQ677936

Table 1. (Continued).

Taxon	voucher/culture[1]	SSU	LSU	*RPB1*	*RPB2*	*TEF1*
Pyrenophora phaeocomes	DAOM 222769	DQ499595	DQ499596		DQ497614	DQ497607
Pyrenophora tritici-repentis 1	OSC 100066		AY544672			DQ677882
Pyrenophora tritici-repentis 2	CBS 328.53					**GU349017**
Quadricrura septentrionalis	CBS 125429	AB524474	AB524615			
Quintaria lignatilis	CBS 117700	**GU296188**	**GU301865**		**GU371761**	
Quintaria submersa	CBS 115553		**GU301866**	**GU357751**		**GU349003**
Racodium rupestre 1	L423	EU048576	EU048581			
Racodium rupestre 2	L424	EU048577	EU048582			
Ramichloridium apiculatum	CBS 156.59	**GU296189**			**GU371770**	
Ramichloridium cerophilum	CBS 103.59	**GU296190**	EU041855			
Rasutoria tsugae	ratstk	EF114730	EF114705	**GU371809**		
Rhytidhysterium rufulum 2	CBS 306.38	**GU296191**	FJ469672	FJ238444		**GU349031**
Rhytidhysteron rufulum 1	GKM 361A	**GU296192**	**GU301867**			
Rimora mangrovei	JK 5246A	**GU296193**	**GU301868**		**GU371759**	
rock isolate TRN 111	CBS 118294	**GU323193**	**GU323220**	**GU357783**	**GU371751**	**GU349088**
rock isolate TRN 123	CBS 117932	**GU323194**	**GU323219**	**GU357784**	**GU371753**	
rock isolate TRN 137	CBS 118300	**GU323195**	**GU323218**	**GU357782**	**GU371749**	
rock isolate TRN 138	CBS 118301	**GU323196**	**GU323217**		**GU371750**	
rock isolate TRN 152	CBS 118346	**GU323197**	**GU323223**		**GU371752**	
rock isolate TRN 211	CBS 117937	**GU323198**	**GU323222**	**GU357785**	**GU371754**	
rock isolate TRN 235	CBS 118605	**GU323199**		**GU357787**	**GU371756**	**GU349087**
rock isolate TRN 43	CBS 117950	**GU323200**	**GU323221**	**GU357786**	**GU371755**	**GU349086**
Roussoella hysterioides 1	MAFF 239636	AB524480	AB524621		AB539101	AB539114
Roussoella hysterioides 2	CBS 125434	AB524481	AB524622		AB539102	AB539115
Roussoella pustulans	MAFF 239637	AB524482	AB524623		AB539103	AB539116
Roussoellopsis tosaensis	MAFF 239638		AB524625		AB539104	AB539117
Saccharata proteae	CBS 115206	**GU296194**	**GU301869**	**GU357753**	**GU371729**	**GU349030**
Saccothecium sepincola	CBS 278.32	**GU296195**	**GU301870**		**GU371745**	**GU349029**
Schismatomma decolorans	DUKE 0047570	AY548809	AY548815		DQ883715	DQ883725
Schizothyrium pomi 1	CBS 406.61	EF134949	EF134949			
Schizothyrium pomi 2	CBS 486.50	EF134948	EF134948			
Schizothyrium pomi 3	CBS 228.57	EF134947	EF134947			
Scorias spongiosa	CBS 325.33	DQ678024	DQ678075		DQ677973	DQ677920
Setomelanomma holmii	CBS 110217	**GU296196**	**GU301871**		**GU371800**	**GU349028**
Setosphaeria monoceras	AY016368		AY016368			
Spencermartinsia viticola (teleomorph *Botryosphaeria viticola*)	CBS 117009	DQ678036	DQ678087	**GU357795**	DQ677985	
Sporormiella minima	CBS 524.50	DQ678003	DQ678056		DQ677950	DQ677897
Stagonospora macropycnidia	CBS 114202	**GU296198**	**GU301873**			**GU349026**
Stylodothis puccinioides	CBS 193.58		AY004342	FJ238427		DQ677886
Sydowia polyspora	CBS 116.29	DQ678005	DQ678058	**GU357791**	DQ677953	DQ677899
Teratosphaeria associata (as *Teratosphaeria jonkershoekensis*)	CBS 112224	**GU296200**	**GU301874**	**GU357744**	**GU371723**	**GU349025**
Teratosphaeria cryptica (as *Mycosphaerella cryptica*)	CBS 110975	GU214602	GQ852682			
Teratosphaeria fibrillosa 1	CBS 121707	**GU296199**	**GU323213**	**GU357767**		
Teratosphaeria fibrillosa 2	CPC 1876		GU214506			
Teratosphaeria stellenboschiana (as *Colletogloeopsis stellenboschiana*)	CBS 116428	GU214583	EU019295			

Table 1. (Continued).

Taxon	voucher/culture[1]	SSU	LSU	*RPB1*	*RPB2*	*TEF1*
Teratosphaeria suberosa (as *Mycosphaerella suberosa*)	CPC 11032	GU214614	GQ852718			
Tetraplosphaeria sasicola	MAFF 239677	AB524490	AB524631			
Thyridaria rubronotata	CBS 419.85		**GU301875**		**GU371728**	**GU349002**
Tremateia halophila	JK 5517J	**GU296201**			**GU371721**	
Trematosphaeria pertusa	CBS 122371	**GU348999**	**GU301876**		**GU371801**	**GU349085**
Trichodelitschia bisporula 1	CBS 262.69	**GU349000**	**GU348996**	**GU371812**	**GU371802**	**GU349020**
Trichodelitschia bisporula 2 (duplicate)	CBS 262.69	**GU296202**				
Trichodelitschia munkii	Kruys201	DQ384070	DQ384096			
Triplosphaeria maxima	MAFF 239682	AB524496	AB524637			
Trypethelium nitidiusculum 1	139		GU327728			GU327732
Trypethelium nitidiusculum 2	AFTOL 2099		FJ267701			
Trypethelium tropicum	25		GU327730			
Tubeufia cerea	CBS 254.75	DQ471034	DQ470982	DQ471180	DQ470934	DQ471105
Tubeufia paludosa	CBS 120503	**GU296203**	**GU301877**	**GU357754**	**GU371731**	**GU349024**
Tubeufia paludosa (as anamorph *Helicosporium phragmitis*)	CBS 245.49	DQ767649	DQ767654		DQ767643	DQ767638
Tyrannosorus pinicola	CBS 124.88	DQ471025	DQ470974	DQ471171	DQ470928	DQ471098
Ulospora bilgramii	CBS 110020	DQ678025	DQ678076		DQ677974	DQ677921
Venturia inaequalis 1	CBS 594.70	**GU296205**	**GU301879**	**GU357757**		**GU349022**
Venturia inaequalis 2	CBS 815.69	**GU296204**	**GU301878**	**GU357756**		**GU349023**
Venturia inaequalis 3 (as *Spilocaea pomi*)	CBS 176.42		**GU348998**			**GU349089**
Venturia populina	CBS 256.38	**GU296206**	**GU323212**	**GU357769**		
Verrucisporota daviesiae	CBS 116002	**GU296207**	GQ852730			
Verruculina enalia	JK 5253A	DQ678028	DQ678079		DQ677977	DQ677924
Westerdykella angulata (as *Eremodothis angulata*)	CBS 610.74	DQ384067	DQ384105	**GU371805**		**GU371821**
Westerdykella cylindrica	CBS 454.72	AY016355	AY004343	DQ471168	DQ470925	DQ497610
Westerdykella ornata	CBS 379.55	**GU296208**	**GU301880**		**GU371803**	**GU349021**
Wettsteinina lacustris	CBS 618.86	DQ678023			DQ677972	DQ677919
Wicklowia aquatica	AF289-1		GU045446			
Wicklowia aquatica	CBS 125634	GU266232	GU045445	**GU371813**		
Zasmidium cellare	CBS 146.36	EF137362	EU041878			
Zopfia rhizophila	CBS 207.26	DQ384086	DQ384104			

[1]BCC: Belgian Coordinated Collections of Microorganisms; CABI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, U.K.; CBS: Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; DAOM: Plant Research Institute, Department of Agriculture (Mycology), Ottawa, Canada; DUKE: Duke University Herbarium, Durham, North Carolina, U.S.A.; HHUF: Herbarium of Hirosaki University, Japan; IFRDCC: Culture Collection, International Fungal Research & Development Centre, Chinese Academy of Forestry, Kunming, China; MAFF: Ministry of Agriculture, Forestry and Fisheries, Japan; NBRC: NITE Biological Resource Centre, Japan; OSC: Oregon State University Herbarium, U.S.A.; UAMH: University of Alberta Microfungus Collection and Herbarium, Edmonton, Alberta, Canada; UME: Herbarium of the University of Umeå, Umeå, Sweden; Culture and specimen abbreviations: ANM: A.N. Miller; CPC; P.W. Crous; EB: E.W.A. Boehm; EG: E.B.G. Jones; GKM: G.K. Mugambi; JK: J. Kohlmeyer; KT: K. Tanaka; SMH: S.M. Huhndorf.

SUPPLEMENTARY INFORMATION

Table 2. Genomes used for phylogenetic profile. All are opisthokonts; remaining classifications used in Fig. 4 are indicated in columns: Do – *Dothideomycetes,* ED - *Eurotiomycetes* & *Dothideomycetes*, S – Saccharomyceta, A – *Ascomycota,* Di – *Dikarya,* MD - *Mucoromycotina & Dikarya*, CMD - *Chytridiomycota,* F - *Fungi*.

Genomes	**Classifications**							
Alternaria brassicicola	Do	ED	S	A	Di	MD	CMD	F
Cochliobolus heterostrophus	Do	ED	S	A	Di	MD	CMD	F
Mycosphaerella fijiensis	Do	ED	S	A	Di	MD	CMD	F
Mycosphaerella graminicola	Do	ED	S	A	Di	MD	CMD	F
Pyrenophora tritici-repentis	Do	ED	S	A	Di	MD	CMD	F
Stagonospora nodorum	Do	ED	S	A	Di	MD	CMD	F
Aspergillus fumigatus		ED	S	A	Di	MD	CMD	F
Aspergillus nidulans		ED	S	A	Di	MD	CMD	F
Aspergillus terreus		ED	S	A	Di	MD	CMD	F
Coccidioides immitis		ED	S	A	Di	MD	CMD	F
Histoplasma capsulatum		ED	S	A	Di	MD	CMD	F
Uncinocarpus reesii		ED	S	A	Di	MD	CMD	F
Ashbya gossypii			S	A	Di	MD	CMD	F
Botrytis cinerea			S	A	Di	MD	CMD	F
Candida albicans			S	A	Di	MD	CMD	F
Candida glabrata			S	A	Di	MD	CMD	F
Candida guilliermondii			S	A	Di	MD	CMD	F
Candida lusitaniae			S	A	Di	MD	CMD	F
Chaetomium globosum			S	A	Di	MD	CMD	F
Debaryomyces hansenii			S	A	Di	MD	CMD	F
Fusarium graminearum			S	A	Di	MD	CMD	F
Fusarium oxysporum			S	A	Di	MD	CMD	F
Fusarium verticillioides			S	A	Di	MD	CMD	F
Kluyveromyces lactis			S	A	Di	MD	CMD	F
Laccaria bicolor			S	A	Di	MD	CMD	F
Lodderomyces elongisporus			S	A	Di	MD	CMD	F
Magnaporthe grisea			S	A	Di	MD	CMD	F
Nectria haematococca			S	A	Di	MD	CMD	F
Neurospora crassa			S	A	Di	MD	CMD	F
Pichia stipitis			S	A	Di	MD	CMD	F
Podospora anserina			S	A	Di	MD	CMD	F
Saccharomyces cerevisiae			S	A	Di	MD	CMD	F
Sclerotinia sclerotiorum			S	A	Di	MD	CMD	F
Sporobolomyces roseus			S	A	Di	MD	CMD	F
Trichoderma atroviride			S	A	Di	MD	CMD	F
Trichoderma reseei			S	A	Di	MD	CMD	F
Trichoderma virens			S	A	Di	MD	CMD	F
Verticillium dahliae			S	A	Di	MD	CMD	F
Yarrowia lipolytica			S	A	Di	MD	CMD	F
Schizosaccharomyces japonicus				A	Di	MD	CMD	F
Schizosaccharomyces octosporus				A	Di	MD	CMD	F
Schizosaccharomyces pombe				A	Di	MD	CMD	F
Coprinus cinereus					Di	MD	CMD	F
Cryptococcus neoformans					Di	MD	CMD	F
Phanerochaete chrysosporium					Di	MD	CMD	F

Table 1. (Continued).

Genomes	Classifications			
Postia placenta	Di	MD	CMD	F
Puccinia graminis f. *sp. tritici*	Di	MD	CMD	F
Ustilago maydis	Di	MD	CMD	F
Phycomyces blakesleeanus		MD	CMD	F
Rhizopus oryzae		MD	CMD	F
Batrachochytrium dendrobatidis			CMD	F
Encephalitozoon cuniculi				F
Drosophila melanogaster				