Molecular systematics of the marine Dothideomycetes

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Abstract: Phylogenetic analyses of four nuclear genes, namely the large and small subunits of the nuclear ribosomal RNA, transcription elongation factor 1-alpha and the second largest RNA polymerase II subunit, established that the ecological group of marine bitunicate ascomycetes has representatives in the orders Capnodiales, Hysteriales, Jahnuales, Mytiliniidales, Patellariales and Pleosporales. Most of the fungi sequenced were intertidal mangrove taxa and belong to members of 12 families in the Pleosporales: Aigialaceae, Dodyelliaeaceae, Leptosphaeriaceae, Lentilholisciacae, Lophiotomataceae, Massarinaceae, Montagulaceae, Morosphaeriaceae, Plesporaceae, Testudinaceae and Trematosphaeriaceae. Two new families are described: Aigialaceae and Morosphaeriaceae, and three new genera studied: Halomassarina, Morosphaeria and Rimora. Few marine species are reported from the Dothideomycetidae (e.g. Mycophagellaceae, Capnodiales), a group poorly studied at the molecular level. New marine lineages include the Testudinaceae and Mangilica guatemalensis in the Jahnuales. Significantly, most marine Dothideomycetes are intertidal tropical species with only a few from temperate regions on salt marsh plants (Spartina species and Juncus roemarianus), and rarely totally submerged (e.g. Halothria positionae and Pontoporeia biturnbina on the seagrasses Posidonia oceanica and Cymodocea nodosum). Specific attention is given to the adaptation of the Dothideomycetes to the marine milieu, new lineages of marine fungi and their host specificity.

Key words: Dothideomycetes, ecology, marine fungi, multi-locus, new genera, systematics.

Taxonomic novelties: Aigialaceae Suetrong, ecotagropon, E.B.G. Jones, Kohlm., Volk.-Kohlm. & Schoch, fam. nov., Halomassarina Suetrong, Sakayaroj, E.B.G. Jones, Kohlm., Volk.-Kohlm. & Schoch, gen. nov., Halomassarina hallassiae (Kohlm. & Volk.-Kohlm.), Suetrong, Sakayaroj, E.B.G. Jones, Kohlm., Volk.-Kohlm. & Schoch, comb. nov., Suetrong, Sakayaroj, E.B.G. Jones, Kohlm., Volk.-Kohlm. & Schoch, comb. nov., Suetrong, Sakayaroj, E.B.G. Jones, Kohlm., Volk.-Kohlm. & Schoch, comb. nov., Clade V. Morosphaeriaceae Suetrong, Sakayaroj, E.B.G. Jones, & Schoch, fam. nov., Morosphaeria velataspora (K.D. Hyde & Borse) Suetrong, Sakayaroj, E.B.G. Jones & Schoch, comb. nov., Morosphaeria ramunculicola (K.D. Hyde) Suetrong, Sakayaroj, E.B.G. Jones & Schoch, comb. nov., Rimora mangrovi (Kohlm. & Vittai) Kohlm., Volk.-Kohlm., Suetrong, Sakayaroj, E.B.G. Jones, comb. nov.

INTRODUCTION

Most marine Dothideomycetes are intertidal, primarily from mangrove habitats and rely on the active discharge of their ascospores. They are frequently found as saprobes of decaying woody materials in the marine environment. The species that occur completely submerged in the sea are mostly parasites or symbionts of seagrasses or marine algae. It is not clear how ascospore discharge occurs in these species as their hosts are primarily from temperate regions on salt marsh plants (Spartina species and Juncus roemarianus), and rarely totally submerged (e.g. Halothria positionae and Pontoporeia biturnbina on the seagrasses Posidonia oceanica and Cymodocea nodosum). Specific attention is given to the adaptation of the Dothideomycetes to the marine milieu, new lineages of marine fungi and their host specificity.

Scolecosporiella typhae, Stenphyllum triglochinolica and Phialophora cf. olivacea and molecular data indicates that the telemorphs of Amorosia littoralis, dendryphilla salina and D. arenaria may be in the Pleosporales (Mantle et al. 2006, Jones et al. 2008). This paucity of marine anamorphic fungi is in marked contrast to freshwater fungi and terrestrial genera of the class (Cai et al. 2006, Shenoy et al. 2007, Shearer et al. 2009; this volume).

Marine Dothideomycetes occur on a wide range of substrata: mangrove wood, twigs and leaves; sea and marsh grasses (especially Spartina spp. and Juncus roemarianus) (Kohlmeyer et al. 1995a–c, 1996, 1997a–b). Culms and leaves of sea and marsh grasses are ideal substrata for saprobic fungi because they may remain standing for several years during and after senescence (Christian et al. 1990, Kohlmeyer & Volkmann-Kohlmeier 2001). Other species are found on brown and red seaweeds, e.g. Loldtia danica and Pleospora gracilariaceae (Schatz 1984, Simmons & Schatz 1989), on wood associated with sand e.g. Caryospora australiensis and Decaisnella formosa (Abdel-Wahab & Jones 2003) or on the brackish water palm Nypa fruticans, e.g. Canispora nypae, Herpotrichia nypicola, Tirisporella beccariana and Heliscascus nypae (Jones et al. 1996, Hyde & Alias 2000). Few marine Dothideomycetes produce elaborate appended ascospores, and...
most possess gelatinous sheaths that swell in water when released from the asc (Massarina velataspore and Trematelia halophila). Genera with appended ascospores, although generally modifications of a gelatinous sheath, include: Carinaspore nypae, Decorospora gaudejouryi and Falcoformispersa lignatis.

The main objective of this study is to provide information on the taxa that are unique to the marine milieu, e.g. Aegialus spp., Manglicola guatemalensis, Halothia positioniae and Pontoporia biturbinata and confirm the taxonomic assignment of other marine ascomycetes within the context of a well sampled analysis with other related fungi.

**MATERIAL AND METHODS**

**Collection of fungi**

Drift and attached wood, culms and leaves of marsh plants, seagrasses and seaweeds were collected from a variety of habitats and geographical locations, placed in clean plastic bags and returned to the laboratory. After washing with freshwater to remove sediments, the samples were examined for fungi. Samples were kept moist by spraying with sterilised distilled water. Sporulating fungi were examined, identified, illustrated and single-spore isolations made. Most of the fungi sequenced in this study were obligate species, but some facultative and halotolerant terrestrial taxa from Juncus roemerianus have also been included so as to increase the sampling diversity.

**Fungal isolates and culture characteristics**

A selection of specimens were isolated by cutting the top of an ascospora with a sterilised razor blade, removing the contents of the centrum by making a spore suspension and then streaking the spores on antibiotic seawater agar (Kohlmeyer & Kohlmeyer 1979, Schoch et al. 2007) and germinating spores picked up. Other single ascospore isolations were made on cornmeal seawater agar (CMA/S) and an equal volume of phenol-chloroform (PIERCE) added. The mixture was kept at -20 °C for 30 min, or until the DNA had precipitated, chilled absolute ethanol and 7.5 M ammonium acetate. The mixture upper liquid phase was transferred to a new microtube containing an equal volume of phenol-chloroform (PIERCE) added. The mixture was incubated at 70 °C for 30 min, allowed to germinate overnight. Germinating spores on antibiotic seawater agar (Kohlmeyer & Kohlmeyer 1979, 2007) were used to facilitate the selection of other fungal sequences to be used in the analyses. Alignments were checked and manually optimised along with other sequences obtained from the GenBank nucleotide database. The dataset was refined visually in BioEdit v. 7.0.1 (Hall 2004) to facilitate the selection of other fungal sequences to be used in the analyses. Alignments were checked and manually optimised along with other sequences obtained from the GenBank nucleotide database. The dataset was refined visually in BioEdit v. 7.0.1 (Hall 2004) to facilitate the selection of other fungal sequences to be used in the analyses.
Molecular phylogenies

The BLAST search based on SSU and LSU sequences revealed the closest matches with taxa in *Dothideomycetes* and SSU, LSU, TEF1, and RPB2 sequences generated as part of this study are listed in Table 1. These sequences were combined with previously published data from various orders of the *Dothideomycetes* (Botryosphaeriales, Capnodiales, Dothideales, Hysteriales, Pleosporales and Myriangiales) obtained from GenBank (Table 1). The data set consisted of 199 taxa, with *Opegrapha dolomitica* and *Roccella fuciformis* included as the outgroup taxa. The maximum parsimony dataset consists of 4 141 total characters, 1 890 (45.6 %) characters are constant, 532 (12.8 %) characters are parsimony informative and 1 791 (41.6 %) characters are parsimony uninformative. The heuristic search resulted in a single most parsimonious tree (MPT) with a length of 18 715 steps (CI = 0.208, RI = 0.623, RC = 0.130; data not shown). One hundred successive searches using a rapid hill-climbing algorithm from distinct randomised starting trees in RAxML yielded a best scoring likely tree (Fig. 1) with a log likelihood –84765.605900. The matrix had 2 985 alignment patterns with 32 % of the characters consisting of gaps or undetermined characters. The alignment patterns were distributed across seven partitions as follows: LSU – 859, SSU – 217, TEF1 codon1 – 195, TEF1 codon2 – 309, TEF1 codon3 – 309, RPB2 codon1 – 230, RPB2 codon2 – 203, RPB2 codon1 – 254.

Phylogenetic trees obtained from maximum likelihood, Bayesian and maximum parsimony analyses yielded trees with similar overall topology at subclass, order and family relationship in agreement with previous work based on maximum likelihood (Schoch et al. 2006). However, the internal node relationships of some taxa were resolved differently between the maximum likelihood, Bayesian and maximum parsimony trees. For example: the taxonomic position of *Biatrospora marina* differed between the maximum likelihood, Bayesian and Maximum parsimony trees in the maximum likelihood and Bayesian tree, *B. marina* grouped in a basal part of Clade XIV- Residual paraplychete assemblage. But in the maximum parsimony tree, *B. marina* grouped in a basal clade to the *Testudinacaeae*. This is not unexpected as divergence in evolutionary rates and the presence of missing data affects all these methods differently. Nevertheless, we describe new taxa based on agreement in support for all three computational methods.

Taxonomy

This study resulted in the sampling of 51 marine dothideomycetous species (Table 1) with most of the marine genera belonging in the *Plesosporomycetidae*, and only two taxa (*Mycosphaerella, Scirrhia*) referred to the *Dothideomycetidae*. Only clades with marine taxa (in blue bold in the tree) are discussed in the text.

*Marine Dothideomycetes* show great variation in the morphology of the ascomata, asci and ascospores as illustrated in Figs 2–3. Many genera possess ascospores with a mucilaginous sheath that swells in water, once released from the asci. In others the sheath are drawn out to form appendages (e.g. *Carinispora nypae, Decorospora gaudrefroyi, Falciformispora lignitilis*).

Plesosporomycetidae

1. *Pleosporales*, Fig. 1.

Delineation of families in the *Pleosporales* previously relied extensively on morphological characters which resulted in 17 to 19 families (Kirk et al. 2001, Lumbsch & Huhndorf 2007). These were poorly resolved at the molecular level and Schoch et al. (2006) could only find reasonable support for seven families in a phylogeny generated from four genes: *Leptosphaeriaceae, Lophiostomataceae, Phaeosphaeriaceae, Pleosporaceae, Sporormiaceae, Testudinaceae* and *Trematosphaeriaceae*. A major reassessment of these taxa is needed and attempts are underway to complete this (see Mugambi et al. 2009a, and Zhang et al. 2009, this volume). As part of this process we attempted to place a diverse selection of marine *Dothideomycetes* using phylogenetic
Fig. 1. RAxML tree of marine Dothideomycetes with bootstrap support values for maximum likelihood and maximum parsimony above the nodes. The values below the nodes are Bayesian posterior probabilities. Relevant clades are highlighted in colour.
reconstruction. This resulted in 11 supported clades corresponding to families, with marine representatives (Fig. 1) (Didymellaceae-Clade IX, Lentitheciaceae-Clade I, Leptosphaeriaceae-Clade VIII, Lophiotomataceae-Clade XII, Massarinaceae-Clade II, Montagulaceae-Clade III, Phaeosphaeriaceae-Clade VII, Pleosporaceae-Clade VI, Sporormiaceae-Clade XIII, Testudinaceae-Clade XV, Trematosphaeriaceae-Clade IV) and two new families: 1) Aigialaceae (Clade XVII) for Aigialus and related taxa (Ascomycota mangicola and Lophiotoma mangrove), and 2) Morosphaeriaceae (Clade V) for the species Morosphaeria (Massarina ramunculicola, Massarina velatapsora), Helicascus nypae, H. kanaloanus and Kirschsteiniothelia elaterasus. Further clades are also identified, but their position remains unresolved, e.g. the familial position of the taxa Halothia posidioniae, Mauritiana rhizophorae and Pontoporeia biturbinalta in clade XIV.

Clade I. Lentitheciaceae

The marine Massarina species are not monophyletic which is in agreement with observations on terrestrial and freshwater members of the genus (Zhang et al. 2009b). Consequently a number of taxonomic changes are proposed in this chapter. Zhang et al. (2009a; this volume) erected the family Lentitheciaceae. However the monophyly of Lophiotoma is not supported in the current study. Massarina phragmiticola was described from the saltmarsh grass Phragmites australis (Poon et al. 1998), and groups within this family. It grouped with M. arundinacea with 84 % MLBP and 98 % MPBP support (Fig. 1). However Zhang et al. (2009a; this volume) refers M. arundinacea to the new genus Lentitheciaceae and we place M. phragmiticola in synonymy with Lentitheciaceae arundinacea.

Keissleriella (type species K. aesculi) comprises some 25 species (Kirk et al. 2008) and two species group with Lentitheciaceae in clade I, with high support. Keissleriella rara was described from the salt marsh species Juncus roemerianus, a rare halotolerant species (Kohlmeyer et al. 1995c). Zhang et al. (2009a) also included Keissleriella linearis in their phylogenetic analysis and transferred it to Lentitheciaceae.

Clade II. Massarinaceae

Aptroot (1998) reviewed the genus Massarina and reduced the 160 names in the literature to 43 taxa, while others (especially those from aquatic habitats) have been transferred to Lophiotoma (Hyde & Aptroot 1998, Hyde et al. 2002b, Liew et al. 2002). However, subsequent studies indicate that Massarina and Lophiotoma species are polyphyletic (Zhang et al. 2009b; this volume). These genera and the families Lophiotomataceae / Massarinaceae are difficult to separate and often have overlapping characters (Zhang et al. 2009b). In our analysis the type species Massarina eburnea forms a well supported clade (Clade II) with two Heliminthosporium species (H. velutinum, H. solani) as a sister group.

Jones et al. (2009) referred the genus Massarina to the Lophiotomataceae based on the molecular evaluation of Hyde et al. (2002b) and Liew et al. (2002). Lophiotoma has been reported as a monophyletic genus (Tanaka & Harada 2003, Tanaka & Hosoya 2008) while Zhang et al. (2009b) have shown that Lophiotoma is phylogenetically divided into two groups: Lophiotoma I which includes the type species L. macrostomum (voucher Lundqvist 20504), and Lophiotoma II which also contains sequences of L. macrostomum (voucher HHUF 27293 and HHUF 27290). Zhang et al. (2009b) were unable to verify the identity of the different strains of L. macrostomum and consequently could not determine the taxonomic position of Lophiotoma s. str. The paraphyletic nature of the Lophiotomataceae has previously been noted (Schoch et al. 2006) and clade XII is likely to represent the narrow concept of the Lophiotomataceae, although it is still too early to draw this conclusion until type material of Lophiotoma (L. macrostomum) is obtained (Zhang et al. 2009b). In our analysis we have selected the accession numbers AB433273 and AB433274 from the voucher specimens HHUF 27290 and HHUF 27293, respectively, and regard this clade as representing the family Lophiotomataceae (Clade XII).

Clade III. Montagulaceae

Based on morphological data, Jones et al. (2009) referred the genus Tremataeia to the Pleosporaceae, but molecular data places it with high support in the Montagulaceae (100 % MLBP, 94 % MPBP, 1.00 BYPP) with Bimuria novae-zelandiae as a sister
taxon. Kohlmeyer et al. (1995a) described Tremateia halophila from senescent leaves of Juncus roemerianus and regarded it as a facultative marine ascomycete. Characteristic features include an apical cap on the ascus, I- ocular chamber, and muriform ascospores with a wide mucilaginous sheath, and a Phoma-like anamorph.

Clade IV. Trematosphaeriaceae

This clade comprises four strains of Massarina thalassiae, a common species on mangrove wood, from Aldabra, Australia, Belize, Brunei, Florida, Galapagos, India, Malaysia, Mexico, Thailand (Kohlm. & Volkmann-Kohlmeyer 1987, Hyde 1992d, 1993, Alias & Jones 2000, Jones et al. 2006), with Trematosphaeria pertusa as a sister taxon. Falciformispora lignitellis (Fig. 2T, W) also groups in this clade with high support (94 % MLBP, 90 % MPBP, 1.00 BYPP); a species found on mangrove wood as well as on the fronds of the terrestrial oil palm (U. Pinruan, pers. comm.). As Massarina thalassiae cannot be accommodated in the genus Massarina based on molecular evidence, a new genus Halomassarina, is described.

Halomassarina Suetrong, Sakayaroj, E.B.G. Jones, Kohlm., Volkm.-Kohlm. & C.L. Schoch, gen. nov. MycoBank MB515951. Fig. 2AF.

Etymology: From the Greek hals = salt, in reference to the marine origin of the fungus.

Ascomata subglobosa ad pyriformia, immersa vel erumpentia, ostiolata, peripherysata, papillata vel epipapillata, clypeata, coriacea, brunnea, singularia. Peridium cellulis applanatis pachydermisque, texturam angularem formans. Hamathecium pseudoparaphysibus simplicibus, rarer anastomosantibus. Asci octospori, cylindrici ad clavati, pedunculati, pachydermi, fissitunicati, camera oculare, sine apparatu apicali, I non reagentes. Ascospores distichiae, ellipsoidæae, triseptatæ, hyalinae, tunica gelatinosa tectæ.

Ascomata subglose to pyriform, immersed or erumpent, ostiolate, peripherysata, papillata or papillaplate, clypeate, coriaceous, brown, single. Peridium of flattened, thick-walled cells, forming a textura angularis. Hamathecium of simple, rarely anastomosing pseudoparaphyses. Asci 8-spored, cylindrical to clavate, pedunculate, thick-walled, fisitunicate, with an ocular chamber but without apical apparatus, I-negative. Ascospores distichous, ellipsoidal, 3-septate, hyaline, surrounded by a gelatinous sheath.

Type species: Halomassarina thalassiae Kohlm. & Volkm.-Kohlm.), Suetrong, Sakayaroj, E.B.G. Jones, Kohlm., Volkm.-Kohlm. & C.L. Schoch.

Halomassarina thalassiae (Kohlm. & Volkm.-Kohlm.) Suetrong, Sakayaroj, E.B.G. Jones, Kohlm., Volkm.-Kohlm. & C.L. Schoch, comb. nov. MycoBank MB515952. Basionym: Massarina thalassiae Kohlm. & Volkm.-Kohlm. Canad. J. Bot. 65: 575. 1987.

This is a widely collected tropical species from intertidal and subtidal mangrove wood or fishing crafts (Kohlmeyer & Volkmann-Kohlmeyer 1987).

Clade V. Morosphaeriaceae

This clade, comprising four marine species Massarina ramunculicola, M. velataspora, Helicascus kanalosanus and H. nygae, is well supported (100 % MLBP, 100 % MPBP, 1.00 BYPP) with the Massarinaeaeae, Montagulanaceae and Trematosphaeriaceae as sister clades. As M. ramunculicola and M. velataspora do not group with other Massarina species, a new family and genus Morosphaeria are proposed.

Morosphaeriaceae Suetrong, Sakayaroj, E.B.G. Jones & C.L. Schoch, fam. nov. MycoBank MB515953.

Familia Pleosporales. Ascomycota. Ascomata subglobosa, conica, lenticularia, immersa ad superficia, ostiolata, papillata, peripherysata, brunnea vel nigra, coriacea vel carbonacea, solitaria, vel gregaria, cum 3–4 loculi, ostilosi communi ad centrum. Hamathecium pseudoparaphysibus filamentosus, numerosus, ramosis ad basem, ramosis anastomosantibus supra ascos. Asci octospori, clavati vel cylindrici pedunculati, pachydermi, fisitunicati, persistentes, camera apicale et disco apicale, IKI non-reagentes. Ascospores biseriatae, hyalinae ad brunnea, septatae constrictae ad leviter constrictae, tunica vel calyptra gelatinosa tectae, vel sine turica.

Family in the Pleosporales, Ascomycota. Ascomata subglobose, conical, lenticular, immersed to superficial, ostiolate, papillate, peripherysate, brown to black, coriaceous or carbonaceous, single to gregarious, stromatic with 3–4 loculi with a common central ostiole. Hamathecium with filamentous pseudoparaphyses, unbranched to branched at the base, anastomosing above the asc, embedded in a gelatinous matrix. Asci 8-spored, clavate to cylindrical, pedunculate, thick-walled, fisitunicate, with an ocular chamber and apical ring, non-amyloid, persistent. Ascospores biseriate, hyaline to brown, septate, with or without a gelatinous sheath or cap.

Type genus: Morosphaeria Suetrong, Sakayaroj, E.B.G. Jones & C.L. Schoch.

Morosphaeria Suetrong, Sakayaroj, E.B.G. Jones & C.L. Schoch, gen. nov. MycoBank MB515954.

Etymology: Named after Mor = sea in Welsh in reference to its marine habitat and sphearia in reference to the perithecial ascomata

Ascomata solitaria vel gregaria, subglobosa vel lenticularia, immersa, erumpentia, ostiolata, papillata, coriacea, brunnea ad nigra, pseudoparaphysibus angusti, hyaliniis, simplicibus et numerosis. Asci octospori, clavati vel cylindrici, pedunculati, bifurcatis, pachydermi, fisitunicati, cum camera apicale et apicale, IKI non reagentes. Ascospores uniseriatae vel biseriatae, fusiformes vel ellipsoidales, 1–3 septatae, constrictae ad septa, cum tunica gelatinosae.

Ascomata solitaria or gregarious, subglose to pyriform, immersed becoming superficial, ostiolate, papillate, coriaceous, brown to black, pseudoparaphyses filamentous, anastomosing, branching, and numerous. Asci 8-spored, clavate to cylindrical, short pedunculate, thick-walled, bifurcate, fisitunicate, with an ocular chamber and apical apparatus, persistent. Ascospores hyaline, 1–3 septate, constricted at the septa, fusiform to ellipsoid, surrounded by a mucilaginous sheath.

Type species: Morosphaeria velataspora (K.D. Hyde & Borse) Suetrong, Sakayaroj, E.B.G. Jones & C.L. Schoch.

Morosphaeria velataspora (K.D. Hyde & Borse) Suetrong, Sakayaroj, E.B.G. Jones & C.L. Schoch, comb. nov. MycoBank MB515955. Fig. 2AG. Basionym: Massarina velataspora K.D. Hyde & Borse, Mycotoxan 27: 163. 1986.
**Morosphaeria ramunculicola** (K.D. Hyde) Suetrong, Sakayaroj, E.B.G. Jones & C.L. Schoch, **comb. nov.** MycoBank MB515956. Fig. 3A, H.

*Basionym:* Massarina ramunculicola K.D. Hyde, Mycologia 83: 839. 1992.

Both species are common and frequently collected on dead wood of various mangrove trees in tropical and subtropical localities (Hyde & Borse 1986b, Hyde 1992a, Schmit & Shearer 2003, Jones & Abdel-Wahab 2005, Jones et al. 2006). Ascospores of both species possess a well-developed sheath (Au *et al.* 2001, Au & Vrijmoed 2002), while in *M. ramunculicola* polar appendages are formed as outgrowth of the fibrillar material within the inner regions of the sheath through polar discontinuities (Read *et al.* 1997a, b). The taxa *Helicascus kanaloanus* and *H. nypae* form a sister group to *Morosphaeria* species with high bootstrap support. Jones *et al.* (2009) referred this genus to the Pleosporaceae as in previous analyses (Tam *et al.* 2003) and grouped it with *Kirschsteiniothelia*...
elaterascus (Shearer 1993a). However, Kirschsteiniothelia is polyphylectic with the marine species K. maritima grouping in our analysis in the Mytilinidaceae (Clade XIX, Fig. 1). In addition to this the type species of the genus, K. aethiops and its anamorph, Dendryphiopsis atra, are placed outside of the Pleosporales as currently defined, always in close association with an isolate of Phaeosphaeria olivacea (Jones et al., 2002). This genus has four species that form a sister group to Phaeolus and Phaeosphaeria, but molecular data suggests that species in some currently accepted genera sensu Lumbsch & Huhndorf (2007) e.g. Comminutispora, are unrelated (Schoch et al. 2009a; this volume).

Zhang et al. (2009a; this volume) included the following marine species in the Phaeosphaeriaceae: Leptosphaeria albopunctata, Ph. spartinae, Ph. spartinica, Ph. typharum as well as Amarenomyces ammophilae, a facultative marine species collected on Juncus roemerianus throughout the year (Kohlmeier et al. 1997a). Of the marine taxa included in this family all occur on salt marsh plants: L. aestuarii, Ph. olivacea on J. roemerianus, Ph. spartinae, and Ph. spartinica on Spartina spp., while Ph. ammophilae occurs on a range of grasses and sedges, but primarily on Ammophila arenaria (Kohlmeier & Kohlmeyer 1979).

Clade VIII. Leptosphaeriaceae

Currently five Leptosphaeria species are referred to this family (Jones et al., 2009), but no sequences of marine Leptosphaeria are available for any of these, and therefore their taxonomic position cannot be verified.

Clade IX. Didymellaceae

The family Didymellaceae was recently described for the teleomorph genera Didymella, Leptosphaerula, including several Phoma anamorphs (de Gruyter et al. 2009). Four marine Didymella species have been described, three from brown or red seaweeds and D. avicenniae from wood of Avicennia (Patil & Borse 1985, Jones et al. 2009). In our analyses it forms a well-supported
basal clade (99 % MLBP, 97 % MPBP, 1.00 BYPP) to the families Phaeosphaeriaceae, Pleosporaceae, and Leptosphaeriaceae. Kohlmeyer & Volkman-Kohlmeeyer (2003) questioned the taxonomic position of Didymella magnei, a species found on the red seaweed Palmaria palmata, because the ascospores differed morphologically from those of other Didymella species.

Clade X. Julella clade

The genus Julella was previously assigned to the Pleosporales incertae sedis and Phaeosphaeriaceae, respectively (Jones et al. 2009). Julella avicenniae (Fig. 2 AE) was initially described as a Pleospora species but because the ascomata develop on woody substrata, immersed beneath a clypeus with narrow pseudoparaphyses, Hyde (1992b) transferred it to Julella.
However, ascomata can be superficial on well-decayed mangrove wood. Although regarded as an obligate marine ascomycete (Hyde 1992b), it may be implicated in the dieback of young shoots of Avicennia marina, at Morib mangrove, Malaysia, not submerged in seawater (Jones 2007). Julella avicenniae strains form a monophyletic clade with an unidentified pleosporaceous sequence (OSC 100706). This forms a moderately supported clade separated from other families in the Pleosporales (67 % MLBP).

Clade XII. Lophiostomataceae

In our analyses the families Lophiostomataceae and Massarinaeae are distinct, and distantly placed within the Pleosporales. This is confirmed elsewhere (Zhang et al. 2009a; this volume). Jones et al. (2009) referred seven genera with marine species to this family (Decaisnella-Clade XIV, Unresolved, Herpotrichia-Clade XI, Melanommataceae, Lophiostoma, Massarina-Clade II, Massarinaeae, Paralomyces, Platystomum, Quintaria-Clade XVI Residual assemblage). However, molecular data places some of these in other families, as indicated in the above sentence (Fig. 1). Of these genera, only Platystomum and Paralomyces (Tam et al. 2003) were included in the present analysis. Currently four marine Lophiostoma species are recognised: L. acrostichi, L. armatisporum, L. rhizophora and Platystomum scalarisporum; however, Su et al. (pers. obs.) propose the transfer of the latter species to Lophiostoma based on morphological and molecular data. Other Lophiostoma species have been transferred to Astrosphaeriella (A. asiana, A. mangrovis) by Hyde et al. (2002b) and Liew et al. (2002). In our analysis, based on molecular data, Lophiostoma mangrovi is referred to the family Agialaceae (Clade XV, Fig. 1), while other Massarina species are placed in the Lentitheciaceae (Clade I) [Lentitheicum (Massarina) phragmiticola], or the new family Morosphaericeae (clade V) [Morosphaeria (Massarina) ramunculicola, M. (Massarina) velataspores]. No molecular data is available for the marine species Herpotrichia nycicola which occurs on the palm Nypa fruticos, while Quintaria lignatilis forms a sister group to the Testudinaceae with low support (Schoch et al. 2006).

Clade XIV. Residual paraphyletic assemblage

Several unresolved species form part of a poorly resolved group that includes the Testudinaceae and it is not clear whether missing data played a role in this. The genera in question include: Carinispora (Fig. 2AV), Massarina ricifera, Passeriniella, Salsuginea and Quintaria (Fig. 2F). Jones et al. (2009) referred Salsuginea ramicola (Fig. 2M, X) to the Pleosporales incertae sedis; a genus with similarities to Helicascus (Kohlmeyer 1969, Hyde 1991) while Hyde (1991) suggested the Dothideales incertae sedis. Both genera occur on mangrove wood but differ in that Salsuginea lacks a stroma, the ascomata form under a clypeus, asci have a distinctive ocular chamber and ascospores with prominent apical pores and lacking a mucilaginous sheath. It is a species collected from various mangrove tree species with ascospore measurements differing, but whether this is in response to the host remains to be evaluated (Hyde 1991).

The genera Acrocordiopsis (Fig. 3P) and Passeriniella form an unsupported clade with both taxa known from mangrove wood in the tropics (Hyde & Mouzouris 1988, Borse & Hyde 1989, Alias et al. 1999) and referred previously to the Melanommataceae and Dothideales incertae sedis, respectively (Jones et al. 2009). Morphologically they would appear to share few common characters. Acrocordiopsis species are characterised by large (<2 mm) ascospores that are conical, superficial on the host and carboxenous with the ascospores forming on a thin layer of peridial tissue on the host substratum while the ascospores are hyaline and 1-septate (Alias et al. 1999). Currently two Passeriniella species are accepted (Jones et al. 2009), namely P. mangrovi and P. savoryellipsoid, with coriaceous, globose to subglobose, immersed ascospore, and ascospores that are 3-septate, central cells brown, and hyaline end cells (Hyde & Mouzouris 1988, Maria & Sridhar 2002). The taxonomic characterisation of the genus Passeriniella is confusing and has been discussed by Hyde & Mouzouris (1988) and Kohlmeyer & Volkmann-Kohlmeyer (1991).

Byssothecium (Passeriniella) obiones, a common species on senescent culms of Spartina, has a checkered history, assigned to Pleospora, Leptosphaeria, Didymosphaeria, Melasphaeria and Passeriniella (Jones et al. 2009). Khashnosh & Shearer (1996) showed that based on ITS sequence data, Byssothecium

The latter are temperate hosts, while D. formosa and M. rhizophora are from the tropics.

Clade XV. Testudinaceae

Verruculina and Massarina ricifera (Fig. 2K, AA) are the only marine genera referred to this family, poorly supported in the current analysis, but confirming the results of a previous study (Schoch et al. 2006). In their analysis the family formed the basal node to the Pleosporales. Members of the Testudinaceae form a monophyletic clade and are characterised by ascospores that are 1-septate, brown without germ slits and with or without ornamentation (Kruys et al. 2006). However, Verruculina enalia shares few characters with members of the Testudinaceae, it differs especially by its marine habitat and persistent asci. Massarina ricifera is an obligate marine ascomycete growing on Juncus roemerianus and referred by Kohlmeyer et al. (1995b) to the Lophiostomataceae “with hesitation” as it did not fully agree with the type species Massarina eburnea. Molecular data presented here clearly indicates that it does not belong in Massarina, but further assignment must await additional collections.
(Passeriella) obiones did not belong in either Leptosphaeria or Phaeosphaeria. Subsequently, Barr (2002) assigned it to Byssothecium, based on the vericolourous ascospores in the Teichosporaceae. In our original data set, it grouped with Mycosphaerella species in the Capnodiales. As the origin of this sequence (JK 4748) cannot be verified, and because of the distinctive morphology of B. obiones which has little in common with those of Mycosphaerella and other members in the Capnodiales, we did not present these data here.

Two sequences of Quintaria lignitilis form a sister group to the Testudinaceae but with moderate support for all analyses. The genus has previously been referred to the Lophiostomataceae (Cai et al. 2006) and shares features in common with Trematosphaeria. Quintaria differs from Trematosphaeria by having completely immersed ascomata with rounded bases, black incrustations lining the sides of the ostiolar canal, a non-amyloid plate in the ascus and hyaline ascospores (Kohlmeyer & Volkmann-Kohlmeyer 1991).

Carinispora nypae is another anomalous taxon whose taxonomic position cannot be resolved at this time. It is placed in the paraphyletic assemblage XVI by maximum likelihood and Bayesian derived phylogenies, but not for those obtained by maximum parsimony. This may be due to artifacts associated with long branch lengths and its placement will require more in-depth analysis. Carinispora nypae is found growing on the marine palm Nypo fruticans and has raised crust-like spots covered in a soft crust-like stroma, with lenticular ascomata under a clypeus, cylindrical and narrow asci, and yellow to pale-brown ascospores with a pronounced sheath drawn out on one side into a spine-like polar appendage (Hyde 1992a). Hyde (1992a) commented that it was close to Phaeosphaeria, but our data do not support this view.

Clade XVII. Aigialaceae Suetrong, Sakayaroj, E.B.G. Jones, Kohlm., Volkm.-Kohlm. & C.L. Schoch, fam. nov. MycoBank MB515957.

Etymology: Named after the type genus.

Family Pleosporaceae. Ascomycotina. Ascomata globosa, conica, immersa ad superficiem, ostiolata, ostiolum rotundum vel fissuriforme, epapillata, periphysata. Hamathecium pseudoparaphysibus trabeculatis, eramosis ad basem, ramosis superficialia, ostiolata, ostiolum rotundum vel fissuriforme, periphysata. Peridium cellulis pachydermis, texturam angularem ad basem, anastomosantibus supra ascos. Asci octospori, cylindrici pedunculati, pachydermi, fissitunicati, disco apicale, IKI non-reagentes. Ascosporae distichae, fusiformes, dissepimentatae, hyalinae, tunica gelatinosa tectae.

Family in the Pleosporales, Ascomycota. Ascomata globosum and immersed to superficial or conical, ostiolate, ostiolum round to cleft-like, appapillate, black, carbonaceous to coriaceous, single to gregarious. Periphysate. Hamathecium trabeculatum, unbranched at the base, anastomosing above the ascus, embedded in a gelatinous matrix. Asci 8-spored, cylindrical, pedunculate, thick-walled, fissitunicata, with a refractive apical ring, non-amyloid. Ascospores biseriate or monostichous, peripherally, ostiolar, ostiolum round or fissuriforme, epapillate, periphysata.

Type genus: Aigialus Kohlm. & Schatz.

Aigialus Kohlm. & S. Schatz, Trans. Brit. Mycol. Soc. 85: 699. 1985. A. grandis Kohlm. & S. Schatz, Trans. Brit. Mycol. Soc. 85: 699. 1985 (Type species). Fam. 3A–B, L, N. A. mangrovis Borse, Trans. Brit. Mycol. Soc. 88: 424. 1987. Fig. 3D, P. A. parvus S. Schatz & Kohlm., Trans. Brit. Mycol. Soc. 85: 704. 1985. Fig. 3C, F–G, O.

A. rhizophorae Borse, Trans. Brit. Mycol. Soc. 88: 424. 1987. Fig. 3E, Q. A. striatisspora K.D. Hyde, Mycol. Res. 96: 1044. 1992.

Jones et al. (2009) accepted four species in this genus, but rejected A. rhizophorae as it shared a number of features with A. grandis, but only differed in the vertical septation in the subapical cell. Recent collections made in Thailand have enabled us to sequence this species and it is clearly distinct from A. grandis. This is a commonly encountered genus on mangrove wood and widely reported in the literature (Borse 1987, Schmit & Shearer 2003, Abdel-Wahab 2005, Jones et al. 2006). Aigialus striatisspora was described from Ranong mangrove, Thailand, but no further collections have been made (Hyde et al. 1990, 1993).

Asocratera Kohlm., Canad. J. Bot. 64: 3036. 1986. A. manglicola Kohlm., Canad. J. Bot. 64: 3036. 1986 (Type species).

Asocratera manglicola is characterised by carbonaceous, black, gregarious ascomata that are conical, crater-like, superficial on wood, on a black stroma, by trabeculate pseudoparaphyses, by asci with a refractive apical ring, and hyaline ascospores, surrounded by a gelatinous evanescent sheath (Kohlmeyer 1986). It is a common species on mangrove wood in the intertidal zone, and known from various tropical geographic locations (Schmit & Shearer 2003).

Rimora Kohlm., Volkm-Kohlm., Suetrong, Sakayaroj & E.B.G. Jones, gen. nov. MycoBank MB515958.

Etymology: From the Latin rina = cleft, fissure and os = mouth, in reference to the cleft-like ostiole, a unique feature among marine ascomycetes.

Ascomata erumpentia, apice plano, elongata, appilata, ostiolo fissuriforme, periphysata, nigra, gregaria. Peridium cellulis pachydermis, texturam angularem formans. Hamathecium pseudoparaphysibus ramosis. Asci octospori, cylindrici, pedunculati, pachydermi, fissitunicata, sinne apparatu apicali. Ascospores distichae, fusiformes, trisepitae, hyalinae, tunica gelatinosa tectae.

Ascomata erumpent, with flat tops, elongated, appilulate, opening with a periphysate cleft-like ostiole, black, gregarious. Peridium of thick-walled cells, forming a textura angularis. Hamathecium of branched pseudoparaphyses. Asci 8-spored, cylindrical, pedunculate, thick-walled, fissitunicata, without apical apparatus. Ascospores biseriate, fusiform, 3-septate, hyaline, surrounded by an evanescent sheath.

Type species: Rimora mangrovei (Kohlm. & Vittal) Kohlm., Volkm-Kohlm., Suetrong, Sakayaroj, E.B.G. Jones. Rimora mangrovei (Kohlm. & Vittal) Kohlm., Volkm-Kohlm., Suetrong, Sakayaroj & E.B.G. Jones, comb. nov. MycoBank MB515959. Fam. 3K, S. Basionym: Lophiostoma mangrovei Kohlm. & Vittal, Mycologia 78: 487. 1986.
the pseudoparaphyses. However, the aforementioned authors conceded that *A. mangrovis* (and *A. asiatica*) differed from other *Astrosphaeriella* species by their round flattened ascomata, silt-like ostioles and non monocotyledonous hosts.

All three genera *Aigialus*, *Ascoscrotites* and *Rimora* share features such as carbonaceous, apipallate ascomata, trabeculate pseudoparaphyses, cylindrical asci with an apical apparatus and ascospores with a sheath. However, they differ in the morphology of their ascospores: brown and muriform in *Aigialus*, hyaline and 1–3-septate in *Ascoscrotites* and *Rimora*.

2. *Mytilinidiales*, Fig. 1

**Clade XIX. *Mytilinidiales***

The common bitunicate ascomycete *Kirschsteiniothelia maritima* groups with *Lophium mytilum*, with *Mytilinidion mytilillum* and *Hysterium andinense* as a sister group. The genus *Kirschsteiniothelia* has been referred to the *Pleosporaceae* (Eriksson & Hawksworth 1998, Kirk et al. 2001), *Pleomassariaceae* (Barr 1993), and questionably the *Massariaceae* (Kodsueb et al. 2006). The genus appears to be polyphyletic, and Shearer (1993a) and Schoch et al. (2006) are of the opinion that *K. aethiops* does not belong in the *Pleosporaceae*. Kodsueb et al. (2006) show that *K. elaterascus* (a freshwater species) clusters with *Morosphaeria* (*Massarina*) *ramunculicola* in a sister clade to the *Melanomnataceae* (see also clade XI, Fig. 1). However, *K. elaterascus* differs from *K. maritima*, and other *Kirschsteiniothelia* species in ascus structure, its unusual endoascus with a long, coiled base that uncoils during ascus dehiscence, ascospore measurements, the presence of an ascospore sheath and its freshwater occurrence (Shearer 1993a).

**Clade XX. Unresolved taxa**

Included in this clade are three coelomycete species of which *Pseudorobilliadra phragmitis* has been reported from pine and yellow poplar test panels from estuarine waters (Salinity 3–16 ppt) (Jones et al. 2009). This monophyletic group formed a well-supported clade and a sister group to the *Mytilinidiales*. However in the current study they form a weakly supported clade with *Farlowiella camichaeliana* and are basal to the *Mytilinidiales* in all analyses.

3. *Patellariales*, Fig. 1

**Clade XXII. *Patellariaceae***

*Patellaria cf. atrata* (Fig 2B, R, AD), a species found growing on various mangrove wood species collected in Hong Kong and Thailand, forms a sister group to the *Hysteropatella* species, taxa normally assigned to the *Hysteriales*, but recently removed (Boehm et al. 2009a, b; this volume). Morphologically, little distinguishes *Glioniella clavatopora* and *Patellaria atrata*; paraphyses in the latter species are distinctly branched and club-shaped (Suetrong & Jones 2006). The paraphyses illustrated by Steinke & Hyde (1997) are simple and not branched (Suetrong & Jones 2006). Boehm et al. (2009a; this volume) refer *Glioniella* to the *Hysteriales*, and *Patellaria* in the *Patellariaceae*; further collections of the marine taxa are required to resolve their identification.

A number of marine species do not group within existing orders of *Dothideomycetes* and this may indicate new supergeneric taxa not yet circumscribed. The lack of sufficient protein coding gene sequences for these in our analysis and the tendency for these species to be associated with fast evolving branches on our trees further complicates the development of phylogenetic hypotheses for these taxa.

(i) *Biatrospora marina* (Clade XIV), in all analyses, forms a distinct long branch and is a basal taxon to the *Pleosporomycetidae* without any closely related taxa (Fig. 1). It is an unusual species described from *Sonneratia alba* mangrove wood collected in the Seychelles and India (Hyde & Borse 1986a). It has immersed subglobose to pyriform ascocoma that are black and carbonaceous, cylindrical asci and brown, septate ascospores with hyaline, globose refractive chamber or an appendage at each end. Pseptation is unusual in that ascospores are non-septate in the center but septate at both ends and not constricted at the septa. Additional collections have been made from mangroves in Hong Kong, Malaysia and Thailand (Jones et al. 2006, E.B.G. Jones unpubl. data).

(ii) *Saccardoella rhizophorae* Clade XIX. *Saccardoella* species have been regarded as having unitunicate asci and thus classified in the *Cyphosphaeriaceae* (Barr 1994). However, Mathiasson (1989) was of the opinion that the asci are bitunicate and this would appear to be supported by the current study. *Saccardoella* species are known from terrestrial, marine and freshwater habitats (Hyde 1992c, Tsui et al. 1998). However in all phylogenetic analyses to date this species does not group within any known family or order, and further studies are required to determine its phylogenetic relationship.

4. *Jahnulales*

**Aliquandostipitaceae** (data not shown)

The family *Aliquandostipitaceae* was established for species in the genus *Aliquandostipites* based on the phylogenetic analyses of SSU nrDNA sequences (Inderbitzin et al. 2001). Subsequently Pang et al. (2002) introduced the new order *Jahnulales* into the *Dothideomycetes*, *Ascomycota*, based on phylogenetic analysis of SSU nrDNA sequences of *Aliquandostipite*, *Jahnula* and *Patescospora*. More recently, Campbell et al. (2007) studied the phylogenetic relationships of taxa in the *Jahnulales* inferred from SSU and LSU nrDNA sequences and recognised four groups: 1) a basal group with *Megalohypha aqua-dulces*; 2) a *Jahnula* group comprising the type species *J. aquatica*; 3) five *Aliquandostipite* species; and 4) four *Jahnula* species and the anamorphic genera *Brachiosphaera* and *Xylomyces*. They emended the ordinal description to include brown, wide hyphae (>10 µm) and greater variation of ascospore morphology.

Three marine fungi belong in the *Jahnulales*, the teleomorph *Mangicula guatemalensis* and the anamorphic species *Xylomyces chlorydosporus* and *X. rhizophorae* (Suetrong et al. 2010). *Mangicula guatemalensis* is a poorly known species with only three previous collections (Kohlmeier & Kohlmeier 1971, Hyde 1988, Jones et al. 2009, Suetrong et al. 2010). The type strain was collected from dead roots of *Rhizophora mangle* in Guatemala (Kohlmeier & Kohlmeier 1971). Subsequent collections have been made on intertidal prop roots of *Rhizophora apiculata* at Kpg Danau, Brunei (Hyde 1988) and frond bases of *Nypa fruticans* (Jones et al. 2009). Common features *M. guatemalensis* shares with the *Jahnulales* include stipitate ascomata, bitunicate asci, reticulate pseudoparaphyses and 1-septate brown ascospores. *Mangicula guatemalensis* differs from other bitunicate ascomycetes by its large
ascomata, wide ostiole, large unequally 1-septate ascospores and mangrove habitat on *R. mangle* and the frond bases of *N. fruticans*.

Huhndorf (1994) referred *Mangicola* to the Hypsostromataceae, a family with no known relationship to any group in the Dothideomycetes (*Loculoascomycetes*) but “probably with affinities to the Melanommatales” (Mugambi & Huhndorf 2009; this volume). Characteristics that unite *Mangicola* and the Hypsostromataceae include superficial, large, elongate ascomata (stalked) with a soft-texture, trabeculate pseudoparaphyses, stipitate asci attached in a basal arrangement in the centrum and fusiform, septate ascospores (Huhndorf 1994).

**Dothideomycetidae**

5. *Capnodiales*, Fig. 1

Fourteen genera, such as *Belzeana*, *Caryospora*, *Coronopapilla*, *Lautospora*, *Loratospora*, *Pontoporeia* and *Thalassoasculus*, assigned to the subclass *Dothideomycetidae*, have only marine species, and represent new lineages of fungi that may be associated with the *Capnodiales* (Jones et al. 2009). Importantly, few have been studied at the molecular level. Placement of the genera *Passeriniella* and *Pontoporeia* has already been discussed above.

**Clade XXV. Mycosphaerellaceae**

*Mycosphaerella eurypotami*, a halotolerant terrestrial species found on *Juncus roemerianus*, was tentatively referred to the genus by Kohlmeyer et al. (1997b). In the current study it is a sister taxon to all *Mycosphaerella* species with moderate support. Jones et al. (2009) list three marine *Mycosphaerella* species (*M. salicorniae*, *M. staticiola*, *M. suaeidae-australis*) found on salt marsh plants (*Armeria*, *Limonium*, *Salicornia* and *Suaeda*), while *M. pneumatothripe* is a common species on the pneumatophores of *Avicennia* species in Asia and the Caribbean (Kohlmeyer & Kohlmeyer 1979, Jones et al. 2003, E.B.G. Jones, pers. comm.). However recent molecular phylogenies containing a single culture did not support the placement of *M. pneumatothripe* in *Mycosphaerella* (Schoch et al. 2006); instead it was found on a poorly resolved branch within *Dothideomycetidae*.

In our analysis, *Scirrhia annulata*, described from senescent leaves of *Juncus roemerianus* (Kohlmeyer et al. 1996), groups with various *Mycosphaerella* species with moderate support. Diagnostic features are the linear stromata, 1–3 mm long, generally superficial, multiloculate with ascomata in longitudinal rows, asci clavate with apical apparatus (several rings), ascospores 3-septate, brown, with a thin evanescent sheath, and measuring 46–60 x 9–11.5 µm.

**Clade XVIII. Unresolved taxa (Fig. 1)**

(i) The taxonomic position of *Heleiosasa barbatula* (Fig. 1) is unresolved as observed by its swapping position in different analyses (data not shown) and previously referred to the *Dothideales* and *Pleosporales incertae sedis*, respectively (Kohlmeyer et al. 1996, Jones et al. 2009). This species, collected on *Juncus roemerianus*, is rare and is not obligately marine. Characteristics include immersed ostiolate epipalliate ascomata formed beneath a clypeus, with pseudoparaphyses, asci cylindrical with short pedicel, refractive apical apparatus and ascospores that are pale brown, ellipsoidal, 1-septate with 10 or more cilia-like polar appendages at each end.

(ii) The genera *Caryospora*, and *Lineolata* form a basal clade in all analyses with weak support, genera previously assigned to *Melanommatales* and *Pleosporales incertae sedis*, respectively (Jones et al. 2009). Both occur on mangrove substrata and have been widely reported from different geographical locations (Schmit & Shearer 2003).

*Caryospora* was thought to be related to *Caryospora*, with which it shares a number of common features (Kohlmeyer 1985). It is found on dead wood of intertidal roots and branches of mangrove trees and has large ascomata and 1-septate, dark-brown ascospores that are thickened at their apices.

*Lineolata* was initially described as a *Didymosphaeria* but transferred to this genus (Kohlmeyer & Volkmann-Kohlmeyer 1990) as it differs in the following respects: no clypeus, almost superficial ascomata, hamathecium with a gelatinous matrix, asci with an apical ring-like structure around the ocular chamber and ornamented brown ascospores. It remains enigmatically placed here, although three monophyletically placed isolates obtained from different geographic locations heighten our confidence in the provenance of these sequences.

**DISCUSSION**

**Marine lineages of the Dothideomycetes**

The study confirms the occurrence of several marine Dothideomycetes with well supported sequence data. The *Pleosporales* includes ten families and three unresolved clades with marine species, while the orders *Capnodiales*, *Jahnulales*, *Mytilillidiales*, and *Patellariales* are represented by few taxa. This is in common with their known diversity (? in nature (Kohlmeyer & Kohlmeyer 1979, Jones et al. 2009). While many terrestrial genera have marine members, e.g. *Mycosphaerella*, *Passeriniella*, *Lophostoma*, *Massarina*, *Trematosphaeria* and *Phaeosphaeria*, others have no known terrestrial counterparts. The uniqueness of these has necessitated the introduction of two new families in the *Pleosporales*, *Aigialaceae* (all marine genera: *Aigialus*, *Ascoscratera*, *Rimora*) and *Morosphaeriaceae* (marine genera *Helicascus*, *Morosphaeria* and the freshwater species *Kirschsteiniothella elaterascus*). The taxonomic position of other exclusively marine genera/species remains to be resolved e.g. the seagrass ascomycetes *Halotithia posidoniae*, *Pontoporeia biturbinata* (Clade XIV), and *Lineolata rhizophorae* (Clade XVIII) and *Bartirospora marina* (Clade XIV).

A number of new marine lineages have been highlighted as result of molecular studies including *Mangicola guatemalensis*, the first member of the *Jahnulales* reported from marine habitats (Suetrong et al. 2010). This is of particular interest as all other *Jahnulales* members are fresh water or peat swamp species and raises the question as to whether these marine fungi are derived from terrestrial and freshwater taxa that have migrated to the sea. This would support earlier phylogenetic analyses (Spatafora et al. 1998) that strongly suggest a terrestrial origin of another marine ascomycete family in the *Sordariomycetes*, the *Halosphaeriaceae*. A more recent data set (Schoch et al. 2009a; this volume) continues to support this hypothesis. The marine species *M. guatemalensis* occurs in estuarine mangrove habitats on the palm fronds of *Nipa fruticans* and *Rhizophora* wood and may well form a link between lignonous freshwater taxa and species from estuarine to marine environments. Another *Jahnulales* species of interest is the anamorph *Xylomyces rhizophorae*, found on various marine and
mangrove substrata (Kohlmeier & Volkmann-Kohlmeier 1998, S. Swichai, pers. comm.), Campbell et al. (2007) and Prihatini et al. (2008) have shown that Xylomyces chlamydosporus has a telemorph in the Jahnulales.

A second marine lineage is the Agialaceae comprising three genera: Agialus, Ascocratera, and the new genus Rima, a family within the Pleosporales. Morphologically they show few common characteristics but all are to be found in mangrove habitats.

Schoch et al. (2006) showed that Verniculina enalia is a member of the Testudinaceae, and another marine lineage in the Dothideomycetes. Previously referred to the Didymosphaeriaceae (Kohlmeier & Volkmann-Kohlmeier 1990), it forms a well supported basal clade to the Pleosporales. Continued molecular studies of unresolved taxa may yield further lineages of marine ascomycetes.

**Taxa for future phylogenetic study**

Marine Dothideomycetes include a broad spectrum of genera and a wide variety has been sequenced for the current study. However, several remain to be investigated with DNA sequence data, especially the genera Belizeana, Capillatospora and Thalassoascus (Dothideales incertae sedis); Lautospora (Dothideomycetidae incertae sedis); Bicrouania (Melanommataceae?); Lautitia (Phaeosphaeriaceae?) and Tirisporella (Pleosporales incertae sedis). Most are only rarely collected, have yet to be isolated, are intertidal, or rarely totally submerged. Other more frequently collected taxa also require further analysis: Quintania lignitallis (mangrove species), Decaisnella formosa (wood in association with sand) and Byssothecium obiones (on Spartina grass).

**Adaptation to the marine environment**

Of the 64 genera (108 species) of marine Dothideomycetes nearly all are intertidal species found in mangrove habitats, with the exception of those that occur on marine algae, saltmarsh plants or seagrasses, e.g. Thalassoascus, Lautitia, Pharcidia (algae), Bicrouania (marsh plants), Halothelia, Pontoporeia (seagrasses); Caryospora australiensis, Decaisnella formosa and Platystomum scabridisporum (wood associated with sand) (Abdel-Wahab & Jones 2000, 2003). Most of them would appear to be well adapted to intertidal estuarine habitats with active discharge of their ascospores. Although they lack the elaborate ascospore appendages found in the Halosphaeriaceae (Jones 1994, 1995) many have mucilaginous sheaths, often elaborated to form polar appendages (Yusoff et al. 1994, Read et al. 1997a, b, Alias et al. 2001, Au et al. 1999). Ascospores within the ascus are surrounded by a well-defined delimiting membrane which prevents the mucilaginous sheath from expanding, thus ensuring effective ascospore discharge (Read et al. 1994, Yusoff et al. 1994). Once ejected from the ascus the sheaths (and appendages) take up water, swell and help in the attachment of the spores to suitable substrata (Jones 1995).

Some species form ascospore appendages by fragmentation of a sheath e.g. Capronia ciliomaris (Au et al. 1999) and Tirisporella beccariana (Jones et al. 1996). A similar mechanism of appendage unfolding appears to occur in Helcoidea barbatula (Kohlmeier et al. 1996). As with the ensheathed ascospores, the appendages do not dilate until they are dispersed into water.

Few marine anamorphic fungi have been reported in comparison to those found in freshwater habitats (Marvanová 1997, Belliveau & Bårlocher 2005, Cai et al. 2006). Currently some 94 marine anamorphs are known, but only a few have been linked to teleomorphs in the Dothideomycetes: Amorosia littoralis (Mantle et al. 2006), Dendryphiella arenaria, O. salina (Jones et al. 2008), Xylomyces spp. (Campbell et al. 2007, Prihatini et al. 2008), Pseudorobillarda phragmitis (Runjindamai, pers. comm.), and Robillarda rhizophorae (Runjindamai, pers. comm.). A strain of Alternaria maritima groups within the Pleosporaceae in the current study, while other marine anamorphic species e.g. Stemphyllum spp. Stagonospora spp., may also be linked to teleomorphs in the Dothideomycetes.

Freshwater anamorphic fungi are uniquely adapted to their habitat with branched, sigmoid and tetraradiate conidia (Jones 2006, Campbell et al. 2007); many have teleomorphs in the Dothideomycetes (Webster & Descals 1979, Tsui & Berbee 2006, Tsui et al. 2006). In contrast few of the marine hyphomycetes appear to be adapted to their milieu, lacking any elaboration of their conidia (except e.g. Varicosporina ramulosa and Dwayaangam junci). This is particularly so for species with recorded teleomorphs in the Dothideomycetes (Jones et al. 2008).

**Specific habitats of marine Dothideomycetes**

Marine Dothideomycetes are generally intertidal ascomycetes and more common in mangroves, with only a few documented from temperate climates.

(i) Nypa fruticans: Currently some 100 saprophytic fungi have been documented from Nypa fruticans, a brackish water palm that occurs from fully saline conditions to freshwater habitats. Common fungi on this palm include Astrosphaeriella nypae, Astrosphaeriella striatispora, Helicascus nypae, Linocarpon appendiculatum and Tirisporella beccariana. Many of the fungi occurring in Nypa are not found on other mangrove or marine substrata, for example, Linocarpon spp., Astrosphaeriella spp., Oxidothis spp. and Fasciatispora lignicola. Therefore one could ask, are these fungi host-specific or is their occurrence on Nypa determined by the salinity of the habitat? A significant number of fungi on Nypa are unique to the palm, e.g. Helicascus nypae, Tirisporella beccariana and Carinisporella nypae while recently Mangicola guatemalensis has been found to be common on this palm in Thailand.

(ii) Seagrasses: The diversity of fungi in seagrasses has been a neglected field (Raghukumar 2008). Generally, diverse seagrass species support low diversity and density of saprophytic and endophytic fungi, as confirmed by many studies (Wilson 1998, Alva et al. 2002, Devarajan et al. 2002, Rodriguez 2008, Sakayaroj et al. 2010). The most common marine fungi associated with seagrasses include Sordariomycetes, Corollospora maritima, Linda thalassiae, Lulworthia sp. and anamorphic fungi (Kohlmeier & Kohlmeyer 1979, Newell & Fell 1980). Cuomo et al. (1982, 1985) reported that the marine Dothideomycetes, Pontoporeia biturbinata, and Halothelia posidoniana were commonly found on Posidonia oceanica and Cymodocea nodosa from Mediterranean coasts (Cuomo et al. 1982, 1985) and Cyprus (Jones et al. 2009). These two obligate marine Dothideomycetes appear to be host specific and are frequently found on rhizomes of seagrass (Kohlmeier & Kohlmeyer 1979).

Many anamorphic dothideomycetous fungi have been found predominantly as endophytes associated with living seagrass tissues (Sakayaroj et al. 2010). They are mostly sterile mycelia and have only been identified by DNA sequence analysis (Sakayaroj et al. 2010). So far the diversity of marine fungi associated with seagrasses, compared with other substrata, is relatively low (Kohlmeier & Kohlmeyer 1979). This is probably due to 1) growth
inhibiting substances present in seagrass, 2) possibly the frail leaves of seagrass break up before most of the ascomycetes are able to colonise or sporulate and finally 3) they are attacked by other competitors such as bacteria, protozoa, lower fungi, fast growing anamorphic and/or terrestrial fungi (Sakayaroj et al. 2010).

(iii) Saltmarsh plants: Spartina and Juncus roemerianus: The mycota of the saltmarsh plant Juncus roemerianus, endemic to the U.S. east coast and to the Gulf of Mexico, is unique among herbaceous plants and can only be vaguely compared to that of mangrove trees, which also host obligate marine as well as terrestrial species. The terete leaves of J. roemerianus remain standing for three years or more and the extreme conditions of the habitat are the reason for the unique fungal diversity (117 species, 17 families; Kohlmeyer & Volkman-Kohlmeyer 2001). Bitunicates appear to be less abundant than other groups of fungi; they range from obligate marine taxa at the base to terrestrial but halotolerant species at the tip of the leaves.

Spartina species are common saltmarsh plants in temperate climates that support a wide range of fungi. Kohlmeyer & Volkman-Kohlmeyer (2002) list 39 obligate and facultative marine fungi reported from Spartina species, of which 13 are bitunicate species. Phaeosphaeria species appear to be the most common bitunicate genus on this substratum.

(iv) Mangroves: Some 54 species of mangrove trees and 60 associates occur in the new and old world (Tomlinson 1986) with senescent wood, leaves and fruits offering a unique habitat for fungi. It is interesting that magicolous fungi are predominantly bitunicate species, while uniltunicate ascomycetes are more prevalent in other marine habitats. Of the 108 described marine Dothideomycetes, 90 sequences are currently available enabling the taxonomic resolution of a number of genera and species; in particular of Massarina species which are frequently found on mangrove substrata.

Future studies

Many habitats, substrata, geographical locations remain virgin territory for studies on marine fungi. For example, a recent investigation of the fungal diversity associated with the brown alga Fucus serratus found several unknown phylotypes within the Sordariomycetes the prevalence of mangrove fungi in Dothideomycetes is even more noticeable. Does this ecological predominance reflect a radiation event of these fungi in the Dothideomycetes? Or is our sampling still biased towards specific geographies and ecologies? Only a renewed focus on the niches described above will provide us with the answer. It is our hope that a broader scope will provide enough resolution to begin to address ecological shifts in this fascinating group of fungi.

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### SUPPLEMENTARY INFORMATION

Table 1. The list of species used in this study.

| Taxon                   | Substrate     | Collector | Location                                           | Source | SSU       | LSU       | RPB2      | TEF1     |
|-------------------------|---------------|-----------|----------------------------------------------------|--------|-----------|-----------|-----------|----------|
| Acrocordiopsis patilii | Mangrove wood | J. Sakayaroj | Thailand, Hat Khanom Mu Ko Thale Tai National Park | BCC 28166 | GU479736 | GU479772  | GU479811  | –         |
| Acrocordiopsis patilii | Mangrove wood | J. Sakayaroj | Thailand, Hat Khanom Mu Ko Thale Tai National Park | BCC 28167 | GU479737 | GU479773  | GU479812  | –         |
| Aigialus grandis        | Mangrove wood | E.B.G. Jones | Malaysia, Morib                                  | BCC 18419 | GU479738 | GU479774  | GU479813  | GU479838  |
| Aigialus grandis        | Mangrove wood | E.B.G. Jones | Malaysia, Morib                                  | BCC 20000 | GU479739 | GU479775  | GU479814  | GU479839  |
| Aigialus grandis        | Mangrove wood | J. Kohlmeyer | Belize, Stewart Island                            | JK 5244A | GU296131 | GU301793  | GU371762  | –         |
| Aigialus grandis        | Mangrove wood | J. Kohlmeyer | Bahamas, Mores Island                             | JK 4770  | GU479740 | –         | –         | –         |
| Aigialus grandis        | Mangrove wood | E.B.G Jones | Malaysia, Morib                                  | CY 2909  | AF441172 | –         | –         | –         |
| Aigialus grandis        | Mangrove wood | S. Suetrong  | Thailand, Kung Krabaen Bay Royal development Study Center | BCC 33563 | GU479741 | GU479776  | GU479815  | GU479840  |
| Aigialus mangrovei      | Mangrove wood | S. Suetrong  | Thailand, Kung Krabaen Bay Royal development Study Center | BCC 33564 | GU479742 | GU479777  | GU479816  | GU479841  |
| Aigialus parvus         | Mangrove wood | E.B.G. Jones | Malaysia, Morib                                  | BCC 18403 | GU479743 | GU479778  | GU479817  | GU479842  |
| Aigialus parvus         | Mangrove wood | E.B.G. Jones | Malaysia, Morib                                  | BCC 32558 | GU479744 | GU479779  | GU479818  | GU479843  |
| Aigialus parvus         | Mangrove wood | E.B.G. Jones | Malaysia, Morib                                  | CY 5061  | AF441173 | –         | –         | –         |
| Aigialus rhizophorae    | Mangrove wood | S. Suetrong  | Thailand, Mu Ko Chang National Park              | BCC 33572 | GU479745 | GU479780  | GU479819  | GU479844  |
| Aigialus rhizophorae    | Mangrove wood | S. Suetrong  | Thailand, Mu Ko Chang National Park              | BCC 33573 | GU479746 | GU479781  | GU479820  | GU479845  |
| Allewia eureka          |              |           |                                                    | DAOM 195275 | DQ677994 | DQ678044  | DQ677938  | DQ677883  |
| Alternaria alternata    |              |           |                                                    | CBS 916.96  | DQ678031 | DQ678082  | DQ677980  | DQ677927  |
| Alternaria maritima     |              |           | Ubiquitous                                        | CBS 126.60  | GU456294 | GU456317  | –         | –         |
| Amorosia littoralis     |              |           | Littoral zone                                     | P.G. Mantle | NN 6654 | AM292056  | AM292055  | –         | –         |
| Ascochyta pisi          |              |           |                                                    | CBS 126.54  | DQ678018 | DQ678070  | DQ677867  | DQ677913  |
| Ascocrratera manglicola |              |           |                                                    | CBS 120023  | GU296136 | GU301799  | GU371763  | –         |
| Ascocrratera manglicola |              |           |                                                    | K. Tanaka | HHUF 30032 | GU479748  | GU479783  | GU479822  | GU479847  |
| Ascocrratera manglicola | Mangrove wood | E.B.G. Jones | Thailand, Ranong Mangrove forest                  | BCC 09270  | GU479747 | GU479782  | GU479821  | GU479846  |
| Ascocrratera manglicola |              |           |                                                    | J. Kohlmeyer | JK 5262C, | GU296136  | GU301799  | GU371763  | –         |
| Aureobasidium pullulans |              |           |                                                    | CBS 584.75  | DQ471004 | DQ470956  | DQ470906  | DQ471075  |
| Berkleasmium micronesulm|              |           |                                                    | CBS 8141  | DQ280268 | DQ280272  | –         | –         |
| Berkleasmium nigroapicale|              |           |                                                    | CBS 8220  | DQ280269 | DQ280273  | –         | –         |
| Batrionospora marina    | Mangrove wood | E.B.G. Jones | Singapore, Singapore mangrove forest             | CY 1228  | GQ925835 | GQ925848  | GU479823  | GU479848  |
| Bimuria noavea-zelandiae |              |           |                                                    | CBS 107.79  | DQ677998 | DQ678051  | DQ677944  | DQ767637  |
| Botryosphaeria dothidea  |              |           |                                                    | CBS 115476 | DQ677998 | DQ678051  | DQ677944  | DQ767637  |
| Botryosphaeria ribis     |              |           |                                                    | CBS 115475 | DQ678000 | DQ678053  | DQ677947  | DQ677993  |
| Botryosphaeria stevensii |              |           |                                                    | CBS 431.82  | DQ678012 | DQ678064  | DQ677960  | DQ677907  |
| Botryosphaeria tsugae    |              |           |                                                    | CBS 418.64  | AF271127 | DQ766755  | DQ767644  | DQ677914  |
| Taxon                     | Substrate                     | Collector | Location                        | Source                  | SSU       | LSU       | RPB2         | TEF1        |
|--------------------------|-------------------------------|-----------|---------------------------------|-------------------------|-----------|-----------|--------------|-------------|
| Byssothecium cirinnans   | Mangrove wood (Nypa fruticans) | A. Loilong | Thailand, Tambon Bang Pao       | CBS 36316               | GU479749  | –         | –             | GU479849    |
| Capnodium coffeae        | Mangrove wood                 | J. Kohlmeyer | Fiji, Suva                    | JK 5020A                | GU479750  | GU479784  | –             | –           |
| Capnodium salicinum      | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Carinispora nypae       | Mangrove wood                 | A. Loilong | Thailand, Tambon Bang Pao       | CBS 36316               | GU479749  | –         | –             | GU479849    |
| Carylporinae             | Mangrove wood                 | J. Kohlmeyer | Fiji, Suva                    | JK 5020A                | GU479750  | GU479784  | –             | –           |
| Cladosporium             | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Columnosphaeria          | Mangrove wood                 | J. Kohlmeyer | Fiji, Suva                    | JK 5020A                | GU479750  | GU479784  | –             | –           |
| Decaisnella formosa      | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Decorospora gaudefroyi   | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Delitschia winteri      | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Delphinella strobiligena | Mangrove wood                 | J. Kohlmeyer | Fiji, Suva                    | JK 5020A                | GU479750  | GU479784  | –             | –           |
| Dendryphiella arenaria   | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Dendryphiella salina     | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Didymella cucurbitacearum| Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Didymella fucicola       | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Dothidea hippophaes      | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Dothidea insculpta       | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Dothidea sambuci         | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Dothiora cannabinae      | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Elsinoe centrolobi       | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Elsinoe phaseoli         | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Elsinoe veneta           | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Falciformispora lignantii| Mangrove wood                 | U. Pinruan | Thailand, Ban Bang Sak          | BCC 21118               | GU371835  | GU371827  | –             | –           |
| Falciformispora lignantii| Mangrove wood                 | U. Pinruan | Thailand, Ban Bang Sak          | BCC 21117               | GU371834  | GU371826  | –             | –           |
| Farlowiella carmichaeliana| Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Floricola striata        | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Gloniopsis praelonga     | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Gloniopsis subrugosa     | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Guignardia bidwellii     | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Guignardia gauthieri     | Mangrove wood                 | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Halomassarina (Massarina) thalassiae | Mangrove wood | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
| Halomassarina (Massarina) thalassiae | Mangrove wood | E.B.G. Jones | Australia, The Mornington Peninsula National Park | BCC 25617 | GQ925834 | GQ925847 | GU479824 | GU479850 |
Table 1. (Continued).

| Taxon                                    | Substrate                  | Collector       | Location                          | Source            | SSU             | LSU             | RPB2 | TEF1 |
|------------------------------------------|----------------------------|-----------------|-----------------------------------|-------------------|-----------------|-----------------|------|------|
| Halomassarina (Massarina) thalassiae     | Mangrove wood              | E.B.G. Jones    | U.S.A., Florida                   | BCC 17055         | GQ925843        | GQ925850        | –    | –    |
| Halomassarina (Massarina) thalassiae     | Mangrove wood              | E.B.G. Jones    | U.S.A., Florida                   | BCC 17054         | GQ925842        | GQ925849        | –    | –    |
| Halothia posidoniae                      | Seagrasses (Posidonia oceanica) | E.B.G. Jones    | Cyprus                            | BBH 22481         | GU479752        | GU479786        | –    | –    |
| Heleiosa barbatula                       | Juncus roemeranus          | J. Kohlmeyer, B. Kohlmeyer | U.S.A., North Carolina, Carteret County | JK 5548I         | GU479753        | GU479787        | –    | –    |
| Helicascus kanaloanus                    | Mangrove wood              | A. Loilong      | Thailand, Tambon Bang Pao         | BCC 36751         | GU479754        | GU479788        | GU479826 | GU479854 |
| Helicascus nypae                         | Mangrove wood              | A. Loilong      | Thailand, Tambon Bang Pao         | BCC 36752         | GU479755        | GU479789        | GU479827 | GU479855 |
| Helicascus nypae                         | Mangrove wood              | E.B.G. Jones    | Malaysia, Kuala Selangor          | PP 6066           | AF441174        | –              | –    | –    |
| Helminthosporium solani                  |                            |                 |                                    |                   |                 |                 | –    | –    |
| Helminthosporium velutinum               |                            |                 |                                    |                   |                 |                 | –    | –    |
| Herpotrichia diffusa                     |                            |                 |                                   | CBS 250.62        | DQ678019        | DQ678071        | DQ677968 | DQ677915 |
| Herpotrichia juniperi                    |                            |                 |                                   | CBS 200.31        | DQ678029        | DQ678080        | DQ677978 | DQ677925 |
| Hysterium andinense                      |                            |                 |                                   | CBS 123562        | FJ161159        | FJ161199        | FJ161125 | FJ161107 |
| Hysterium angustatum                     |                            |                 |                                   | CBS 236.34        | –              | FJ161180        | FJ161117 | FJ161096 |
| Hysterium pulicare                       |                            |                 |                                   | CBS 123377        | FJ161161        | FJ161201        | FJ161127 | FJ161109 |
| Hysterobrevium mori                      |                            |                 |                                   | CBS 123564        | FJ161158        | FJ161198        | –      | FJ161106 |
| Hysterobrevium smilacis                  |                            |                 |                                   | CBS 114601        | FJ161135        | FJ161174        | FJ161114 | FJ161091 |
| Hysteropatella clavispora                |                            |                 |                                   | CBS 247.34        | DQ678006        | AY541493        | DQ677955 | DQ677901 |
| Hysteropatella elliptica                 |                            |                 |                                   | CBS 935.97        | EF495114        | DQ767657        | DQ767647 | DQ767640 |
| Julella avicenniae                       | Mangrove wood              | E.B.G. Jones    | Thailand, Mu Ko Chang National Park | BCC 18422        | GU371831        | GU371823        | GU371787 | GU371816 |
| Julella avicenniae                       | Mangrove wood              | E.B.G. Jones    | Thailand, Mu Ko Chang National Park | BCC 20173        | GU371830        | GU371822        | GU371786 | GU371815 |
| Julella avicenniae                       | Mangrove wood              | J. Kohlmeyer    |                                   | JK 5236A          | GU479756        | GU479790        | –      | –      |
| Julella avicenniae                       | Mangrove wood              | E.B.G. Jones    | Hong Kong Tingkok                 | CY 2462           | AF441175        | –              | –      | –      |
| Keissleriella cladophila                 | Mangrove wood              |                 |                                   | CBS 104.55        | GU298155        | GU301822        | GU371735 | GU349043 |
| Keissleriella rara                       | Juncus roemeranus          | J. Kohlmeyer, B. Kohlmeyer | U.S.A., North Carolina, Carteret County | CBS 118429       | GU479757        | GU479791        | –      | –      |
| Kirschsteiniothelia elaterascus          |                            |                 |                                   | HKUCC 7769 & A22-5A | AF053727        | AY787934        | –      | –      |
| Kirschsteiniothelia maritima             | Driftwood                  | J. Kohlmeyer, B. Kohlmeyer | U.S.A., Washington, Friday Harbor Laboratories | CBS 221.60        | –              | GU323203        | –      | GU349001 |
| Lentitheciun (Massarina) phragmiticola    | Phragmites, grass          | C. Tsui         | Hong Kong Tai, O Lantau Island    | CBS 110446        | DQ813512        | DQ813510        | –      | –      |
| Lentitheciun arundinaceum (Massarina arundinacea) | Phragmites, grass          | C. Tsui         | Hong Kong Tai, O Lantau Island    | CBS 619.86        | DQ813513        | DQ813509        | –      | –      |
| Leptosphaeria biglobosa                  |                            |                 |                                   | CBS 303.51        | –              | GU301826        | –      | GU349010 |
| Leptosphaeria doliolum                   |                            |                 |                                   | CBS 505.75        | U43447          | U43474          | –      | –      |
| Leptosphaeria maculans                   |                            |                 |                                   | DAOM 2220267      | DQ470993        | DQ470946        | DQ471062 | DQ471062 |
| Leptosphaerulina australis               |                            |                 |                                   | CBS 939.69        | EU754068        | EU754167        | –      | –      |
Table 1. (Continued).

| Taxon                          | Substrate          | Collector  | Location                                  | Source        | SSU            | LSU            | RPB2 | TEF1     |
|-------------------------------|--------------------|------------|-------------------------------------------|---------------|----------------|----------------|------|----------|
| Lewia infectoria              | Mangrove wood      | J. Kohlmeyer | U.S.A., Florida                           | IMI 303186    | U43465         | U43482         | –    | –        |
| Lineolata rhizophorae         | Mangrove wood      | J. Kohlmeyer | Australia, Queensland                      | CBS 641.66    | GU479758       | GU479792       | GU479828 | –        |
| Lineolata rhizophorae         | Mangrove wood      | J. Kohlmeyer | Belize, Blue Ground Range                 | CBS 118422    | –              | GU479805       | –    | –        |
| Lophiostronga (Platystomum)   | Wood, sand         | E.B.G. Jones | Australia, The Momington Peninsula National Park | BCC 22836    | GG025832       | GG025845       | GU479829 | GU479856   |
| Lophiostronga (Platystomum)   | Wood, sand         | E.B.G. Jones | Australia, The Momington Peninsula National Park | BCC 22835    | GG025831       | GG025844       | GU479830 | GU479857   |
| Lophiostronga arundinis       |                    |            |                                           | CBS 621.86    | DQ782383       | DQ782384       | DQ782386 | DQ782387 |
| Lophiostronga bipolarae       |                    |            | (Massarina bipolaris)                     | HKUCC 1053    | AF164365       | –              | –    | –        |
| Lophiostronga crenatum        |                    |            |                                           | CBS 629.86    | DQ678017       | DQ678069       | DQ677965 | DQ677912 |
| Lophiostronga fuckellii       |                    |            |                                           | CBS 113432    | –              | EU552139       | –    | –        |
| Lophiostronga fuckellii       |                    |            |                                           | CBS 101952    | –              | DQ399531       | –    | –        |
| Lophiostronga macrostromum    |                    |            |                                           | KT 709        | AB521732       | AB433274       | –    | –        |
| Lophiostronga macrostromum    |                    |            |                                           | KT 635        | AB521731       | AB433273       | –    | –        |
| Lophiostronga sagittiforme    |                    |            |                                           | HHUFO 29754   | –              | AB369267       | –    | –        |
| Lophium mytilinum             |                    |            |                                           | CBS 269.34    | DQ0678030      | DQ0678081      | DQ677979 | DQ677926 |
| Loratospora aestuarii         | Juncus roemerianus | J. Kohlmeyer, B. Kohlmeyer | U.S.A., North Carolina, Carteret County | JK 5535D     | GU296168       | GU301838       | GU371760 | –        |
| Macrohomina phaseolina        |                    |            |                                           | CBS 277.33    | DQ678037       | DQ678088       | DQ677986 | DQ677929 |
| Massarina platani             |                    |            |                                           | CBS 221.37    | DQ678013       | DQ678065       | DQ677961 | DQ677908 |
| Massarina eburnea             |                    |            |                                           | CBS 473.64    | AF164367       | –              | –    | –        |
| Massarina eburnea             |                    |            |                                           | HKUCC 4054    | AF164366       | –              | –    | –        |
| Massarina igniaria            |                    |            |                                           | CBS 845.96    | DQ813511       | DQ810223       | –    | –        |
| Massarina ricifera            | Juncus roemerianus | J. Kohlmeyer, B. Kohlmeyer | U.S.A., North Carolina, Carteret County | JK 5535F     | GU479759       | GU479793       | –    | –        |
| Mauritiana rhizophorae        | Mangrove wood      | S. Suetrong | Thailand, Kung Krabaen Bay Royal development Study Center | BCC 28866    | GU371832       | GU371824       | GU371796 | GU371817 |
| Mauritiana rhizophorae        | Mangrove wood      | S. Suetrong | Thailand, Kung Krabaen Bay Royal development Study Center | BCC 28867    | GU371833       | GU371825       | GU371797 | GU371818 |
| Melanomma pulvis-pyrius       |                    |            |                                           | CBS 109.77    | AF164389       | DQ384095       | –    | –        |
| Melanomma radicans            |                    |            |                                           | ATCC 42522    | U43461         | U43479         | AY485625 | –        |
| Montagnula opulenta           |                    |            |                                           | CBS 168.34    | AF164370       | DQ678086       | DQ677984 | –        |
| Morosphaeria (Massarina)      | Mangrove wood      | J. Kohlmeyer | U.S.A., North Carolina, Carteret County | JK 5304B     | GU479760       | GU479794       | GU479831 | –        |
| Morosphaeria (Massarina)      | Mangrove wood      | E.B.G. Jones | Malaysia, Monib                          | BCC 18405    | GG025839       | GG025854       | –    | –        |
| Morosphaeria (Massarina)      | Mangrove wood      | E.B.G. Jones | Malaysia, Monib                          | BCC 18404    | GG025838       | GG025853       | –    | –        |
| Morosphaeria (Massarina)      | Mangrove wood      |            |                                           | HKUCC 7649    | –              | DQ528762       | –    | –        |
| Taxon                          | Substrate                  | Collector   | Location                              | Source | SSU          | LSU          | RPB2 | TEF1   |
|-------------------------------|----------------------------|-------------|---------------------------------------|--------|--------------|--------------|------|--------|
| Morosphaeria (Massarina) velataspora | Mangrove wood              | E.B.G. Jones | U.S.A., Florida                       | BCC 17059 | GQ925841     | GQ925852     | –    | –      |
| Morosphaeria (Massarina) velataspora | Mangrove wood              | E.B.G. Jones | U.S.A., Florida                       | BCC 17058 | GQ925840     | GQ925851     | –    | –      |
| Mycosphaerella eurypotami     | Juncus roemerianus         | J. Kohlmeyer, B. Kohlmeyer | U.S.A., North Carolina, Carteret County | JK 5586J | GU479761     | GU301852     | GU371722 | GU371722 |
| Mycosphaerella fijiensis      |                            |             |                                       | OSC 100622 | DQ767552     | DQ678098     | DQ677993 | –      |
| Mycosphaerella graminicola    |                            |             |                                       | CBS 292.38  | DQ678033     | DQ678094     | DQ677982 | –      |
| Mycosphaerella punctiformis   |                            |             |                                       | CBS 113265  | DQ471017     | DQ470968     | DQ470920 | –      |
| Myxangiogloea duriaeii        |                            |             |                                       | CBS 260.36  | AY016347     | DQ678059     | DQ677954 | DQ677900 |
| Myxangiogloea hispanicum      |                            |             |                                       | CBS 247.33  | GU296180     | GU301854     | GU371744 | GU349055 |
| Myxangiogloea eurypotami      |                            |             |                                       | CBS 303.34  | FJ161144     | FJ161184     | FJ161119 | FJ161100 |
| Myxangiogloea rossii          |                            |             |                                       | CBS 690.82  | DQ384069     | DQ384107     | –    | –      |
| Oedohysterium inalens         |                            |             |                                       | CBS 238.34  | FJ161142     | FJ161182     | FJ161118 | FJ161097 |
| Oedohysterium sinense         |                            |             |                                       | EB 0333     | FJ161169     | FJ161209     | FJ161130 | –      |
| Opegrapha dolomitica          |                            |             |                                       | –          | DQ883706     | –           | DQ883714 | DQ883732 |
| Ophiophaerella herpordichus   |                            |             |                                       | ATCC 12279  | U43453       | U43471       | –    | –      |
| Ostreichnicurtisii            |                            |             |                                       | CBS 19834   | FJ161137     | FJ161176     | –    | FJ161093 |
| Ostreichniassafras            |                            |             |                                       | CBS 322.34  | FJ161148     | FJ161188     | FJ161122 | –      |
| Paraliomyces lentiferus        | Mangrove wood              | E.B.G. Jones | Hong Kong, North Lantau               | CY 3525   | AF441176     | –           | –    | –      |
| Passeriniella savoryellopsis  | Mangrove wood              | J. Kohlmeyer | Belize, Tobacco Range                 | JK 5167C  | GU479762     | GU479795     | –    | GU479858 |
| Patellaria atrata 1            | Mangrove wood              | S. Suetrong  | Thailand, Kung Krabae Royal development Study Center | BCC 28877 | GU371837     | GU371829     | –    | –      |
| Patellaria atrata 2            | Mangrove wood              | S. Suetrong  | Thailand, Kung Krabae Royal development Study Center | BCC 28876 | GU371836     | GU371828     | –    | –      |
| Phaeodothis winteri           |                            |             |                                       | CBS 182.58  | DQ678021     | DQ678073     | DQ677970 | DQ677917 |
| Phaeosphaeria albopunctata     | Spartina alterniflora      | J. Kohlmeyer | U.S.A., North Carolina, Beaufort      | CBS 254.64 | –           | GU45631     | –    | –      |
|                                  |                            |             |                                       | DAO 226215 | AY544725     | AY544684     | DQ677941 | DQ677885 |
| Phaeosphaeria avenaria         |                            |             |                                       | CBS 576.86  | DQ678011     | DQ678063     | DQ677959 | DQ677906 |
| Phaeosphaeria eustoma          |                            |             |                                       | Juncus romerianus | JK 5540Q | –           | GU479807     | –    | –      |
| Phaeosphaeria olivacea         |                            | J. Kohlmeyer, B. Kohlmeyer | U.S.A., North Carolina, Carteret County | JK 55177A | –           | GU479808     | –    | –      |
| Phaeosphaeria spartincola      | Spartina sp.               | J.Kohlmeyer  | U.S.A., Maryland, Solomons            | JK 5577A  | –           | GU479808     | –    | –      |
| Phoma herbarum                 |                            |             |                                       | CBS 615.75  | EU754067     | EU754186     | –    | –      |
| Phytomyza ulmi                 |                            |             |                                       | CBS 361.52  | EF114726     | EF114702     | –    | –      |
| Pleospora herbarum             |                            |             |                                       | CBS 191.86  | DQ247812     | DQ247804     | DQ247794 | DQ471090 |
| Pleospora sedicola             |                            |             |                                       | CBS 109843  | –           | AY849568     | –    | –      |
| Pleosporaceae sp. 1            |                            |             |                                       | OSC 100706  | –           | GU479809     | –    | –      |
| Pontoporeia biturbinata        | Seagrasses                 | E.B.G. Jones | Cyprus                                | BBH 23338 | GU479763     | GU479796     | GU479837 | –      |
| Preussia minima                |                            |             |                                       | CBS 524.50  | DQ678003     | DQ678056     | DQ677950 | DQ677897 |

*Table 1. (Continued).*
**Table 1.** (Continued).

| Taxon                        | Substrate        | Collector            | Location                      | Source     | SSU          | LSU          | RPB2          | TEF1          |
|------------------------------|------------------|----------------------|-------------------------------|------------|--------------|--------------|---------------|---------------|
| Preussia tericola           |                  |                      |                               | DAOM 230091| AY544726     | AY544686     | DQ470895      | DQ471063      |
| Pseudodobillarda phragmitis  |                  |                      |                               | CBS 842.84 | EU754103     | EU754202     | –             | –             |
| Pseudodobillarda siamensis   |                  |                      |                               | BCC 12531  | FJ825365     | FJ825375     | –             | –             |
| Pseudodobillarda texana      |                  |                      |                               | BCC 12535  | FJ825367     | FJ825377     | –             | –             |
| Paliglumium araucanum        |                  |                      |                               | CBS 112412 | FJ161113     | FJ161112     | FJ161109      | FJ161108      |
| Paliglumium clavisporum      |                  |                      |                               | CBS 123339 | FJ161157     | FJ167526     | FJ161124      | FJ161105      |
| Paliglumium simulans         |                  |                      |                               | CBS 206.34 | FJ161139     | FJ161178     | FJ161116      | FJ161094      |
| Pyrenophora phaeocomes       |                  |                      |                               | DAOM 222769| DQ499595     | DQ499596     | DQ497614      | DQ497607      |
| Pyrenophora tritic-repentis  |                  |                      |                               | OSC 10066  | AY544716     | AY544672     | –             | –             |
| *Quintaria lignatilis*       | Mangrove wood    | J. Kohlmeyer, B. Kohlmeyer | French Polynesia, Moorea       | JK 5390A, CBS 117700 | GU296188 | GU301865 | GU371761 | – |
| *Quintaria lignatilis*       | Mangrove wood    | E.B.G. Jones          | U.S.A., Florida                | BCC 17444 | GU479764     | GU479797     | GU479832      | GU479859      |
| *Quintaria submersa*         | Pattern          |                      |                               | CBS 115553 | –             | –             | –             | –             |
| *Repetophragma ornitense*    |                  |                      |                               | HKUCC 10830| –             | –             | –             | –             |
| *Rimora (Lophiostoma)* mangrovei | Mangrove wood | J. Kohlmeyer          | Belize, Blue Ground Range      | JK 5246A   | GU296193     | GU301868     | GU371759      | –             |
| *Rimora (Lophiostoma)* mangrovei | Mangrove wood | J. Kohlmeyer          | India, Goa                     | JK 5437B   | GU479765     | GU479798     | –             | –             |
| Roccella fuciformis          |                  |                      |                               | DUKE 15572 | AY584678     | AY584654     | DQ782866      | –             |
| Saccardoella rhizophorae     | Mangrove wood    | J. Kohlmeyer, B. Kohlmeyer | Hawaii, Oahu                   | JK 5456A   | GU479766     | GU479799     | –             | –             |
| *Salsigina ramicola*         | Mangrove wood    | K. Tanaka             | Japan, Okinawa                 | KT 2597.1  | GU479767     | GU479800     | GU479833      | GU479861      |
| *Salsigina ramicola*         | Mangrove wood    | K. Tanaka             | Japan, Okinawa                 | KT 2597.2  | GU479768     | GU479801     | GU479834      | GU479862      |
| Scirrhia annulata            | Juncus roemerianus | S. Newell          | U.S.A., Georgia, Sapelo Island  | JK 5546G   | GU479769     | –             | –             | –             |
| Scorias spongiosa            |                  |                      |                               | CBS 325.33 | DQ678024     | DQ678075     | DQ677973      | DQ677920      |
| Styldothia pucciniioides     |                  |                      |                               | CBS 193.58 | AY016353     | AY004342     | –             | –             |
| Sydowi a polyspora           |                  |                      |                               | CBS 116.29 | DQ678005     | DQ678058     | DQ677953      | DQ677999      |
| *Tremateia halophila*        | Juncus roemerianus | J. Kohlmeyer       | U.S.A., North Carolina, Carteret County | JK 5517J   | GU296201     | –             | GU371721      | –             |
| Trematosphaeria (Lophiostoma) heterospora |            |                      |                               | CBS 644.86 | AY016354     | AY016369     | DQ497615      | DQ471049      |
| Trematosphaeria pertusa      |                  |                      |                               | CBS 122371 | FJ201993     | FJ201992     | –             | –             |
| Trematosphaeria pertusa      |                  |                      |                               | CBS 122368 | FJ201991     | FJ201990     | –             | –             |
| Ullospora bilgramii          |                  |                      |                               | CBS 110020 | DQ678025     | DQ678076     | DQ677974      | DQ677921      |
| *Verruculina enalia*         | Mangrove wood    | E.B.G. Jones         | Malaysia, Morib                | BCC 18401  | GU479770     | GU479802     | GU479835      | GU479863      |
| *Verruculina enalia*         | Mangrove wood    | E.B.G. Jones         | Malaysia, Morib                | BCC 18402  | GU479771     | GU479803     | GU479836      | GU479864      |
| *Verruculina enalia*         | Mangrove wood    | J. Kohlmeyer, B. Kohlmeyer | Belize, Blue Ground Range      | JK 5253A   | DQ678028     | DQ678079     | DQ677977      | –             |
| Westerdykella (Eremodothis) angulata |            |                      |                               | CBS 610.74 | DQ384067     | DQ384105     | –             | –             |
| Westerdykella cylindrica     |                  |                      |                               | CBS 454.72 | AY016355     | AY004343     | DQ470925      | DQ497610      |
| Westerdykella dispersa       |                  |                      |                               | CBS 508.75 | U42488       | DQ468050     | –             | –             |
| Wittsteinina lacustris       |                  |                      |                               | CBS 618.86 | DQ678023     | –             | DQ677972      | DQ677919      |