available online at www.studiesinmycology.org
doi:10.3114/sim.2009.64.09

Studies in Mycology 64: 155–173. 2009.

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*, *Jahnulales*, *Mytilinidiales*, *Patellariales* and *Pleosporales*. Most of the fungi sequenced were intertidal mangrove taxa and belong to members of 12 families in the *Pleosporale*s: *Aigialaceae*, *Didymellaceae, Leptosphaeriaceae*, *Lenthitheciaceae*, *Lophiostomataceae*, *Massarinaceae, Montagnulaceae*, *Morosphaeriaceae*, *Phaeosphaeriaceae*, *Pleosporaceae*, *Testudinaceae* and *Trematosphaeriaceae*. Two new families are described: *Aigialaceae* and *Morosphaeriaceae*, and three new genera proposed: *Halomassarina*, *Morosphaeria* and *Rimora.* Few marine species are reported from the *Dothideomycetidae* (e.g. *Mycosphaerellaceae*, *Capnodiales*), a group poorly studied at the molecular level. New marine lineages include the *Testudinaceae* and *Manglicola guatemalensis* in the *Jahnulales*. Significantly, most marine *Dothideomycetes* are intertidal tropical species with only a few from temperate regions on salt marsh plants (*Spartina* species and *Juncus roemerianus*), and rarely totally submerged (e.g. *Halotthia posidoniae* and *Pontoporeia biturbinata* 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, Sakayaroj, E.B.G. Jones, Kohlm., Volkm.-Kohlm. & Schoch, fam. nov., *Halomassarina* Suetrong, Sakayaroj, E.B.G. Jones, Kohlm., Volkm.-Kohlm. & Schoch, gen. nov., *Halomassarina thalassiae* (Kohlm. & Volkm.-Kohlm.), Suetrong, Sakayaroj, E.B.G. Jones, Kohlm., Volkm.-Kohlm. & Schoch, comb. nov., Suetrong, Sakayaroj, E.B.G. Jones, Kohlm., Volkm.-Kohlm.,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* Kohlm., Volkm-Kohlm., Suetrong, Sakayaroj, E.B.G. Jones, gen. nov., *Rimora mangrovei* (Kohlm. & Vittal) Kohlm.,Volkm-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 often submerged for most of the time. Jones *et al*. (2009) list 64 genera and *ca.* 108 species of marine *Dothideomycetes* that fall into three accepted orders (*Capnodiales*, *Dothideales*, *Pleosporales*), three orders *incertae sedis* (*Hysteriales*, *Patellariales*, *Jahnulales*) and 23 genera not assigned with confidence to any order. Most of these higher order taxa are represented by a single genus or species while most are members of the *Pleosporales* with 25 genera and 61 species (+ 13 genera, 20 species, *incertae sedis*). Taxa that can not be assigned with confidence to either an order or family include *Aigialus*, *Halotthia, Lautospora, Manglicola*, *Mauritiana*, *Passeriniella*, *Pontoporeia*, and *Tirisporella*. A notable feature of the marine *Dothideomycetes* is how few anamorphs are known. Examples include *Amarenographium metableticum*, *Scolecosporiella typhae*, *Stemphylium triglochinicola* and *Phialophora* cf. *olivacea* and molecular data indicates that the teleomorphs of *Amorosia littoralis*, *Dendryphiella 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 roemerianus*) (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-Kohlmeyer 2001). Other species are found on brown and red seaweeds, *e.g*. *Lautitia danica* and *Pleospora gracilariae* (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. Carinispora nypae*, *Herpotrichia nypicola*, *Tirisporella beccariana* and *Helicascus nypae* (Jones *et al*. 1996, Hyde & Alias 2000). Few marine *Dothideomycetes* produce elaborate appendaged ascospores, and

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most possess gelatinous sheaths that swell in water when released from the asci (*Massarina velataspora* and *Tremateia halophila*). Genera with appendaged ascospores, although generally modifications of a gelatinous sheath, include: *Carinispora nypae*, *Decorospora gaudefroyi* and *Falciformispora lignatilis*.

The main objective of this study is to provide information on the taxa that are unique to the marine milieu, *e.g. Aigialus* spp., *Manglicola guatemalensis*, *Halotthia posidoniae* and *Pontoporeia 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 ascoma 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/SW) with added antibiotics (streptomycin sulfate 0.5g/L, penicillin G 0.5 g/L) and allowed to germinate overnight. Germinating spores were transferred to a fresh agar plate and incubated for 2 wk at 25 ºC and deposited in relevant culture collections (Table 1 - see online Supplementary Information).

DNA extraction, amplification and sequencing

Fungal genomic DNA from a selection of cultures was isolated by filtering mycelia grown in seawater broth at 22 ºC with subsequent lyophilisation (Spatafora *et al*. 1998). DNA was then extracted using the FastDNA kit and cells were ground on the Fast-Prep instrument from MPI Biochemicals (Irvine, CA, U.S.A.) following manufacturer recommendations. Fungal biomass was harvested for a different set of isolates by filtering through cheesecloth, and washed several times with sterile distilled water. The harvested mycelium was stored at -20 °C and ground to a fine powder with a mortar and pestle. Fifty to 100 mg ground fungal mycelium was placed into 400 mL lysis buffer (O'Donnell *et al*. 1997) and DNA extracted as follows: the tube was incubated at 70 °C for 30 min, and an equal volume of phenol-chloroform (PIERCE) added. The upper liquid phase was transferred to a new microtube containing chilled absolute ethanol and 7.5 M ammonium acetate. The mixture was kept at -20 °C for 30 min, or until the DNA had precipitated, and then centrifuged at 14 000 rpm, 4 °C, for 15 min. The DNA pellet was washed twice with chilled 75 % ethanol and air dried. The DNA was resuspended in 50 mL TE buffer and checked for quantity and quality by 1 % agarose gel electrophoresis.

The following four genes were chosen for this study: small (18S) and large subunit (28S) of the nuclear ribosomal DNA (SSU, LSU) plus the gene fragments from the second largest subunit of RNA polymerase (*RPB2*) and the translation elongation factor 1-alpha (*TEF1*) gene. The rDNA was amplified with *Taq* DNA polymerase from FERMENTAS (Cat.No. MBDOEPO402) using PCR Model MJ Research DYAD ALD *ALD* 1244 thermocycler (*MJ Research*, Waltham, MA). Primers used for amplification include the SSU, LSU, *RPB2* and *TEF1* (White *et al*. 1990, Bunyard *et al*. 1994, Liu *et al.* 1999, Rehner 2001, respectively). The PCR products were purified using a NucleoSpin Extraction Kit (Macherey-Nagel, Germany), following the manufacturer's instructions. The characterisation of PCR products was performed via agarose gel electrophoresis on 1 % agarose gel containing ethidium bromide as the staining agent. PCR products were directly sequenced by Macrogen Inc., Korea. The sequencing primers used for as the different regions are SSU: NS1, NS3, NS4, NS6 (White *et al*. 1990); LSU: JS1, JS8, LROR and LR7 (Bunyard *et al.* 1994); *TEF1*: 983F, 2218R, CEFF2 and CEFR2 (Rehner 2001); *RPB2*: 5F1, 5F2, 7cR and 7R (Liu *et al.* 1999). Each sequence was checked for ambiguous bases and assembled using BioEdit v. 6.0.7 (Hall 2004) and SeqMerge, forming part of the GCG v. 10 software suite (Accelrys, San Diego, U.S.A.).

Sequence alignment and phylogenetic analyses

A total of 51 species (90 new sequences – Table 1) from the *Dothideomycetes*, representing 46 teleomorphic genera and five anamorphic genera were analysed along with reference fungal sequences from fungal families that were downloaded from the GenBank (listed in Table 1).

The consensus sequences for each DNA region were initially aligned with ClustalW v. 1.6 (Thompson *et al*. 1994) and improved in MUSCLE (Edgar 2004) (as part of Geneious Pro v. 4.7.4 (Biomatters, Auckland, N.Z.). When necessary new sequences were added to a core set of seed sequences using MAFFT v. 6.708b (Katoh & Toh 2008) using the e-insi option. Sequence homologies were also analysed using BLAST (Altschul *et al*. 1990) 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). Incomplete data at the 5´- and 3´-end of partial sequences were coded as missing. Following Wiens (2006), we included taxa in our multi-locus matrix even if they did not have all genes present. All absent genes were coded as missing data, forming at least 30 % of the total characters. Two members of the *Arthoniomycetes*, namely *Roccella fuciformis* and *Opegrapha dolomitica*, were chosen as outgroup sequences based on their placement as sister to the *Dothideomycetes* (Schoch *et al*. 2009).

Phylogenetic trees based on individual SSU, individual LSU, combined SSU and LSU and combined SSU, LSU and TEF datasets (data not shown) were congruent with the combined SSU, LSU, *RPB2* and *TEF1* data sets. However the position of the taxa *Biatriospora marina* and *Quintaria lignatilis* (in Clades XIV and XVI, respectively) and *Saccardoella rhizophorae* (unresolved taxon) were not constant. The phylogenetic analyses of the combined SSU, LSU, *RPB2* and *TEF1* data were performed using parsimony, Bayesian and maximum likelihood algorithms.

(i) Maximum parsimony (MP) analyses: MP analyses were performed using PAUP v. 4.0b10 (Swofford 2003). Gaps were treated as missing data with 100 replicates of random stepwise addition of sequences and tree-bisection reconnection (TBR) branch-swapping. All characters were given equal weight. The consistency indices (CI; Kluge & Farris 1969), retention indices (RI; Farris 1989) and rescaled consistency indices (RC; Farris 1989) were calculated for each tree generated. Bootstrap support values (Felsenstein 1985) were calculated for all parsimony analyses by 1000 bootstrap replicates (full heuristic searches, 10 replicates of random stepwise addition of sequences). Maximum parsimony bootstrap values (MPBP) equal or greater than 50 % are given above each node (Fig. 1).

(ii) Bayesian analyses (Larget & Simon 1999): The model of substitution used for Bayesian analyses was chosen with MrModeltest v. 2.2 (Nylander 2004). Independent Bayesian phylogenetic analyses were performed in MrBayes v. 3.1.2 (Huelsenbeck & Ronquist 2001) using a uniform [GTR+I+G] model, lset nst = 6 rates = invgamma; prset statefreqpr = dirichlet (1,1,1,1). The Metropolis-Coupled Markov Chain Monte Carlo (MCMC) sampling approach was used to calculate posterior probabilities (PP). Four Markov chains were run from a random starting tree for 5 000 000 generations and trees sampled every 100 generations. The first 5 000 trees were discarded as burn-in prior to convergence of the four chains. The remaining trees were used to construct a 50 % majority rule consensus tree and to calculate Bayesian Posterior Probabilities (BYPP) with those equal or greater than 0.95 given below each node (Fig. 1).

(iii) Maximum likelihood analyses (ML) were conducted in RAxML v. 7.2.2 (Stamatakis 2006). The dataset was partitioned according to each gene and separate codons (eight partitions) as previously done in Schoch *et al*. (2009). A general time reversible model (GTR) with a discrete gamma distribution and four rate classes was applied to each partition. A tree was obtained by simultaneously running a fast bootstrap search of 1 000 pseudoreplicates followed by a search for the most likely tree under functional setting "a". We also did 100 successive searches in RAxML under the GTR model with gamma rate distribution and starting each search from a randomised tree. Maximum Likelihood bootstrap values (MLBP) equal or greater than 50 % are given above each node (Fig. 1).

Phylogenetic trees were drawn using Treeview v. 1.6.6 (Page 2001) and TreeDyn 198.3 (Chevenet *et al*. 2006). Sequences derived in this study are deposited in GenBank, and the alignments in TreeBASE (www.treebase.org).

RESULTS

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*, *Hysteriale*s, *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 *Biatriospora 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 paraphyletic assemblage. But in the maximum parsimony tree, *B. marina* grouped in a basal clade to the *Testudinaceae*. 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 beloning in the *Pleosporomycetidae*, 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 sheaths are drawn out to form appendages (*e.g. Carinispora nypae*, *Decorospora gaudefroyi*, *Falciformispora lignatilis*).

Pleosporomycetidae

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

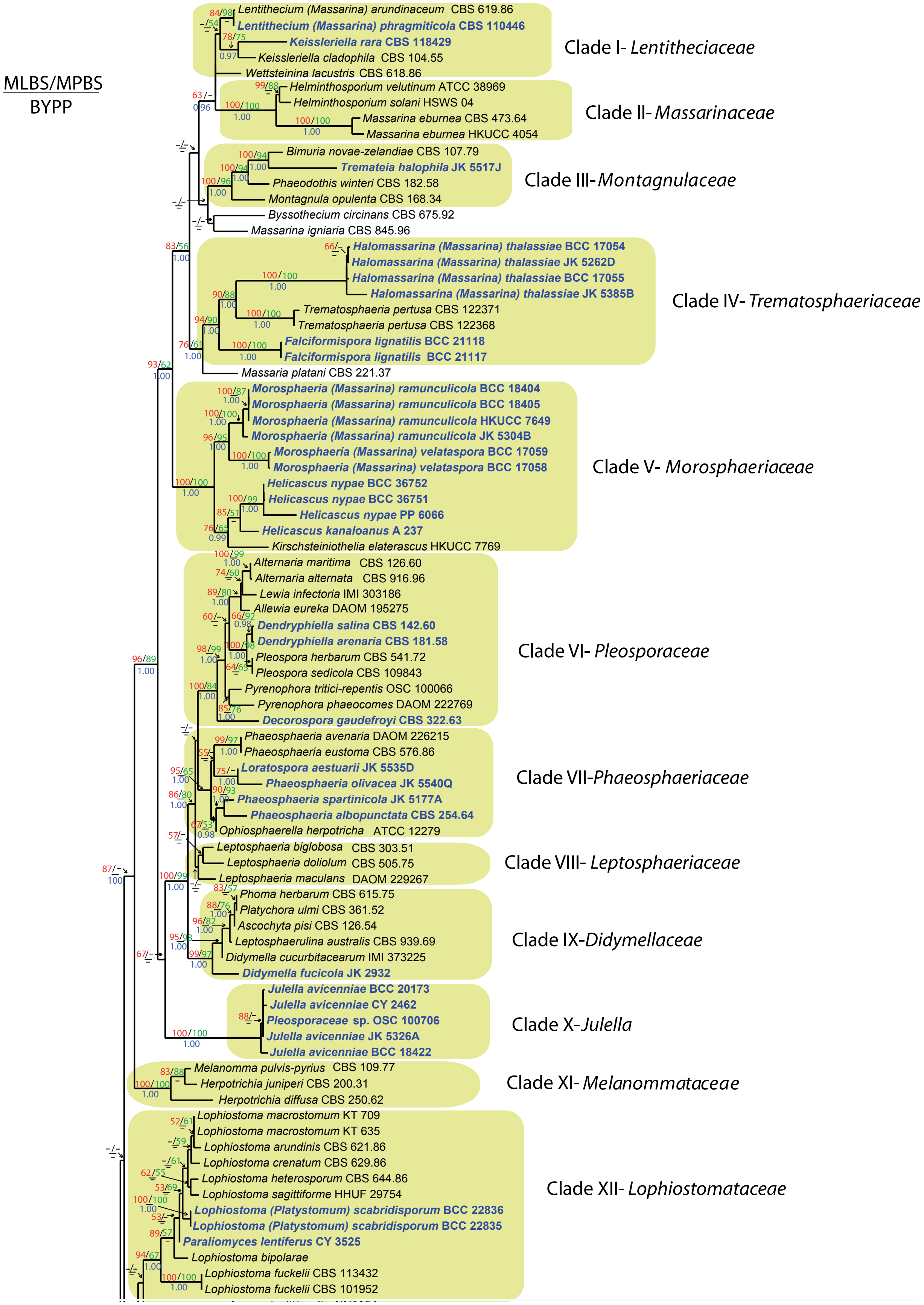


Fig. 1. RAxML tree of marine *Dothideomycetes* with bootstrap support values for maximum likelihood and maximum parsimony above the nodes. The values below the nodes are Bayesian posterior probalities. Relevant clades are highlighted in colour.

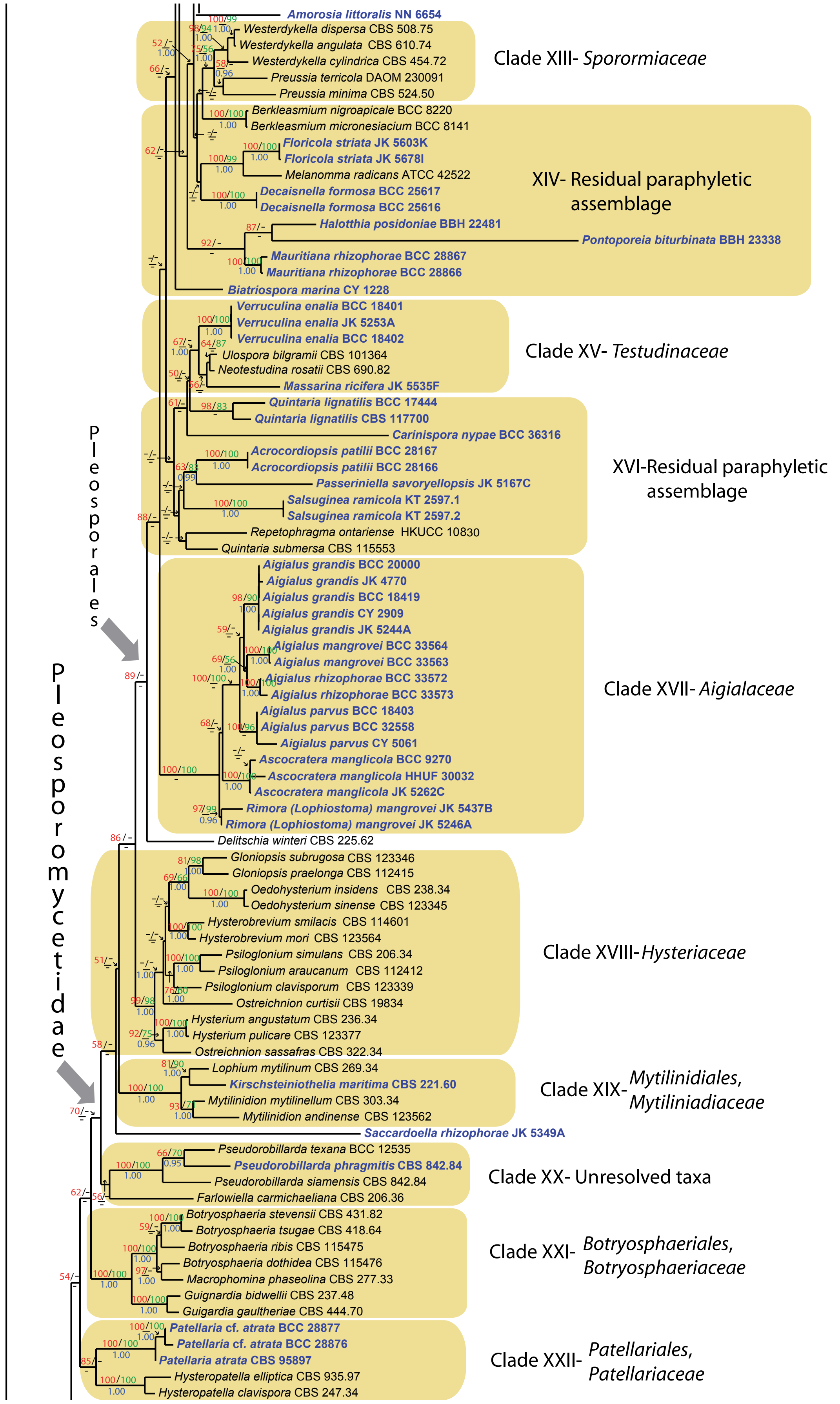


Fig. 1. (Continued).

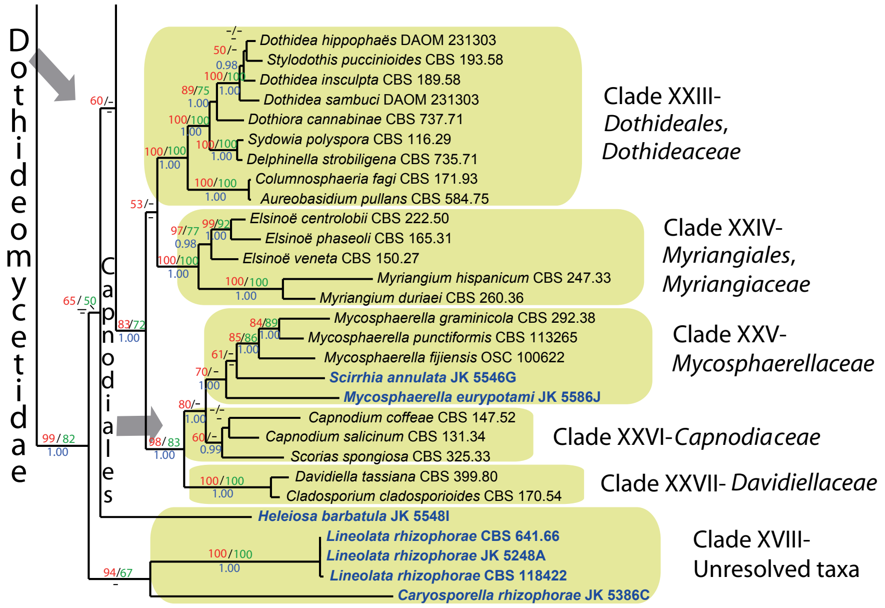


Fig. 1. (Continued).

reconstruction. This resulted in 11 supported clades corresponding to families, with marine representatives (Fig. 1) (*Didymellaceae*-Clade IX, *Lentitheciaceae*-Clade I, *Leptosphaeriaceae*-Clade VIII, *Lophiostomataceae*-Clade XII, *Massarinaceae*-Clade II, *Montagnulaceae*-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 (*Ascocratera manglicola* and *Lophiostoma mangrovei*), and 2) *Morosphaeriaceae* (Clade V) for the species *Morosphaeria* (*Massarina ramunculicola*, *Massarina velataspora*), *Helicascus nypae*, *H. kanaloanus* and *Kirschsteiniothelia elaterascus*. Further clades are also identified, but their position remains unresolved, *e.g.* the familial position of the taxa *Halotthia posidoniae*, *Mauritiana rhizophorae* and *Pontoporeia biturbinata* 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*, and the genus *Lentithecium* for *Massarina* that do not group in the *Massarinaceae*. However the monophyly of *Lentithecium* 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 *Lentithecium* and we place *M. phragmiticola* in synonymy with *Lentithecium arundinaceum.*

Keissleriella (type species *K. aesculi)* comprises some 25 species (Kirk *et al.* 2008) and two species group with *Lentithecium* 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 *Lentithecium.*

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 *Lophiostoma* (Hyde & Aptroot 1998, Hyde *et al.* 2002b, Liew *et al.* 2002). However, subsequent studies indicate that *Massarina* and *Lophiostoma* species are polyphyletic (Zhang *et al.* 2009a; this volume). These genera and the families *Lophiostomataceae* / *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 *Helminthosporium* species (*H. velutinum*, *H. solani*) as a sister group.

Jones *et al.* (2009) referred the genus *Massarina* to the *Lophiostomataceae* based on the molecular evaluation of Hyde *et al.* (2002b) and Liew *et al.* (2002). *Lophiostoma* has been reported as a monophyletic genus (Tanaka & Harada 2003, Tanaka & Hosoya 2008) while Zhang *et al.* (2009b) have shown that *Lophiostoma* is phylogenetically divided into two groups: *Lophiostoma* I which includes the type species *L. macrostomum* (voucher Lundqvist 20504), and *Lophiostoma* 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 *Lophiostoma s. str.* The paraphyletic nature of the *Lophiostomataceae* has previously been noted (Schoch *et al.* 2006) and clade XII is likely to represent the narrow concept of the *Lophiostomataceae*, although it is still too early to draw this conclusion until type material of *Lophiostoma* (*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 *Lophiostomataceae* (Clade XII).

Clade III. *Montagnulaceae*

Based on morphological data, Jones *et al.* (2009) referred the genus *Tremateia* to the *Pleosporaceae*, but molecular data places it with high support in the *Montagnulaceae* (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 (Kohlmeyer & Volkmann-Kohlmeyer 1987, Hyde 1992d, 1993, Alias & Jones 2000, Jones *et al*. 2006), with *Trematosphaeria pertusa* as a sister taxon. *Falciformispora lignatilis* (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, periphysata, papillata vel epapillata, clypeata, coriacea, brunnea, singularia. Peridium cellulis applanatis pachydermisque, texturam angularem formans. Hamathecium pseudoparaphysibus simplicibus, rariter anastomosantibus. Asci octospori, cylindrici ad clavati, pedunculati, pachydermi, fissitunicati, camera oculare, sine apparatu apicali, I non reagentes. Ascosporae distichae, ellipsoideae, triseptatae, hyalinae, tunica gelatinosa tectae.

Ascomata subglobose to pyriform, immersed or erumpent, ostiolate, periphysate, papillate or apapillate, 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, fissitunicate, with 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 kanaloanus* and *H. nypae,* is well supported (100 % MLBP, 100 % MPBP, 1.00 BYPP) with the *Massarinaceae*, *Montagnulaceae* 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 Pleosporalium, Ascomycetium. Ascomata subglobosa, conica, lenticulara, immersa ad superficialia, ostiolata, papillata, periphysata, brunnea vel nigra, coriacea vel carbonacea, solitaria, vel gregaria, cum 3–4 loculis, ostiolo communi ad centrum. Hamathecium pseudoparaphysibus filamentosis, numerosis, ramosis ad basem, ramosis anastomosantibusque supra ascos. Asci octospori, clavati vel cylindrici pedunculati, pachydermi, fissitunicati, persistentes, camera apicale et disco apicale, IKI non-reagentes. Ascosporae biseriatae, hyalinae ad brunneae, septatae constrictae ad leviter constrictae, tunica vel calyptra gelatinosa tectae, vel sine tunica.

Family in the *Pleosporales*, *Ascomycota*. *Ascomata* subglobose, conical, lenticular, immersed to superficial, ostiolate, papillate, periphysate, brown to black, coriaceaous 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 asci, embedded in a gelatinous matrix. Asci 8-spored, clavate to cylindrical, pedunculate, thick-walled, fissitunicate, 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.

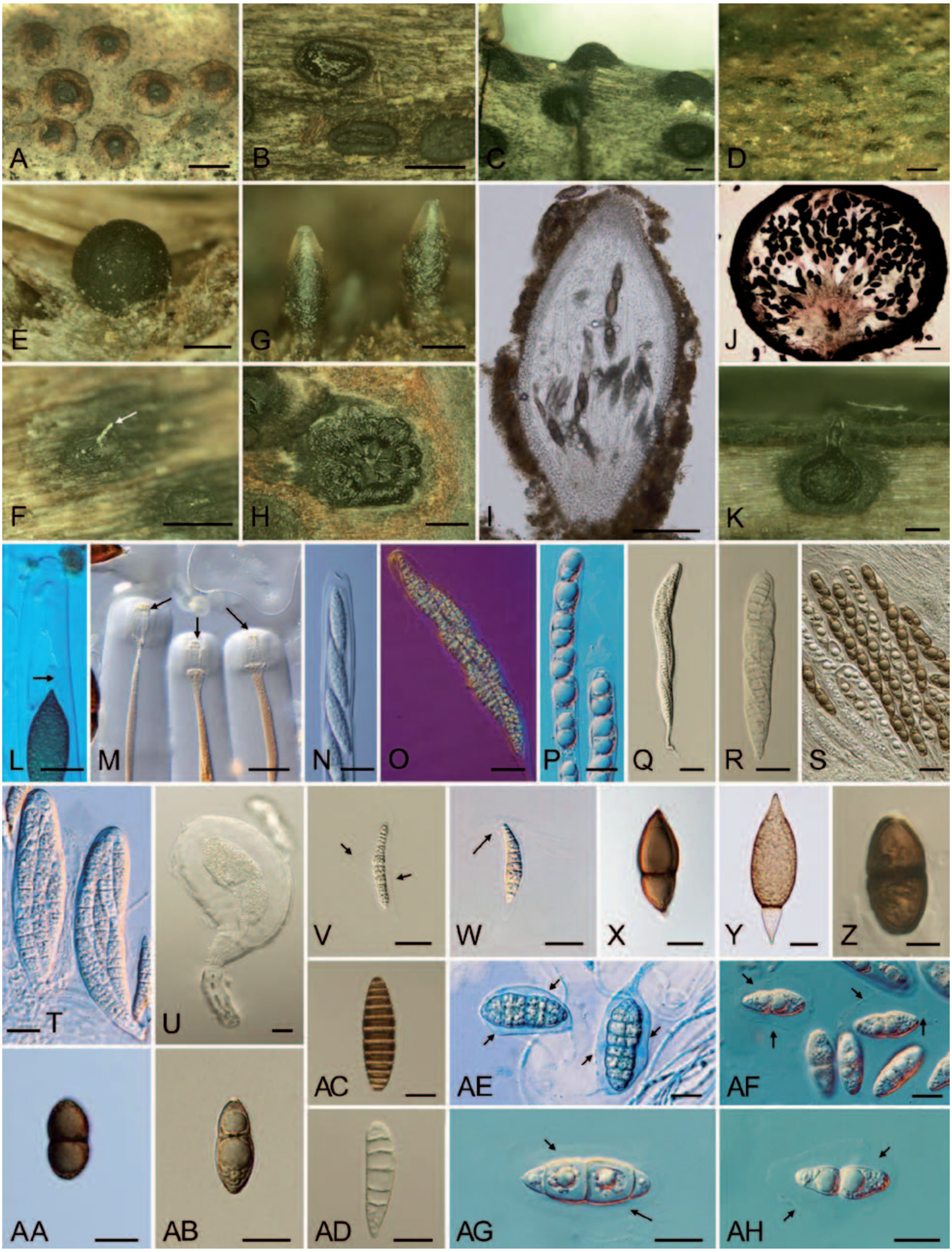
Etymology: Named after *Mor* = sea in Welsh in reference to its marine habitat and *sphaeria* in reference to the perithecial ascomata

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

Ascomata solitary or gregarious, subglobose to lenticular, immersed becoming superficial, ostiolate, papillate, coriaceous, brown to black, pseudoparaphyses filamenatous, anastomosing, branching, and numerous. *Asci* 8-spored, clavate to cylindrical, short pedunculate, thick-walled, bitunicate, fissitunicate, with an ocular chamber and apical apparatus, persistent. *Ascospores* hyaline, 1–3 septate, constricted at the septa, fusiform to ellipsoidal, 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. 2 AG.
Basionym: *Massarina velataspora* K.D. Hyde & Borse, Mycotaxon 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*

Fig. 2. (p. 162) Morphological features of marine *Dothideomycetes*. A. Immersed lenticular ascomata beneath clypeus of *Carinispora nypae*. B. Apothecium of *Patellaria* cf. *atrata* (*Patellariales*). C. Broadly conical ascomata of *Halotthia posidoniae*. D. Immersed ascomata of *Helicascus nypae*. E. Globose ascoma of *Pontoporeia biturbinata*. F. Immersed ascomata of *Quintaria lignatilis*. Released asci (arrow) from ostiole. G. Mature ascomata of *Manglicola guatemalensis* (*Jahnulales*). H. Tangential section of *Helicascus nypae* through stroma with several loculi. I. Longitudinal section (l.s.) of *Manglicola guatemalensis* ascoma with asci and pseudoparaphyses. J. *Pontoporeia biturbinata*, non-ostiolate ascoma, asci originating at the periphery of a hemispherical basal pulvinus. K. Longitudinal section through ascoma of *Verruculina enalia*. Asci. L–U. Ascus tip of *Manglicola guatemalensis*. Ascospores show the apical appendage (arrow) in ascus. M. Ascus tip of *Salsuginea ramicola*, consisting of a large distinctive ocular chamber and prominent ring (arrows). N. Clavate ascus of *Quintaria lignatilis* with apical plate. O. Clavate ascus of *Quintaria lignatilis*, with biseriate ascospores, in Nomarski and Quartz. P. Ovoidal or ellipsoidal ascospores in cylindrical asci of *Acrocordiopsis patilii*. Q. Clavate to long-cylindrical ascus of *Carinispora nypae*. R. Clavate ascus of *Patellaria* cf. *atrata*. S. Subcylindrical asci with pseudoparaphyses of *Helicascus nypae*. T. Clavate asci of *Falciformispora lignatilis* (*Trematosphaeriaceae*). U. Broadly clavate ascus of *Pontoporeia biturbinata*. V–AH. Ascospores of marine *Dothideomycetes*: V. *Carinispora nypae*. Cylindrical and multiseptate ascospore with keel-like mucilaginous sheath (arrows). W. *Falciformispora lignatilis*. Fusiform ascospores surrounded by thin mucilaginous sheath and single scythe-like appendage (arrow) at the base. X. *Salsuginea ramicola*. Ovoid, dark brown ascospore with hyaline apical germ pores. Y. *Manglicola guatemalensis*. Fusiform ascospore with lager, pale brown apical cell and hyaline turbinate basal cell. Z. *Halotthia posidoniae*. Ellipsoidal, dark brown ascospores, darker around septum. AA. *Verruculina enalia*. Ellipsoidal, dark brown ascospore, 1-septate. AB. *Helicascus nypae*. Obovoidal ascospore with persistent mucilaginous sheath. AC. *Mauritiania rhizophorae*. Fusiform ascospore, 9–13-distoseptate. AD. *Patellaria* cf. *atrata*. Clavate ascospore, 5–7-septate. AE. *Julella avicenniae*. Muriform ascospores with dilated sheath (arrows), straining in ink. AF. *Halomassarina (Massarina) thalassiae*. Ellipsoidal ascospores with gelatinous sheath (arrows). AG. *Morosphaeria (Massarina) velataspora*. Fusiform to ellipsoidal ascospores, 3-septate with mucilaginous sheath (arrows). AH. *Morosphaeria (Massarina) ramunculicola*. Fusiform ascospores with fully dilated mucilaginous sheath (arrows). Habitat: A, D, G, H, I, L, Q, S, V, Y, AB. On the surface of *Nypa fruticans*. B, F, K, M–P, R, X, AA, AC–AD, AF–AH. On mangrove wood. C, E, J, U, Z. On rhizomes of *Posidonia oceanica*. T, W. On oil palm (*Elaeis guineensis*). AE. On *Avicennia* spp. Scale bars: A–C, E–H = 500 mm; D = 1000 mm; I = 250 mm; K = 200 mm; J = 150 mm; L–Z, AB, AF–AH = 20 mm; AA, AC–AE = 10 mm.

elaterascus (Shearer 1993a). However, *Kirschsteiniothelia* is polyphyletic 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 *Phaeotrichum benjaminii*, originally isolated from dung (Lumbsch & Lindemuth 2001, Kruys *et al*. 2006, Schoch *et al*. 2009b). This continues to demonstrate the polyphyletic nature of this genus in agreement with clear morphological differences alluded to earlier (Shearer 1993a). There is great morphological variation in the three genera assigned to this family, especially the ascospores, hyaline in *Morosphaeria*, brown to dark-brown in *K. elaterascus* and *Helicascus* species, respectively.

Clade VI. *Pleosporaceae*

Jones *et al*. (2009) referred five genera with marine representatives in this family: *Decorospora, Helicascus, Falciformispora, Pleospora* and *Tremateia.* The current study confirms the placement of *D. gaudefroyi* in this family (Inderbitzin *et al*. 2002), along with the two anamorphic species, *Dendryphiella arenaria* and *D. salina*, that form a sister group to *Pleospora herbarum* and *Pleospora sedicola* (Jones *et al*. 2008). *Alternaria maritima* groups as a sister taxon with *Alternaria alternata* and *Lewia* species with moderate support (74 % MLBP, 60 % MPBP). The current study refers *Tremateia* to the *Montagnulaceae* (Clade II) and *Helicascus* to the new family *Morosphaeriaceae* (Clade V), respectively, while *Falciformispora* groups in a sister group to *Halomassarina thalassiae* and *Trematosphaeria pertusa* (Clade IV, Fig. 1). (Zhang *et al*. 2009a; this volume). The identity of the *Alternaria maritima* strain is questioned as this taxon was regarded as *nomen dubium* by Kohlmeyer & Kohlmeyer (1979) since there is no type material to verify the original description by Sutherland (1916).

Clade VII. *Phaeosphaeriaceae*

The families *Leptosphaeriaceae* and *Phaeosphaeriaceae* are closely related as recent sequence data have shown (Khashnobish & Shearer 1996, Cámara *et al*. 2002, Kodsueb *et al*. 2006, Schoch *et al*. 2006). The consensus was that they should both be retained (Câmara *et al*. 2002, Cannon & Kirk 2007).

Loratospora aestuarii, *Phaeosphaeria albopunctata, Ph. olivacea,* and *Ph. spartinicola* are the only marine species represented in the *Phaeosphaeriaceae* in this data set. Based on ITS2 and partial 28S nrDNA sequences Khashnobish & Shearer (1996) confirmed the inclusion of *Ph. albopunctata* and *Ph. typharum* in the *Phaeosphaeriaceae*, and suggested that *Leptosphaeria orae-maris* had a closer relationship with *Phaeosphaeria* than *Leptosphaeria*. Jones *et al*. (2009) tentatively referred the genera *Carinispora, Lautitia* and *Phaeosphaeria* to this family, with *Loratospora aestuarii* in the *Planistromellaceae* (*Dothideomycetidae*, family *incertae sedis*), based on morphological observations. Barr (1996) erected the *Planistromellaceae* for six genera in the *Dothideales* based on brown-celled pseudoparenchymatous ascostroma with one or more locules which open schizogeneously and contain asci, which are separated and overtopped by interthecial tissues at maturity. However 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) include the following marine species in the *Phaeosphaeriaceae*: *Leptosphaeria albopunctata, Ph. spartinae*, *Ph. spartinicola, Ph. typharum* as well as *Amarenomyces ammophilae*. Eriksson (1981) established the new genus *Amarenomyces* for *Ph. ammophilae*, but molecular data places it in *Phaeosphaeria* and thus the earlier name as proposed by Kohlmeyer & Kohlmeyer (1965) and Leuchtmann (1984) should be retained. *Phaeosphaeria olivacea* is a facultative marine species collected on *Juncus roemerianus* throughout the year (Kohlmeyer *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. spartinicola* on *Spartina* spp., while *Ph. ammophilae* occurs on a range of grasses and sedges, but primarily on *Ammophila arenaria* (Kohlmeyer & 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 teleomorphic genera *Didymella*, *Leptosphaerulina*, 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

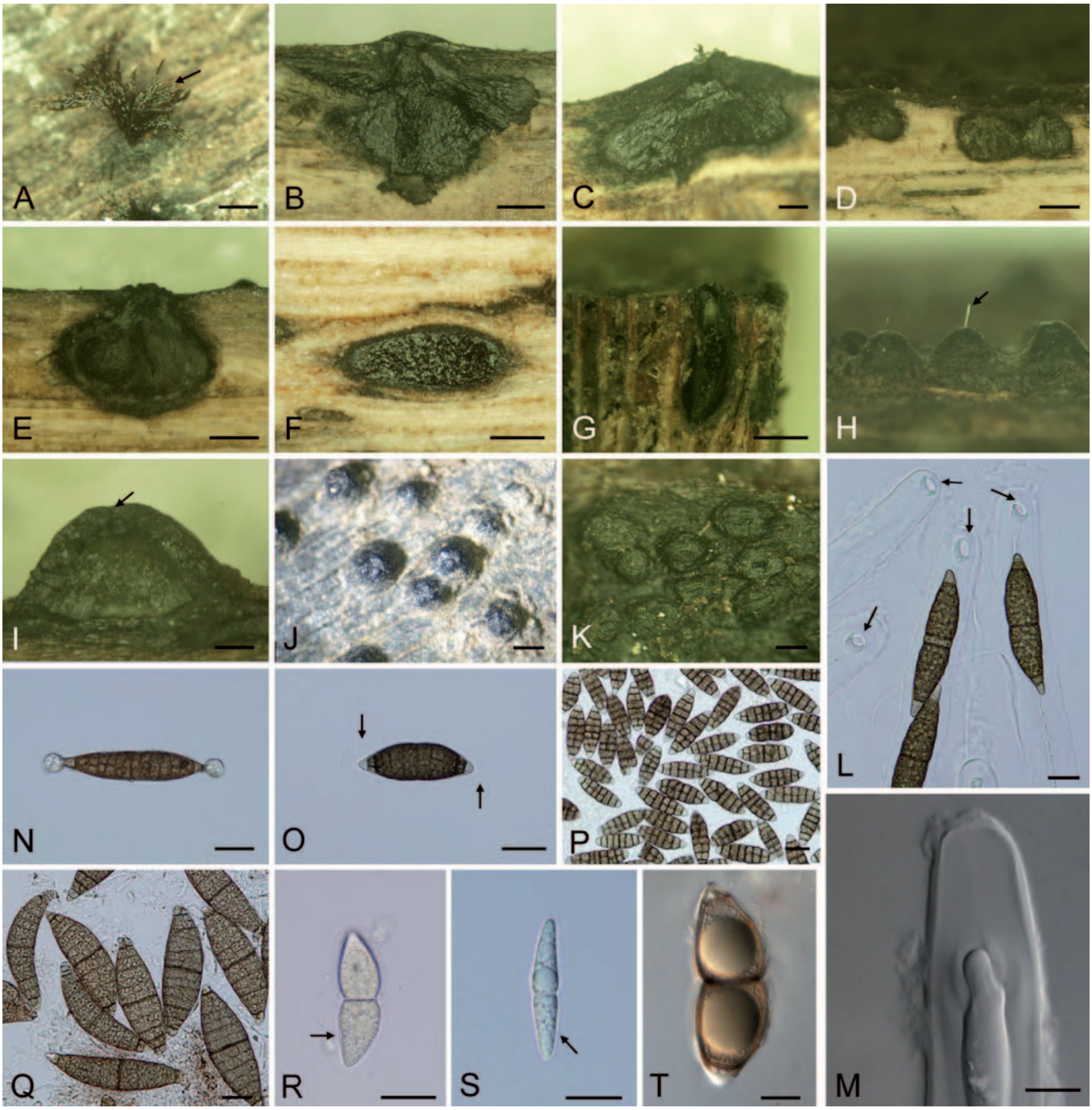


Fig. 3. Morphological features of marine *Dothideomycetes* in the *Aigialaceae* and *Coronopapilla mangrovei*. A. *Aigialus grandis*. Immersed ascomata with ascospores (arrow) released from ostiole. B–E. Longitudinal section (l.s.) through ascomata of *Aigialus grandis* (A), *A. parvus* (B), *A. mangrovis* (C) and *A. rhizophorae* (D). F. *A. parvus*. Surface wood showing ascoma with thick peridium. G. *A. parvus.* Sagittal section through ascoma. H. *Ascocratera manglicola*. Crater-like ascomata with released ascus (arrow) from the ostiole. I. *Ascocratera manglicola*. l.s. of ascoma filled with gelatinous matrix. J. *Coronopapilla mangrovei*. Surface view of ascomata. K. *Rimora (Lophiostoma) mangrovei*. Broadly oblong ascomata. L. *Aigialus grandis.* Asci with apical refractive ring (arrows) and ascospores. M. *Coronopapilla mangrovei*. Ascus tip, thick-walled with ocular chamber. N–T. Ascospores of marine *Dothideomycetes* in *Aigialaceae*: N. *Aigialus grandis*. Broadly fusiform (front view), muriform ascospores with drop of mucilage from end cells. O. *Aigialus parvus.* Ellipsoidal to broadly fusiform (front view), muriform ascospores with a gelatinous cap around apical and subapical cells (arrows). P. *Aigialus mangrovis*. Ellipsoidal to fusiform (front view), muriform ascospores. Q. *Aigialus rhizophorae.* Broadly fusiform (front view), muriform ascospores. R. *Ascocratera manglicola.* Ellipsoidal ascospores, initially 1-septate, later becoming 3-septate with gelatinous sheath (arrow). S. *Rimora (Lophiostoma) mangrovei.* Fusiform ascospore with gelatinous sheath (arrow). T. *Coronopapilla mangrovei*. Ellipsoidal ascospore. Habitat A–T. On mangrove wood. Scale bars: A, D–G, J–K = 500 mm; B–C, H = 250 mm; L, N–S = 25 mm; M, T = 10 mm.

basal clade (99 % MLBP, 97 % MPBP, 1.00 BYPP) to the families *Phaeosphaeriaceae*, *Pleosporaceae*, and *Leptosphaeriaceae*. Kohlmeyer & Volkmann-Kohlmeyer (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 *Massarinaceae* 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, *Massarinaceae*, *Paraliomyces*, *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 *Paraliomyces* (Tam *et al*. 2003) were included in the present analysis. Currently four marine *Lophiostoma* species are recognised: *L. acrostichi*, *L. armatisporum, L. rhizophorae* and *Platystomum scabridisporum*; however, Suetrong *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 mangrovei* is referred to the family *Aigialaceae* (Clade XVII, Fig. 1), while other *Massarina* species are placed in the *Lentitheciaceae* (Clade I) [*Lentithecium* (*Massarina) phragmiticola*], or the new family *Morosphaeriaceae* (clade V) [*Morosphaeria* (*Massarina*) *ramunculicola, M.* (*Massarina*) *velataspora*]. No molecular data is available for the marine species *Herpotrichia nypicola* which occurs on the palm *Nypa fruticosa*, 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 some members of the *Lophiostomataceae* and it is not clear whether missing data influenced this result. One of these is the marine anamorphic species *Amorosia littoralis* (isolated from the littoral zone in the Bahamas) and referred to the *Sporormiacaeae* based on molecular data (Mantle *et al*. 2006). Another anamorphic species, *Floricola striata*, is a facultative marine coelomycete from *Juncus roemerianus,* which grouped with *Melanomma radicans* with high support (100 % MLBP, 99 % MPBP, 1.00 BYPP). The teleomorph genera forming part of this poorly resolved group include: *Decaisnella* (*Lophiostomataceae*), *Halotthia* (Fig. 2C) (*Pleosporales incertae sedis*), *Mauritiana* (*Requienellaceae*) (Fig. 2AC) and *Pontoporeia* (Fig. 2E, J, Z) (*Zopfiaceae*) with weak support and previously assigned to the families listed in brackets (Jones *et al*. 2009). Morphologically they differ radically with perithecioid or cleistothecial ascomata, clavate to cylindrical asci and ascospores that are 3-septate and thick-walled in *Halotthia posidoniae* and *Pontoporeia biturbinata*, muriform in *Decaisnella formosa* and with 9–13 distosepta in *Mauritiana rhizophorae.* They also occur on different substrata: *Decaisnella formosa* on wood associated with sand, *Mauritiana rhizophorae* on mangrove wood, and *Halotthia* and *Pontoporeia* on submerged rhizomes of the seagrasses *Posidonia oceanica* and *Cymodocea nodosa*. The latter are temperate hosts, while *D. formosa* and *M. rhizophorae* 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.

Clade XVI. *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 & Mouzouras 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) ascomata that are conical, superficial on the host and carbonaceous with the asci formed 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. mangrovei* and *P. savoryellopsis*, with coriaceous, globose to subglobose, immersed ascomata, and ascospores that are 3-septate, central cells brown, and hyaline end cells (Hyde & Mouzouras 1988, Maria & Sridhar 2002). The taxonomic characterisation of the genus *Passeriniella* is confusing and has been discussed by Hyde & Mouzouras (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*, *Metasphaeria* and *Passeriniella* (Jones *et al*. 2009). Khashnobish & Shearer (1996) showed that based on ITS sequence data, *Byssothecium*

(*Passeriniella*) *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 lignatilis* 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 *Nypa 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.

Familia Pleosporalium, Ascomycetium. Ascomata subglobosa, conica, immersa ad superficialia, ostiolata, ostiolum rotundum vel fissuriforme, epapillata, periphysata. Hamathecium pseudoparaphysibus trabeculatis, eramosis ad basem, ramosis anastomosantibusque supra ascos. Asci octospori, cylindrici pedunculati, pachydermi, fissitunicati, disco apicale, IKI non-reagentes. Ascosporae biseriatae vel uniseriatae, hyalinae ad atro-brunneae, septatae vel muriformes, constrictae ad leviter constrictae, tunica vel calyptra gelatinosa tectae.

Family in the *Pleosporales*, *Ascomycota*. *Ascomata* subglobose and immersed to superficial or conical, ostiolate, ostiolum round or cleft-like, apapillate, black, carbonaceous to coriaceous, single to gregarious. Periphysate. *Hamathecium* trabeculate, unbranched at the base, anastomosing above the asci, embedded in a gelatinous matrix. *Asci* 8-spored, cylindrical, pedunculate, thick-walled, fissitunicate, with a refractive apical ring, non-amyloid. *Ascospores* biseriate or monostichous, hyaline to brown, septate to muriform, with a gelatinous sheath or cap.

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*). Fig. 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. striatispora 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 striatispora* was described from Ranong mangrove, Thailand, but no further collections have been made (Hyde *et al*. 1990, 1993).

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

Ascocratera 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 *rima* = cleft, fissure and *os* = mouth, in reference to the cleft-like ostiole, a unique feature among marine ascomycetes.

Ascomata erumpentia, apice plano, elongata, epapillata, ostiolo fissuriforme, periphysata, nigra, gregaria. Peridium cellulis pachydermis, texturam angularem formans. Hamathecium pseudoparaphysibus ramosibus. Asci octospori, cylindrici, pedunculati, pachydermi, fissitunicati, sine apparatu apicali. Ascosporae distichae, fusiformes, triseptatae, hyalinae, tunica gelatinosa tectae.

Ascomata erumpent, with flat tops, elongated, apapillate, 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, fissitunicate, without apical apparati. *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. Fig. 3K, S.
Basionym: Lophiostoma mangrovei Kohlm. & Vittal, Mycologia 78: 487. 1986.

≡ *Astrosphaeriella mangrovei* (Kohlm. & Vittal) Aptroot & K.D. Hyde, in K.D. Hyde, Fungi in Marine Environments. Fungal Diversity Press 7: 106. 2002.

Rimora mangrovei was described from collections of bark and wood of mangrove trees from Belize and India (Kohlmeyer & Vittal 1986) as *Lophiostoma*. It was subsequently transferred to *Astrosphaeriella* (Hyde *et al*. 2002b) based on the trabeculate morphology of the pseudoparaphyses. However, the aforementioned authors conceded that *A. mangrovis* (and *A. asiana*) differed from other *Astrosphaeriella* species by their round flattened ascomata, slit-like ostioles and non monocotyledonous hosts.

All three genera *Aigialus*, *Ascocratera* and *Rimora* share features such as carbonaceous, apapillate 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 *Ascocratera* and *Rimora*.

2. *Mytilinidiales*, Fig. 1

Clade XIX. *Mytilinidiaceae*

The common bitunicate ascomycete *Kirschsteiniothelia maritima* groups with *Lophium mytilinum*, with *Mytilinidion mytilinellum* 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 *Massarinaceae* (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 *Melanommataceae* (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 *Pseudorobillarda 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 carmichaeliana* 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 *Hysteropatella* species, taxa normally assigned to the *Hysteriales*, but recently removed (Boehm *et al.* 2009a, b; this volume). Morphologically, little distinguishes *Gloniella clavatispora* 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 *Gloniella* to the *Hysteriaceae*, 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) *Biatriospora 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 ascomata that are black and carbonaceous, cylindrical asci and brown, septate ascospores with hyaline, globose refractive chamber or an appendage at each end. Septation 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 *Clypeosphaeriaceae* (Barr 1994). However, Mathiassen (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 *Aliquandostipite* 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 *Manglicola guatemalensis* and the anamorphic species *Xylomyces chlamydosporus* and *X. rhizophorae* (Suetrong *et al*. 2010). *Manglicola guatemalensis* is a poorly known species with only three previous collections (Kohlmeyer & Kohlmeyer 1971, Hyde 1988, Jones *et al*. 2009, Suetrong *et al*. 2010). The type strain was collected from dead roots of *Rhizophora mangle* in Guatemala (Kohlmeyer & Kohlmeyer 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. *Manglicola 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 *Manglicola* 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 *Manglicola* 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 *Belizeana*, *Caryosporella, Coronopapilla*, *Lautospora*, *Loratospora*, *Pontoporeia* and *Thalassoascus*, 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. suaedae-australis*) found on salt marsh plants (*Armeria*, *Limonium*, *Salicornia* and *Suaeda*), while *M. pneumatophorae* is a common species on the pneumatophores of *Avicennia* species in Asia and the Carribean (Kohlmeyer & Kohlmeyer 1979, Schmit & Shearer 2003, E.B.G. Jones, pers. comm.). However recent molecular phylogenies containing a single culture did not support the placement of *M. pneumatophorae* in *Mycosphaerella* (Schoch *et al*. 2006); instead it was found on a poorly resolved branch within *Dothideomycetes*.

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 *Heleiosa 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 epapillate ascomata formed beneath a clypeus, with pseudoparaphyses, asci cylindrical with short pedicel, refractive apical apparatus and ascospores that are pale brown, ellipsoid, 1-septate with 10 or more cilia-like polar appendages at each end.

(ii) The genera *Caryosporella*, and *Lineolata* form a basal clade in all analyses with weak support, genera previously assigned to *Melanommataceae* 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).

Caryosporella 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*, *Mytilinidiales*, 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*, *Lophiostoma*, *Massarina*, *Trematosphaeria* and *Phaeosphaeria*, others have no known terrestrial counterparts. The uniqeness of these has necessitated the introduction of two new families in the *Pleosporales*, *Aigialaceae* (all marine genera: *Aigialus*, *Ascocratera*, *Rimora*) and *Morosphaeriaceae* (marine genera *Helicascus*, *Morosphaeria* and the freshwater species *Kirschsteiniothelia elaterascus*). The taxonomic position of other exclusively marine genera/species remains to be resolved *e.g.* the seagrass ascomycetes *Halotthia posidoniae*, *Pontoporeia biturbinata* (CladeXIV), and *Lineolata rhizophorae* (Clade XVIII) and *Biatriospora marina* (Clade XIV).

A number of new marine lineages have been highlighted as result of molecular studies including *Manglicola 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 *Nypa fruticans* and *Rhizophora* wood and may well form a link between lignicolous 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 (Kohlmeyer & Volkmann-Kohlmeyer 1998, S. Sivichai, pers. comm.). Campbell *et al*. (2007) and Prihatini *et al*. (2008) have shown that *Xylomyces chlamydosporus* has a teleomorph in the *Jahnulales*.

A second marine lineage is the *Aigialaceae* comprising three genera: *Aigialus*, *Ascocratera*, and the new genus *Rimora*, 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 *Verruculina enalia* is a member of the *Testudinaceae,* and another marine lineage in the *Dothideomycetes*. Previously referred to the *Didymosphaeriaceae* (Kohlmeyer & Volkmann-Kohlmeyer 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: *Quintaria lignatilis* (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)*, Halotthia*, *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 *Heleiosa barbatula* (Kohlmeyer *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 & Bärlocher 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*, *D. salina* (Jones *et al*. 2008), *Xylomyces* spp. (Campbell *et al*. 2007, Prihatini *et al*. 2008), *Pseudorobillarda phragmitis* (Rungjindamai, pers. comm.), and *Robillarda rhizophorae* (Rungjindamai, pers. comm.). A strain of *Alternaria maritima* groups within the *Pleosporaceae* in the current study, while other marine anamorphic species *e.g. Stemphylium* 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., *Oxydothis* 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 *Carinispora nypae* while recently *Manglicola 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, Rodríguez 2008, Sakayaroj *et al*. 2010). The most common marine fungi associated with seagrasses include *Sordariomycetes*, *Corollospora maritima*, *Lindra thalassiae, Lulworthia* sp. and anamorphic fungi (Kohlmeyer & Kohlmeyer 1979, Newell & Fell 1980). Cuomo *et al.* (1982, 1985) reported that the marine *Dothideomycetes*, *Pontoporeia biturbinata*, and *Halotthia posidoniae* 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 (Kohlmeyer & 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 (Kohlmeyer & 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 & Volkmann-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 & Volkmann-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 offereing a unique habitat for fungi. It is interesting that maglicolous fungi are predominantly bitunicate species, while unitunicate 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 *Dothideomycetes*, including some grouping with an anamorph species isolated from leaf litter (*Sporidesmium obclavatulum;* Shenoy *et al.* 2006) without obvious marine assocations (Zuccaro *et al*. 2008). Previously Zuccaro & Mitchell (2005) isolated fungi from living and cast fronds of the alga, with 33 % belonging in the *Dothideomycetes*. Many other niches such as endophytes from marine animals and mangroves await intense study (Pang *et al*. 2008, Schulz *et al*. 2008, Wang *et al*. 2008). Practical applications are also possible as marine endophytes from plants and animals have already yielded a wide range of new chemical structures (Jones 2008, Pan *et al*. 2008). Unknown fungi, including those belonging to the *Dothideomycetes*, have even been isolated from extreme marine environments, *e.g.* ocean sediments and deep sea hydrothermal ecosystems (Burgaud *et al*. 2009). Although it remains to be seen whether these fungi truly qualify as marine fungi the increase in fungal and dothideomycete phylotypes from these environments suggest additional sources of untapped diversity (Le Calvez *et al*. 2009).

In conclusion, marine bitunicate ascomycetes, (as other marine fungi) is a broadly defined ecological group that occupy a wide range of habitats within the maritime environment. Within this study facultative and halotolerant species from *Juncus roemerianus* were also included, as well as two genera on submerged seagrasses from European regions. The vast majority of fungi presented are predominantly tropical/subtropical mangrove species. When compared to the other diverse groups of marine fungi in 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.

ACKNOWLEDGEMENTS

This work was supported by TRF/BIOTEC Special Program for Biodiversity Research and Training Grant BRT R251006, BRT R351004 BRT R352015, and a TOTAL Corporate Foundation, TOTAL E & P Thailand. We thank Y. Zhang and Dr K.D. Hyde for exchange of data and useful discussions. SS acknowledges the Songklanagarind Scholarship for Graduate Studies from the Prince of Songkla University. We thank Prof. M. Tanticharoen, Dr K. Kirtikara and Dr L. Eurwilaichitr for continued support. We thank A. Klaysuban for technical assistance, and U. Pinruan, N. Rungjindamai, R. Choeyklin, A. Loilong, S. Preedanon and O. Supaphon for assistance with the field work. Work performed by CLS after 2008 was supported in part by the Intramural Research Program of the NIH, National Library of Medicine. Part of this work was also funded by a grant from NSF (DEB-0717476) to JWS and CLS (until 2008).

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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 mangrovei	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	Bahamas, Crooked Island	NN 6654	AM292056	AM292055	–	–
Ascochyta pisi				CBS 126.54	DQ678018	DQ678070	DQ677967	DQ677913
Ascocratera manglicola		K. Tanaka	Japan, Okinawa	HHUF 30032	**GU479748**	**GU479783**	**GU479822**	**GU479847**
Ascocratera manglicola	Mangrove wood	E.B.G. Jones	Thailand, Ranong Mangrove forest	BCC 09270	**GU479747**	**GU479782**	**GU479821**	**GU479846**
Ascocratera manglicola		J. Kohlmeyer	Belize, Tobacco Range	JK 5262C, CBS 120023	**GU296136**	**GU301799**	**GU371763**	–
Aureobasidium pullulans				CBS 584.75	DQ471004	DQ470956	DQ470906	DQ471075
Berkleasmium micronescium				BCC 8141	DQ280268	DQ280272	–	–
Berkleasmium nigroapicale				BCC 8220	DQ280269	DQ280273	–	–
Biatriospora marina	Mangrove wood	E.B.G. Jones	Singapore, Singapore mangrove forest	CY 1228	GQ925835	GQ925848	**GU479823**	**GU479848**
Bimuria novae-zelandiae				CBS 107.79	DQ677998	DQ678051	DQ677944	DQ767637
Botryosphaeria dothidea				CBS 115476	DQ677998	DQ678051	DQ677944	DQ767637
Botryosphaeria ribis				CBS 115475	DQ678000	DQ678053	DQ677947	DQ677893
Botryosphaeria stevensii				CBS 431.82	DQ678012	DQ678064	DQ677960	DQ677907
Botryosphaeria tsugae				CBS 418.64	AF271127	DQ767655	DQ767644	DQ677914

Table 1. (Continued).

Taxon	Substrate	Collector	Location	Source	SSU	LSU	*RPB2*	*TEF1*
Byssothecium circinnans				CBS 675.92	AY016339	AY016357	DQ767646	-
Capnodium coffeae				CBS 147.52	DQ247808	DQ247800	DQ247788	DQ471089
Capnodium salicinum				CBS 131.34	DQ677997	DQ678050	–	DQ677889
Carinispora nypae	Mangrove wood (*Nypa fruticans*)	A. Loilong	Thailand,Tambon Bang Pao	BCC 36316	**GU479749**	–	–	**GU479849**
Caryosporella rhizophorae	Mangrove wood	J. Kohlmeyer	Fiji, Suva	JK 5302A	**GU479750**	**GU479784**	–	–
Cladosporium cladosporioides				CBS 170.54	DQ678004	DQ678057	DQ677952	DQ677898
Columnosphaeria fagi				CBS 171.93	AY016342	AY016359	DQ677966	–
Davidiella tassiana				CBS 399.80	DQ678022	DQ678074	DQ677971	DQ677918
Decaisnella formosa		E.B.G. Jones	Australia, The Mornington Peninsula National Park	BCC 25617	GQ925834	GQ925847	**GU479824**	**GU479850**
Decaisnella formosa	Wood, sand	E.B.G. Jones	Australia, The Mornington Peninsula National Park	BCC 25616	GQ925833	GQ925846	**GU479825**	**GU479851**
Decorospora gaudefroyi	Salt marsh plants			CBS 322.63	AF394542	–	–	–
Delitschia winteri				CBS 225.62	DQ678026	DQ678077	DQ677975	DQ677922
Delphinella strobiligena				CBS 735.71	DQ471029	DQ470977	DQ677951	DQ471100
Dendryphiella arenaria	Algae, sand	J. Nicot	France, Gironde, Arcachon area	CBS 181.58	DQ471022	DQ470971	DQ470924	DQ677890
Dendryphiella salina	*Spartina* sp.	E.B.G. Jones	U.K., England; Southampton, Langstone Harbour	CBS 142.60	–	–	DQ435066	DQ414251
Didymella cucurbitacearum				IMI 373225	AY293779	AY293792	–	–
Didymella fucicola	Alga (*Fucus vesiculosus*)	J. Kohlmeyer	U.K., West Looe	JK 2932	–	EF177852	–	–
Dothidea hippophaes				DAOM 231303	U42475	DQ678048	DQ677942	DQ677887
Dothidea insculpta				CBS 189.58	DQ247810	DQ247802	AF107800	DQ471081
Dothidea sambuci				DAOM 231303	AY544722	AY544681	DQ522854	DQ497606
Dothiora cannabinae				CBS 737.71	DQ479933	DQ470984	DQ470936	DQ471107
Elsinoë centrolobi				CBS 222.50	DQ678041	DQ678094	–	DQ677934
Elsinoë phaseoli				CBS 165.31	DQ678042	DQ678095	–	DQ677935
Elsinoë veneta				CBS 150.27	DQ767651	DQ767658	–	DQ767641
Falciformispora lignatilis	Mangrove wood (*Elaeis guineensis*)	U. Pinruan	Thailand, Ban Bang Sak	BCC 21118	**GU371835**	**GU371827**	–	**GU371820**
Falciformispora lignatilis	Mangrove wood (*Elaeis guineensis*)	U. Pinruan	Thailand, Ban Bang Sak	BCC 21117	**GU371834**	**GU371826**	–	**GU371819**
Farlowiella carmichaeliana				CBS 206.36	AY541482	AY541492	DQ677989	DQ677931
Floricola striata	*Juncus roemerianus* (Facultative)	J. Kohlmeyer, B. Kohlmeyer	U.S.A., North Carolina, Carteret County	JK 5678I	**GU296149**	**GU301813**	**GU371758**	**GU479852**
Floricola striata	*Juncus roemerianus* (Facultative)	J. Kohlmeyer, B. Kohlmeyer	U.S.A., North Carolina, Carteret County	JK 5603K	**GU479751**	**GU479785**	–	–
Gloniopsis praelonga				CBS 112415	FJ161134	FJ161173	FJ161113	FJ161090
Gloniopsis subrugosa				CBS 123346	FJ161170	FJ161210	FJ161131	–
Guignardia bidwellii				CBS 237.48	DQ678034	DQ678085	DQ677983	–
Guignardia gaultheriae				CBS 444.70	–	DQ678089	DQ677987	DQ677930
Halomassarina (Massarina) thalassiae	Mangrove wood	J. Kohlmeyer	Fiji, Viti Levu, Suva	JK 5385B	–	**GU479804**	–	**GU479853**
Halomassarina (Massarina) thalassiae	Mangrove wood	J. Kohlmeyer.	Belize, Tobacco Range	JK 5262D	–	**GU301816**	–	**GU349011**

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	–	–
Halotthia posidoniae	Seagrasses (*Posidoniae oceanica*)	E.B.G. Jones	Cyprus	BBH 22481	**GU479752**	**GU479786**	–	–
Heleiosa barbatula	*Juncus roemerianus*	J. Kohlmeyer, B. Kohlmeyer	U.S.A., North Carolina, Carteret County	JK 5548I	**GU479753**	**GU479787**	–	–
Helicascus kanaloanus				A 237	AF053729	–	–	–
Helicascus nypae	Mangrove wood (*Nypa fruticans*)	A. Loilong	Thailand, Tambon Bang Pao	BCC 36751	**GU479754**	**GU479788**	**GU479826**	**GU479854**
Helicascus nypae	Mangrove wood (*Nypa fruticans*)	A. Loilong	Thailand, Tambon Bang Pao	BCC 36752	**GU479755**	**GU479789**	**GU479827**	**GU479855**
Helicascus nypae	Mangrove wood (*Nypa fruticans*)	E.B.G. Jones	Malaysia, Kuala Selangor	PP 6066	AF441174	–	–	–
Helminthosporium solani				HSWS 04	AF120253	–	–	–
Helminthosporium velutinum				ATCC 38969	AF120254	–	–	–
Herpotrichia diffusa				CBS 250.62	DQ678019	DQ678071	DQ677968	DQ677915
Herpotrichia juniperi				CBS 200.31	DDQ678029	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 5326A	**GU479756**	**GU479790**	–	–
Julella avicenniae	Mangrove wood	E.B.G. Jones	Hong Kong Tingkok	CY 2462	AF441175	–	–	–
Keissleriella cladophila				CBS 104.55	**GU296155**	**GU301822**	**GU371735**	**GU349043**
Keissleriella rara	*Juncus roemerianus*	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**
Lentithecium* (*Massarina*) *phragmiticola	*Phragmites*, grass	C. Tsui	Hong KongTai, O Lantau Island	CBS 110446	DQ813512	DQ813510	–	–
Lentithecium arundinaceum (*Massarina arundinacea*)				CBS 619.86	DQ813513	DQ813509	–	–
Leptosphaeria biglobosa				CBS 303.51	–	**GU301826**	–	**GU349010**
Leptosphaeria doliolum				CBS 505.75	U43447	U43474	–	–
Leptosphaeria maculans				DAOM 2229267	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				IMI 303186	U43465	U43482	–	–
Lineolata rhizophorae	Mangrove wood	J. Kohlmeyer	U.S.A., Florida	CBS 641.66	**GU479758**	**GU479792**	**GU479828**	–
Lineolata rhizophorae	Mangrove wood	J. Kohlmeyer	Australia, Queensland	CBS 118422	–	**GU479805**	–	–
Lineolata rhizophorae	Mangrove wood	J. Kohlmeyer	Belize, Blue Ground Range	JK 5248A	–	**GU479806**	–	–
Lophiostoma (Platystomum) scabridisporum	Wood, sand	E.B.G. Jones	Australia, The Mornington Peninsula National Park	BCC 22836	GQ925832	GQ925845	**GU479829**	**GU479856**
Lophiostoma (Platystomum) scabridisporum	Wood, sand	E.B.G. Jones	Australia, The Mornington Peninsula National Park	BCC 22835	GQ925831	GQ925844	**GU479830**	**GU479857**
Lophiostoma arundinis				CBS 621.86	DQ782383	DQ782384	DQ782386	DQ782387
Lophiostoma bipolarae (*Massarina bipolaris*)				HKUCC 1053	AF164365	–	–	–
Lophiostoma crenatum				CBS 629.86	DQ678017	DQ678069	DQ677965	DQ677912
Lophiostoma fuckelii				CBS 113432	–	EU552139	–	–
Lophiostoma fuckelii				CBS 101952	–	DQ399531	–	–
Lophiostoma macrostomum				KT 709	AB521732	AB433274	–	–
Lophiostoma macrostomum				KT 635	AB521731	AB433273	–	–
Lophiostoma sagittiforme				HHUF 29754	–	AB369267	–	–
Lophium mytilinum				CBS 269.34	DQ678030	DQ678081	DQ677979	DQ677926
Loratospora aestuarii	*Juncus roemerianus*	J. Kohlmeyer, B. Kohlmeyer	U.S.A., North Carolina, Carteret County	JK 5535D	**GU296168**	**GU301838**	**GU371760**	
Macrophomina phaseolina				CBS 277.33	DQ678037	DQ678088	DQ677986	DQ677929
Massaria 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	AF164369	DQ384095	–	–
Melanomma radicans				ATCC 42522	U43461	U43479	AY485625	–
Montagnula opulenta				CBS 168.34	AF164370	DQ678086	DQ677984	–
Morosphaeria (Massarina) ramunculicola	Mangrove wood	J. Kohlmeyer	U.S.A., North Carolina, Carteret County	JK 5304B	**GU479760**	**GU479794**	**GU479831**	–
Morosphaeria (Massarina) ramunculicola	Mangrove wood	E.B.G. Jones	Malaysia, Morib	BCC 18405	GQ925839	GQ925854	–	–
Morosphaeria (Massarina) ramunculicola	Mangrove wood	E.B.G. Jones	Malaysia, Morib	BCC 18404	GQ925838	GQ925853	–	–
Morosphaeria (Massarina) ramunculicola	Mangrove wood			HKUCC 7649	–	DQ528762	–	–

Table 1. (Continued).

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	DQ767652	DQ678098	DQ677993	–
Mycosphaerella graminicola				CBS 292.38	DQ678033	DQ678084	DQ677982	–
Mycosphaerella punctiformis				CBS 113265	DQ471017	DQ470968	DQ470920	–
Myrangium duriaei				CBS 260.36	AY016347	DQ678059	DQ677954	DQ677900
Myriangium hispanicum				CBS 247.33	**GU296180**	**GU301854**	**GU371744**	**GU349055**
Mytilinidimytilinellum				CBS 303.34	FJ161144	FJ161184	FJ161119	FJ161100
Neotestudina rosatii				CBS 690.82	DQ384069	DQ384107	–	–
Oedohysterium insidens				CBS 238.34	FJ161142	FJ161182	FJ161118	FJ161097
Oedohysterium sinense				EB 0333	FJ161169	FJ161209	FJ161130	–
Opegrapha dolomitica				–	DQ883706	–	DQ883714	DQ883732
Ophiosphaerella herpotrichus				ATCC 12279	U43453	U43471	–	–
Ostreichnicurtisii				CBS 19834	FJ161137	FJ161176	–	FJ161093
Ostreichnisassafras				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				CBS 958.97	**GU296181**	**GU301855**	–	**GU349038**
***Patellaria* cf. *atrata* 1**	Mangrove wood	S. Suetrong	Thailand, Kung Krabaen Bay Royal development Study Center	BCC 28877	**GU371837**	**GU371829**	–	–
***Patellaria* cf. *atrata* 2**	Mangrove wood	S. Suetrong	Thailand, Kung Krabaen Bay Royal development Study Center	BCC 28876	**GU371836**	**GU371828**	–	-
Phaeodothis winteri				CBS 182.58	DQ678021	DQ678073	DQ677970	DQ677917
***Phaeosphaeria albopunctata* (*Leptosphaeria albopunctata*)**	*Spartina alterniflora*	J. Kohlmeyer	U.S.A., North Carolina, Beaufort	CBS 254.64	–	**GU45631**	–	–
Phaeosphaeria avenaria				DAOM 226215	AY544725	AY544684	DQ677941	DQ677885
Phaeosphaeria eustoma				CBS 576.86	DQ678011	DQ678063	DQ677959	DQ677906
Phaeosphaeria olivacea	*Juncus roemeriaus*	J. Kohlmeyer, B. Kohlmeyer	U.S.A., North Carolina, Carteret County	JK 5540Q	–	**GU479807**	–	–
Phaeosphaeria spartinicola	*Spartina* sp.	J.Kohlmeyer	U.S.A., Maryland, Solomons	JK 5177A	–	**GU479808**	–	–
Phoma herbarum				CBS 615.75	EU754087	EU754186	–	–
Platychora ulmi				CBS 361.52	EF114726	EF114702	–	–
Pleospora herbarum				CBS 191.86	DQ247812	DQ247804	DQ247794	DQ471090
Pleospora sedicola				CBS 109843	–	AY849958	–	–
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).

Taxon	Substrate	Collector	Location	Source	SSU	LSU	*RPB2*	*TEF1*
Preussia terricola				DAOM 230091	AY544726	AY544686	DQ470895	DQ471063
Pseudorobillarda phragmitis				CBS 842.84	EU754103	EU754202	–	–
Pseudorobillarda siamensis				BCC 12531	FJ825365	FJ825375	–	–
Pseudorobillarda texana				BCC 12535	FJ825367	FJ825377	–	–
Psiloglonium araucanum				CBS 112412	FJ161133	FJ161172	FJ161112	FJ161089
Psiloglonium clavisporum				CBS 123339	FJ161157	FJ167526	FJ161124	FJ161105
Psiloglonium simulans				CBS 206.34	FJ161139	FJ161178	FJ161116	FJ161094
Pyrenophora phaeocomes				DAOM 222769	DQ499595	DQ499596	DQ497614	DQ497607
Pyrenophora tritici-repentis				OSC 100066	AY544716	AY544672	–	DQ677882
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				CBS 115553	–	**GU479810**	–	–
Repetophragma ontariense				HKUCC 10830	–	DQ408575	DQ435077	–
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**	–	**GU479860**
Salsuginea ramicola	Mangrove wood	K. Tanaka	Japan, Okinawa	KT 2597.1	**GU479767**	**GU479800**	**GU479833**	**GU479861**
Salsuginea ramicola		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
Stylodothis puccinioides				CBS 193.58	AY016353	AY004342	–	DQ677886
Sydowia polyspora				CBS 116.29	DQ678005	DQ678058	DQ677953	DQ677899
Tremateia halophila	*Juncus roemeriaus*	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	–	–
Ulospora 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	–	–
Wettsteinina lacustris				CBS 618.86	DQ678023	–	DQ677972	DQ677919