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Classification of marine Ascomycota, anamorphic taxa and Basidiomycota

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A comprehensive classification of the filamentous marine fungi is outlined, with reference to recent molecular phylogenetic analyses. The classification includes 530 species (in 321 genera) to order level: Ascomycota 424 species (in 251 genera), anamorphic fungi 94 species (in 61 genera) and Basidiomycota 12 species (in 9 genera). The Halosphaeriales is the largest order of marine fungi with 126 species in 53 genera, of which 35 are monotypic. Several taxa are of uncertain position and cannot be assigned to any higher taxonomic ranks. The decadel index shows that most marine fungi were described in the period 1980-1989 (135) and 1990-1999 (156), with 43 new species and 25 new genera from the past eight years. Keys are provided to the major taxa, genera and species. One new species is described in this paper.

Key words: fungal classification, marine fungi, molecular phylogeny, rDNA, new taxa

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Introduction

Although a few synoptic keys are available for the identification of obligate marine fungi (Kohlmeyer and Volkman-Kohlmeyer, 1991a; Hyde et al., 2000), there has been no attempt to present a classification for them since the book of Kohlmeyer and Kohlmeyer (1979). This monograph addresses this issue.

The number of marine fungi described has increased dramatically since the pioneer study of Barghoorn and Linder (1944) on lignicolous species. Currently some 1,500 names can be found in the literature, but many of these are inadequately described, or may be facultative terrestrial species or synonyms of existing taxa (Jones and Mitchell, 1996). However, Schaumann (pers. comm.) estimates there are some 6,000 marine species, but this figure is not supported by data. The most reliable recent figure is that of Hyde et al. (2000) who listed 444 “higher” obligate marine fungi. However, a number of taxa were not listed, while a further 43 new species in ten new genera have been described over the past eight years. A further 15 new genera have been introduced to accommodate species rejected from existing genera. Other species not previously regarded as marine are included in this monograph. The total now stands at 530 and new taxa continue to be described from this habitat.

Kohlmeyer and Kohlmeyer (1979) stated that: “the decrease of new descriptions of marine fungi during the period 1970-1977 indicates that the most common species have been named and that considerable additions of new taxa in the future are unlikely.” However, as new substrata and geographical locations are being examined for fungi, the number of new species continues to rise (Fig. 1): 135 in 1980-
Fig. 1. Decadal increase in the number of marine fungi.

1989; 156 in 1990-1999 and 43 already recorded for the period 2000-2008. This is certainly noticeable for mangrove species (42 species in Kohlmeyer and Kohlmeyer, 1979; over 170 in Hyde et al., 2000), and tropical locations continue to yield a wide range of new taxa (Jones et al., 2006; Koch et al., 2007). Kis-Papo (2005) has reviewed data on the number of marine fungi and settles on 467 species.

Identification and classification of the marine higher fungi have followed traditional avenues of the evaluation and significance of morphological characters at the light microscope level. For the Ascomycota, ultrastructural characters at the transmission and scanning electron microscope levels have also been used (Jones, 1995). These were specifically applied to ascospore appendage ontogeny of the Halosphaeriales, where delineation of genera was questioned, e.g. *Corollospora* (Kohlmeyer, 1972a; Jones et al., 1983a), and *Ceriosporopsis* (Johnson et al., 1987).

Exploratory studies using TEM and SEM were also used for selected bitunicate marine Ascomycota: *Decorospora gaudefroyi* (as *Pleospora gaudefroyi*) (Yusoff et al., 1994b), *Julella avicenniae* (Au et al., 1999a) and the genus *Massarina* (Au et al., 2001; Read et al., 1994, 1997a, b). Although ultrastructural characters helped in the delineation of a number of genera (e.g. *Corollospora*) others were found to be more difficult to resolve (e.g. *Halosarpehaia*).

Over the last decade, the use of molecular techniques to examine the phylogeny of organisms has advanced considerably (Spatafora and Blackwell, 1994). Molecular techniques have also been applied to examine the relationships of a number of marine taxa at the ordinal level and at the genus/species level. The earliest study was on the phylogeny of *Halosphaeriopsis mediosetigera* (as a representative of the Halosphaeriales), and the Microascales, with both orders sharing a common ancestor (Spatafora and Blackwell, 1994). This relationship has also been supported by other studies (Chen et al., 1999; Kong et al., 2000).

Spatafora et al. (1998) showed that the genus *Lulworthia* did not group within the
Halosphaeriales clade, also noted by Campbell (1999) and Chen et al. (1999). Subsequently, Kohlmeyer et al. (2000) erected the new order Lulworthiales to accommodate the genera Lindra and Lulworthia, while Inderbitzin et al. (2004) showed that the genera Spathulospora and Haloguignardia had affinities with the Lulworthiales. Campbell et al. (2005) erected two monotypic genera within the order to accommodate Lulworthia-like species that did not form a monophyletic group with Lulworthia fucicola, the type species (neotypified by Campbell, 2005). Many taxa in the Halosphaeriales have also been sequenced to infer phylogenetic relationships between morphologically similar taxa. Studies by Kong et al. (2000) and Abdel-Wahab et al. (2001b) confirmed the polyphyly of the genus Halosarphetida and this led to the erection of a number of new genera (Campbell et al., 2003; Pang et al., 2003a, b).

Many genera in the Ascomycota have not been referred to a family or even an order (Hawksworth et al., 1995; Kirk et al., 2001). However, the use of molecular techniques has enabled the resolution of a number of genera. Tam et al. (2003) have shown that the solely known marine bitunicate genera, Aigialus, Helicasca, Julelia and Paraliomyces, with unknown ordinal affinity, can now be classified in the Pleosporales. Similar resolution is possible for the basidiomycetes Calathella, Digittyispora, Halocyphina, Mycaureola and Nia (Binder et al., 2001; Hibbett and Binder, 2001, 2002; Binder et al., 2006). However, many taxa remain to be examined before their assignment to an order can be made. In this monograph we have reviewed the published literature so as to propose the best taxonomic assignment for “obligate” marine fungi. However, conflict may arise between traditional classifications and the need to incorporate phylogenetic analysis, as in the case of the marine Basidiomycota.

We have supplied a key within each genus with more than one species, and added notes on others that may be useful for further research and understanding of their ecology.

Origin of marine fungi

Many theories have been advanced to account for the origin of marine fungi, and in particular the ascomycetes, the Floridean hypothesis being the favoured one (Denison and Carroll, 1966; Kohlmeyer, 1975a; Demoulin, 1985). Spathulospora was considered to be closely related to the Laboulbeniales, a group in turn thought to be related to the Rhodophyta (Kohlmeyer, 1973b). Furthermore, Kohlmeyer (1975a) suggested that Spathulospora, with its marine occurrence and as a parasite of the red alga Ballia, “was close to the hypothetical ancestor of Ascomycetes”. However, in a little cited paper, Walker et al. (1979) questioned the view that Spathulospora belonged to an ancestral group, or along with the Laboulbeniales and Uredinales, could be considered “living fossils”.

That marine fungi are an ecological group has never been in dispute, but did they evolve in the sea or were they secondly adapted to life in the marine milieu? While the latter view has gained in acceptance, there has been little evidence to support it. Spatafora et al. (1998) however have advanced the discussion by demonstrating that the Halosphaeriales at least has made the transition from terrestrial to marine habitats with the consequent loss of dehiscing asci. They also concluded that this was not a solitary episode, as the Lulworthiales was also a transitional group, arising independently of the Halosphaeriales (Kohlmeyer et al., 2000).

Sakayaroj (2005) and Schoch et al. (2006) indicated that within the unitunicate ascomycetes seven and three lineages, respectively, have migrated into the sea. Furthermore five lineages of marine bitunicate ascomycetes are also indicated from analyses of molecular data (Suetrong et al., unpublished data) and may be intermediate forms with many retaining active ascospore discharge. The latter group is particularly prevalent in mangrove habitats where ascus discharge can take place during the intertidal period. Likewise, other groups can be shown to have evolved from
terrestrial to marine habitats: at least three lineages of the Basidiomycota (Binder et al., 2006), as well as ascomycetes with cleistothecial ascomata, but for which no phylogenetic data is available: e.g. Biflua and Marisolaris (Koch and Jones, 1989).

The most primitive true marine fungi are the Chytridiomycota, or as their sometimes referred “the lower fungi”. They are characterized by uniflagellate zoospores that require water for dispersal. They occur in aquatic habitats, both marine and freshwater, and also in terrestrial habitats such as forests, agriculture, desert soils, and acidic bogs (James et al., 2006a, b) and highly adapted multiflagellate anaerobic rumen chytrids (Ho and Barr, 1995; Ho, 2007). The Chytridiomycota have long been regarded as the ancestral group of other fungi (Barr, 1992; Margulis and Schwartz, 1998; Slack et al., 1999). Molecular studies confirm the early evolution of the fungi with the chytrids as the ancestral group (James et al., 2000). As most molecular studies of chytrids have been of taxa from freshwater or terrestrial origin, it is unclear whether ancestral forms were marine (James et al., 2006b). However, it seems likely that they evolved in freshwater habitats. Most marine chytrids are parasitic on algae, are few in number and diversity and may well be secondary invaders of marine habitats. Some of these are clearly derived from terrestrial groups, e.g., Rhizophydidium littoreum (James, pers. comm.). Undoubtedly marine chytrids warrant further study to determine their ancestral phylogeny, as little is known about their phylogenetic position.

Recently, Bass et al. (2007) have recovered novel lineages of chytrids from environmental DNA from marine ecosystems. The origin of Rozella and the related group microsporidia, and Thalassochytrium gracilariopsis, parasitic on the alga Gracilaripsis sp. (Nyvall et al., 1999) raises interesting questions as to the origin of marine chytrids.

James et al. (2006b) state that the earliest fungi were primarily aquatic and lacked aerial spore dispersal, with at least four independent losses of the flagellum, and giving rise to fungi with aerial dispersal of their spores.

There is no data to indicate when marine fungi evolved from terrestrial species, although Vijaykrishna et al. (2006) predicted that fungi became adapted to freshwater some 390 million years ago. Many lineages of marine fungi have been noted, while freshwater fungi occur in only three classes (Vijaykrishna et al., 2006).

Substrata supporting marine fungi

Early records of marine fungi were on drift and decaying algae (Cotton, 1909; Sutherland, 1915, 1916a, b), but the study of Barghoorn and Linder (1944) highlighted the existence of a diverse fungal communities occurring on driftwood. Subsequently dead attached or drift mangrove wood was shown to support a wide range of taxa, that differed appreciably from wood in coastal and oceanic waters (Kohlmeyer, 1984; Hyde and Jones, 1989a, b, 1992a; Jones, 2000). Other marine substrata have also been investigated for the occurrence of marine fungi: coral rocks (Kohlmeyer and Volkmann-Kohlmeyer, 1987b), mangrove leaves, hydrozoan tubes, intertidal marsh grasses (Kohlmeyer, 1972b; Gessner and Kohlmeyer, 1976; Cuomo et al., 1982, 1985), man-made materials (Jones and Le Campion-Alsumard, 1970) and further observations on algicolous marine fungi (Kohlmeyer and Volkmann-Kohlmeyer, 2003b; Zuccaro and Mitchell, 2006). Morrison-Gardiner (2002) isolated a wide range of fungi from Australian coral reefs, many were typical terrestrial genera but these could not be identified using the available taxonomic keys, and might well represent new taxa. Many other substrata await investigation: tropical marine grasses, mollusk shells and soft rocks (Golubic et al., 2005; Raghukumar, 2008).

Materials and Methods

Specimen collection and incubation

Various substrata supporting marine fungi, as mentioned earlier in “Substrata supporting marine fungi”, were collected randomly at different coastal areas in Thailand and other countries e.g. Bahamas, China,
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Denmark, Guam (Micronesia, USA), England and Wales (UK). Samples were placed in plastic bags in order to avoid moisture loss. Samples with a thick sediment layer or other debris were washed thoroughly with running tap water. Surface fouling organisms were scraped off, followed by rinsing with tap water. Samples were then incubated in a plastic box and kept moist by spraying with sterile seawater.

**Microscopic examination**

Initial examination was carried out using a stereomicroscope with magnifications between 10-40×. The surface of the wood was sliced away in order to locate the buried ascomata or pycnidia. Spore mass contents were scooped out on a slide for examination. The observation of sporulating structures was examined in sterile seawater under a compound microscope. The ascoma structure, ascomal wall, the presence or absence of catenophyses, paraphyses, pseudoparaphyses and periphyses, ascus structure and morphology of ascospores are the most important clues for the identification of ascomycetes (Vrijmoed, 2000). For anamorphic fungi, the morphology of conidiomata and the mode of conidiation are vital for identification, in addition to the conidial characteristics. For basidiomycetes, the morphology of the basidiomata serves as an essential feature for identification. Therefore, keys are provided to the major phyla in this monograph.

**Isolation of fungi**

The routine isolation procedure was obtained by single spore isolation (Jones and Hyde, 1988; Choi et al., 1999; Vrijmoed, 2000). Fruiting bodies were picked up with fine forceps or needles and transferred to a small volume of sterile seawater on a glass slide. The fruiting bodies were then crushed to release the spores. The spore suspension was then agitated to ensure a homogenous spore distribution and checked under a compound microscope at low magnification for appropriate density and identity. The suspension was then transferred with a Pasteur pipette onto the isolation agar medium. The spores on the agar were left to dry in a closed plate at room temperature and incubated overnight. A low nutrient medium (e.g. corn meal agar) with antibiotics added (a mixture of Penicillin G and Streptomycin in 1g/l) was used in this procedure. Germinating spores were “picked up” and transferred to a fresh agar plate. At least 5-10 isolates of each species were prepared. Their general colony morphology and growth rate were compared to ensure that the isolates obtained were the same species. Axenic cultures were kept at BIOTEC Culture Collection (BCC) (Thailand), City University of Hong Kong (CY) and University of Portsmouth (PP) (UK).

**Molecular and phylogenetic analysis**

Fungal isolates were obtained from BIOTEC Culture Collection (Thailand), City University of Hong Kong (Hong Kong SAR) and University of Portsmouth (UK) and cultured into GYP sea water broth (4 g/l glucose, 4 g/l yeast extract, 2 g/l peptone). Mycelium (~100 mg) was harvested by filtration, washed twice with sterile distilled water, blotted dry by filter paper and immediately frozen in liquid nitrogen. Mycelial pellets were ground into fine powder using a mortar and pestle, and DNA was extracted using the DNeasy Plant DNA Extraction Kit (QIAGEN) according to the manufacturer’s instructions.

Nuclear ribosomal rRNA genes were amplified using the following primers: small subunit (SSU)- NS1, NS2, NS3, NS5, NS6, NS8 (White et al., 1990) and large subunit (LSU)- JS1, JS5, JS8, LROR, LR7, NL3, NL4, NL4R (Bunyard et al., 1994; Landvik, 1996). PCR reactions were performed in 50 μl using FINNZYMES, DyNAzyme II DNA Polymerase Kit (Macherey-Nagel, Product code F-551S) in a Perkin Elmer thermal cycler. The amplification cycle consisted of an initial denaturation step of 94°C for 2 min followed by 35 cycles of (i) denaturation (94°C for 1 min), (ii) annealing (55°C for 1.5 min) and (iii) elongation (72°C for 2.5 min) and a final 10
min elongation step at 72°C. The PCR products were analyzed by agarose gel electrophoresis and purified using a NucleoSpin Plant DNA Purification Kit (Macherey-Nagel, Catalogue No. 740 570. 50) according to the manufacturer’s instructions. PCR products were sent to Macrogen Inc., Korea, for direct sequencing.

Returned sequences were checked for ambiguity and assembled. Sequences were programme-aligned in Clustal W 1.6 (Thompson et al., 1994) and manually adjusted in Se-Al v1.0a1 (Rambaut, 1999) and BioEdit version 5.0.6. and 6.0.7 (Hall, 2001, 2004). The tree construction procedure was performed in PAUP* 4.0b10 in Macintosh and Window versions (Swofford, 2002).

SSU and LSU rRNA gene sequences were analyzed individually using equally weighted maximum parsimony method (heuristic searches with a stepwise starting tree, a random stepwise addition of 10 replicates and TBR branch-swapping algorithm). Gaps were treated as missing data. Combined SSU and LSU dataset was analyzed using equally weighted parsimony and weighted parsimony approaches. Weighted parsimony analysis was performed using a step matrix to weight nucleotide transformations based on the transition : transversion (ti:tv) ratio estimated from the dataset using maximum likelihood score in PAUP* (Swofford, 2002). Finally, 1,000 replicates of bootstrapping analysis (Felsenstein, 1985) were performed on each dataset (full heuristic searches, stepwise addition of sequence, 100 replicates of random addition of sequence and TBR branch-swapping algorithm).

Layout of the classification of the marine Ascomycota and Basidiomycota

Three fungal groups are treated: Section A: Basidiomycota, Section B: Ascomycota and Section C: anamorphic species (hyphomycetes and coelomycetes). Most of the latter have no known teleomorphs, but this aspect is advancing with the aid of molecular techniques (Chatmala et al., 2002; Shenoy et al., 2007). Where anamorph/teleomorph connections have been established, we have included the anamorphic name under its teleomorph name. The anamorphic name is also included in Section C, with the teleomorph in a lower font, thus enabling the reader to cross-reference the taxonomic names in current use. Molecular sequences where available in the GenBank, are denoted by the prefix ◙ to each species.

Each section is divided into higher-level classification and orders according to that outlined by Hibbett et al. (2007) and where known, the families (Hibbett, 2006; Spatafora et al., 2006; Zhang et al., 2006; Cannon and Kirk, 2007). Genera and species of unknown affinities are referred to incertae sedis. Anamorphic fungi are listed alphabetically under hyphomycetes and coelomycetes, but as in common practice, no lower taxonomic rank is given. However, teleomorphs are listed under species where they are known.

We appreciate that the rapid progress in molecular phylogeny may change the placement of some of the taxa listed here, but hope it will help researchers focus on taxa needing further evaluation and resolution. Many of the taxa listed are known only from their original description, and attention is drawn to these in the hope that further efforts can be made to collect them. Many may occur in specific niches that would require further exploration.

Classification of many marine fungi remains a confused and an unresolved issue, and is particularly acute for the Ascomycota, the largest group. This is well demonstrated by the fact that some 70 genera are referred to as taxa incertae sedis in this monograph. Clearly much effort is required to improve on this state of affairs.

In this treatise we primarily deal with species that have been labelled as obligate marine fungi and those marine derived taxa isolated from submerged substrata or sediments. The latter is not comprehensive but a start must be made to recognize them as true marine fungi. However, we have not included facultative taxa as they are not found under submerged conditions. As much as we dislike these arbitrary designations, it has been necessary to limit the scope of this work. A clear distinction of what is obligate/facultative depends largely on personal opinion, and this
applies very much to species saprophytic on decaying culms of maritime grasses, such as *Spartina* species, *Juncus roemerianus*, *Phragmites communis*, mangrove fungi, especially those on the palm *Nypa fruticans* which can occur in almost freshwater; and taxa isolated from marine sediments (often brackish water habitats) (Udea, 1980, 1995a, b; Udea and Udagawa, 1983). Because the latter group has been isolated onto agar media, they are largely ignored by marine mycologists and simply labelled facultative. The fact that some are repeatedly isolated from such habitats argues for a re-evaluation of their status, but this remains outside the scope of this treatise (Jones, 2000). Kohlmeyer and Volkmann-Kohlmeyer (2003c) are critical of recent studies where fungi have been isolated from coral reefs (Kendrick et al., 1982; Höller et al., 2000; Verbist et al., 2000; Morrison-Gardiner, 2002; Nieves-Rivera, 2002; Raghukumar, 2008) because they were isolated onto media, rather than observed sporulating on the substratum. Care must be taken as some marine fungi may be present in the substratum and do not sporulate under the conditions under observation (Pang and Mitchell, 2005). It is possible that some of these fungi may exist in a similar way to terrestrial endophytes (Zuccaro et al., 2003; Zuccaro and Mitchell, 2005). Also there is evidence emerging that these “so-called” terrestrial species may have evolved into marine forms, and further molecular studies are required to elucidate this (Alker et al., 2001; Zuccaro et al., 2004).

Kohlmeyer and Volkmann-Kohlmeyer in their papers on fungi growing on *Juncus roemerianus*, have attempted to characterize fungi according to their position on the culms and this reflects their degree of inundation by seawater: **obligate**: 6-52 cm above the rhizome e.g. *Phaeosphaeria roemerianii*; **facultative**: 15-56 cm above the rhizome e.g. *Floricola striata*; and **terrestrial or halotolerant**: 45-120 cm above the rhizome, e.g. *Septoriella unigalerita* (Kohlmeyer et al., 1997; Kohlmeyer and Volkmann-Kohlmeyer, 2000). However, as noted, there is a considerable overlap in their position with respect to the rhizome. Although we include fungi from inland lakes, e.g. Salton Sea (Anastasiou, 1963a, b), we have excluded those reported from hypersaline saltterns (Gunder-Cimerman et al., 2000) and the Dead Sea where some 70 filamentous species have been isolated, none typically marine (Buchalo et al., 1998; Nevo et al., 2003; Wasser et al., 2003; Kis-Papo et al., 2003; Kis-Papo, 2005).

Some mangrove fungi are regarded as obligately marine but also occur on parts of the trees not inundated by seawater, e.g. *Julellaavicenniae*, reported on drift/submerged mangrove wood (Hyde, 1992c) but frequently collected on damaged twigs of *Avicennia marina* above the high tide water mark (Jones, personal observation). Conversely, *Mauritiana rhizophorae* (Poonyth et al., 2000b) was described from terrestrial *Rhizophora mucronata*, but has also been collected on intertidal mangrove wood (Alias, pers. comm.). We have therefore adopted a broad interpretation of what we consider to be obligately marine and this may differ significantly from those of others. We have listed a few species that we consider to be borderline species that may also be able to survive exposure to seawater. This has been extended to include taxa isolated from sediments, but cannot be consistently rejected because of their mode of isolation. However, we excluded those considered as halotolerant (Fletcher, 1975; Kohlmeyer et al., 2005). Kohlmeyer and Kohlmeyer (1979), Kohlmeyer and Volkmann-Kohlmeyer (1991a), and Hyde and Sarma (2000) have provide synoptic keys for the identification of marine fungi. All new taxa published since these publications (some 43 species) are illustrated by line drawings and photographs.

**Marine lichens**

Lichens have been largely ignored in the marine mycology literature. Johnson and Sparrow (1961) provide a general account of their occurrence, but without a taxonomic treatment of the taxa. Species included *Arthopyrenia sublitoralis* (on limpet shells), *Lichina pygmaea*, *L. confinis*, *Verrucaria ditmarsica*, *V. maura*, *V. microspora*, and *V. striatula* (all on rock), the discussion focusing
on lichen zonation. Kohlmeyer and Kohlmeyer (1979) document submarine lichens and lichen-like associations, listing 18 species in the genera *Arthopyrenia*, *Lichina*, *Stigmidium*, and *Verrucaria*, on *Littorina*, barnacles and algae. *Verrucaria maura* can also be found on marine wood piles and ironwork (Fletcher, pers. comm.). However, there is no taxonomic treatment of these taxa. Jones (1976) did not include marine lichens in his treatise on marine fungi, while Hyde et al. (2000) list only two. The best account of marine lichens is that of Fletcher (1973a, b) who details some 80 names of littoral and supralittoral lichens. However, he was unable to examine all of these (Fletcher, pers. comm.). Erichsen (1930) described some twelve marine *Verrucaria* species from the Elbe Estuary in the 1930’s, this list is conservative. Therefore the number of lichens listed in this monograph is still conservative.

Nearly all of the species listed here have all been collected in the intertidal zone and thus subject to inundation by seawater. They are cosmopolitan, especially polar to temperate, but rarely recorded from the tropics (Harada, 1995). Hawksworth (2000) comments on the marine and freshwater lineages of lichens, in particular the genera *Lichina*, *Pyrenocollema* and *Verrucaria*. This aspect will be considered later in this volume.

**Marine yeasts**

Marine yeasts also have fared poorly in texts dealing with marine fungi: Johnson and Sparrow (1961) and Kohlmeyer and Kohlmeyer (1979) list eight and twenty three species, respectively of obligate marine yeasts. Kohlmeyer and Kohlmeyer (1979) list a further 140 facultative yeasts. Most of these have been isolated by plating out seawater on to various media or from marine animals and sediments (van Uden and Castello-Branco, 1963; Meyers et al., 1967; Fell, 1976). More recent treatment of marine fungi have been confined to filamentous species (Kohlmeyer and Volkmann-Kohlmeyer, 1991a; Hyde et al., 2000) and we follow this in this volume.

Techniques for the study of yeasts are polyphasic, phenotypic and molecular, with considerable emphasis on the later, while for filamentous fungi morphology still pays a significant role (Statzell-Tallman et al., 2008). Therefore yeasts are best left to specialist’s texts, e.g., Kurtzman et al., 5th edition of *The Yeasts, a Taxonomic Study* (2009). The study of yeasts has also been plagued by the arguments as to whether they are obligate or facultative marine. As for filamentous fungi this is an arbitrary division and emphasis should be placed on habitat and niches within the marine ecosystem. Yeasts isolated from the sea can grow equally well on freshwater media (Fell, pers. comm.).

The number of yeasts documented has steadily increased and with an estimated 1,500 species. Taxa such as *Leucosporidium* spp., *Rhodosporidium* spp., *Candida austromarina*, *C. natalensis*, *Kwoniella mangroviensis* and *Sympodiozymes parvus* are undoubtedly autochthonous species as they are recovered in relatively high numbers from ocean samples (Lachance and Starmer, 1998). Their role in nature is to break down a wide range of organic matter, including lignin. Yeast communities in the open ocean are extensive and much greater that filamentous fungi. This may be accounted for by the ratio of surface to volume of the yeasts, enabling greater uptake of nutrients (Fell, pers. comm.). In mangrove swamps there are a large number of yeasts per unit of water, actively involved in recycling mangrove leachates and in turn acting as a food source for filter feeding invertebrates (Statzell-Tallman et al., 2008). As with filamentous fungi, many yeasts remain to be described, especially in mangrove swamps (Fell et al., 2004). Statzell-Tallman et al. (2008) reported 55 species of ascomycetes and 58 species of basidiomycetes yeasts from three mangrove habitats, 50% of which are undescribed.

Many marine yeasts are also secondary invaders of the sea, and a number of phylogenetic lineages have been reported (Jones and Choeyklin, 2008). For example, basidiomycete lineages: 1. **Tremellomyctes, Cystofilobasidiales**: *Cystofilobasidium bisporidii, C. capitatum* (Fell et al., 2001), *Rhodosporidium diobovatum*, *Rh. paludigenum*, and *Rh. sphaerocarpum* (Fell et al., 2001); 2. **Agaricostilbomyctes**,
**Agaricostilbales**: *Sterigmatomyces halophilus* (Kurtzman and Fell, 2006); 3. **Microbotryomycetes, Sporidiobolales**: *Saccharomycetes, Leucosporidiales*: *Leucosporidium* spp. (Fell et al., 2006; Kurtzman and Fell, 2006) and, ascomycete lineage: *Sakaguchia dacryoidea*, *Leucosporidium* spp. (Fell et al., 2006; Kurtzman and Fell, 2006) and, ascomycete lineage: *Saccharomycetes, Saccharomycetales*: *Saccharomyces* spp., *Metschnikowia* spp.

**Key to the major phyla of marine fungi**

1. Meiospores primarily exogenous, born on basidia or similar structures,
   Section A: **Basidiomycota**……………….. 14
2. Meiospores produced endogenously, formed in asci,
   Section B: **Ascomycota**……………... 21
3. Mitosporces exogenous, or in pycnidia,
   Section C: **Anamorphic fungi**
   (hyphomycetes and coelomycetes)…………… 146

The following classification is based on the publication “A higher-level phylogenetic classification of the Fungi” by Hibbett et al. (2007) for higher order ranks and Cannon and Kirk (2007) for familial placement.

**Classification of the marine fungi**

Phylum: **BASIDIOMYCOTA**
Subphylum: **Ustilaginomycotina**
Class: **Ustilaginomycetes**
Subclass: **Ustilaginomycetidae**
1. Urocystales 2. Ustilaginales

1. Urocystales
   Urocystaceae………………………………… 14
   *Flamingomyces* …………………………….. 14

2. Ustilaginales
   Ustilaginaceae………………………………… 14
   *Parvulago*…………………………………… 14

Subphylum: **Agaricomycotina**
Class: **Agaricomycetes**
Subclass: **Agaricomycetidae**

**Agaricales**
Lachnellaceae………………………………… 15

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*Calathella*……………………………………... 15
*Halocyphina*………………………………… 15
*Nia*…………………………………………… 15

Physalacriaceae……………………………… 16
*Physalacia*…………………………………. 16
*Mycaureola*………………………………… 16

**Agaricomycetes incertae sedis**
**Russulales**

**Digitatispora clade**
*Digitatispora*…………………………………. 17

Peniophoraceae……………………………… 17
*Haloadeurodiscus*………………………… 17

Phylum: **ASCOMYCOTA**
Subphylum: **Pezizomycotina**
Class: **Dothideomycetes**
Subclass: **Dothideomycetidae**

Pleosporomycetidae
Subclass: **Dothideomycetidae**
1. Capnodiales 2. Dothideales

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Hypocreomycetidae
Sordariomycetidae

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Section A:
PHYLUM: BASIDIOMYCOTA

Key to the Basidiomycota

1. Basidiome reduced, parasite, hyphal septum lacking a dolipore and no parthenosomes............................. .
   ........................................................................... Ustilaginomycotina

1. Visible basidiome, saprophytes, symbionts or parasites, basidiospores ballistosporic or statimosporic, clamp-connections present or absent............
   ........................................................................... Agaricomycotina

Subphylum: USTILAGINOMYCOTINA

USTILAGINOMYCETES
USTILAGINOMYCETIDAE
Two orders with marine species

1. Parasitic on dicotyledonous hosts ........ Urocystales
1. Parasitic on members of the Poaceae... Ustilaginales

UROCYSTALES
Urocystaceae


Sori dark on stems and leaves of the host, initially covered by the host epidermis, rupturing at maturity, spores dark, single with no germ pores. Teliospores produced singly, smooth, spore wall comprising and electron-opaque exosporium and an electron-transparent endosporium. Teliospores germinate apically. Initial collection of this species was on Ruppia maritima (Ruppiaceae), at the Etang du Canet, Pyrénées Orientales, France (Feldmann, 1959), with a subsequent collection at Bassin d’Arcachon, Gironde, France (Bauer et al., 2007). The new genus was placed in the Urocystales (Bauer et al., 2007), but earlier placed in the Ustilaginales (Begerow et al., 2006; Matheny et al., 2006). This was confirmed by the molecular study of Bauer et al. (2007). The genus is characterized by the formation of haustoria with an electron-opaque, vesicular matrix coating the fungal cell wall and pigmented teliospores (Bauer et al., 2007).

USTILAGINALES
Ustilaginaceae


Sporulation is at the base of the host plant culms, in the intercellular space underneath the 2-layered epidermis, forming bulbous swelling, sori not covered by a presidium (after Bauer et al., 2007). This species is known from Eleocharis parvula (Cyperaceae) and was recently collected at the Bassin d’Arcachon, Gironde, France (Bauer et al., 2007). It is the only member of the Ustilaginaceae occurring on the Cyperaceae and sporulating at the base of the culms of the host plant under the epidermis (Bauer et al., 2007).

Subphylum: AGARICOMYCOTINA

AGARICOMYCETES
AGARICOMYCETIDAE
Two orders with marine representatives, with reduced basidiomes:

1. A group with large pileate-stipitate basidiomes......
   ........................................................................... Agaricales
1. A group of pileate to resupinate basidiomes .............
   ........................................................................... Russulales incertae sedis

AGARICALES

After Matheny et al. (2006) and equivalent to euagarics clade (Hibbett and Binder, 2001; Binder et al., 2006).

1. Basidioma resupinate, basidiospores filiform......
   ........................................................................... Mycaureola
1. Basidioma not resupinate, ascospores not filiform ....
   ........................................................................... 2
2. Basidioma cyphelloid, funnel-shaped.................
2. Basidioma sub-globose, puff ball-like, no stalk, basidiospores with appendages \( Nia \)
2. Basidioma globose on a stalk, basidiospores non-appendaged \( Physalacria \)
3. Basidioma white, surface hairs smooth, basidium 13-22 × 5-9.5 µm \( Halocyphina \)
3. Basidioma yellowish to ochre yellow, cup-like, wall with surface hairs, brownish, dextrinoid, minutely encrusted, basidia 60-80 × 5-8.5 µm \( Calathella \)

Lachnellaceae

After Matheny et al. (2006) and equivalent to \( Nia \) clade (Hibbett and Binder, 2001; Binder et al., 2006)

**Calathella** D.A. Reid, Persoonia 3: 122, 1964.


Basidiomes cyphelloid, pedunculate, superficial on wood, yellowish with a reddish tinge, older specimens ochre-yellow, leathery, tomentose, solitary or gregarious, mycelium with clamp connections, sterile hairs form a ring around the mouth of the basidiocarp that are simple, brownish, non-septate, dextrinoid, round and minutely encrusted, basidia suburniform to cylindrical, hyaline, with 4 sterigmata, basidiospores subglobose, unicellular, smooth, hyaline, nonamyloid, accumulating at the tip of the basidiome and washed away by the incoming tide. Detailed account of the basidiome and the release of basidiospores is given by Nakagiri and Ito (1991). Classified in the Polyporales, Cyphellaceae (Kirk et al., 2001) while Girms and Malloch (1977) recorded it as a cyphelloid basidiomycetes. Calathella mangrovei shares a common ancestor with \( Nia \) and Cyphellopsis (Hibbett and Binder, 2001). Molecular data confirm its assignment to the euagaric clade and \( Nia \) clade (Binder et al., 2001).


\( N. \) vibrissa R.T. Moore & Meyers, Mycologia 51: 874, 1959 (Type species).

Basidiomes subglobose, superficial, cylindrical, pedicellate, light coloured becoming yellow, pink or orange, soft tissue, smooth, peridium ruptures at maturity, with clamp connections, basidia subglobose to oval with 4-8 basidiospores, hyaline, lacking sterigmata, basidiospores ovoid to ellipsoidal, unicellular, hyaline, with variable number of appendages, one terminal the others lateral. Initially \( N. \) vibrissa was classified as a deuteromycete (Moore and Meyers, 1959) but with the demonstration of basidia and clamp connections and a dolipore septum, it clearly belongs in the homobasidiomycetes (Doguet, 1967, 1968; Brooks, 1975). Subsequently it has been referred to the Melanogastriales (Torrendiaceae: Dring, 1973, or Melanogastriaceae: Doguet, 1967); Nidulariaceae (Rossello et al., 1993) and the Niaceae (Jülich, 1981). Binder et al. (2001) placed \( N. \) vibrissa in the euagarics clade, forming a sister group with Henningsomyces candidus. In a subsequent paper, Hibbett and Binder (2001) confirm the placement of \( N. \) vibrissa in the euagarics clade, along with two other marine basidio-mycetes: C. mangrovei and H. villosa. They opined that the shift from a terrestrial to an aquatic habitat can be accounted for by three or four
Independent transitions, the three shift scenarios giving rise to the terrestrial species *Cyphellopsis anomala* (i.e. derived from a marine ancestor).

*Nia* and *Halocyphina* are strongly supported in a clade (bootstrap value of 100%) with *C. mangrovei* and two terrestrial species: *Cyphellopsis anomala* and *Favolaschia intermedia*. Hibbett and Binder (2002) speculate that *Physalacria maipoensis* may represent an early stage in the transition from terrestrial to the marine environment for these basidiomycetes. This is based on the terrestrial habitat of most *Physalacria* species, with *Ph. maipoensis* often found in the intertidal zone of tropical mangroves. However, we have collected *Physalacria* species on palm rachis submerged or in amphibious habitats in a peat swamp in Thailand (Pinnoi and Jones, pers. comm.).

There is evidence to suggest that *N. vibrissa* is a species complex and further studies are required to resolve this (Jones and Jones, 1993; Binder and Hibbett, 2001).

*Calathella, Halocyphina* and *Nia* consistently group together and all are adapted for life in aquatic habitats (Hibbett and Binder, 2001). All have reduced basidiomes, possibly as an adaptation to an aquatic environment where large fruit bodies would not survive (Jones, 1988). Hibbett (2007) considers the minute forms of cyphelloid basidiomycetes to be related to selection of spore production from minimal substrates.

1. Basidiomata lack sterile hairs/appendages (4.8-8 μm) .............................................................. *N. globospora*
2. Basidiomata with sterile hairs/appendages ................................. 2
3. Basidiospores 11-12 × 7-8 μm, appendages 25-35 μm ....................................................... *N. vibrissa*
4. Basidiospores 6-7 × 3-4 μm, appendages 21-28 μm.. .................................................. *N. epidermoidea*

**Physalaciaceae**


- **Ph. maipoensis** Inderb. & Desjardin, Mycologia 91: 666, 1999.

Basidiomes stipitate-capitate, solitary to gregarious, capitulum globose to subglobose to pyxie-like, white becoming yellow, stipe central, cylindrical, pruinose, arising from a short cushion (Fig. 2), basidia 4-spored, clavate with sterigmata, basidiospores elongate-ellipsoid, smooth, hyaline, non-amyloid, thin-walled, hymenium with gloeo-cystidia. *Physalacria maipoensis* produces a “capitate” fruiting body with a globose head and a short stalk (Fig. 2), and molecular data assign it to the euagarics within a clade comprising *Henningsomyces candidus* and a sister clade to *Schizophyllum commune* but not within the family *Marasmiaceae* (Binder *et al.*, 2001). Inderbitzin and Desjardin (1999) consider the genus as representing “reduced” agarics allied to the genus *Gloiocephala* in the Tricholomataceae.


Basidiomes globose, hemispherical to ellipsoidal, sessile, white, smooth, ostiolate, with up to 12 formed in a circle around the edges of decaying algal tissue, basidia are cylindrical to subclavate, no sterigmata, lacking cystidia, each basidium produces 4 sigmoid basidiospores, unicellular, hyaline, smooth-walled, lacking a sheath or appendages (Porter and Farnham, 1986; Stanley, 1992).

Originally referred to the Ascomycota, but ultrastructural studies confirm its assignment to the Basidiomycota (Porter and Farnham, 1986). *Myc Aureola*, a monotypic genus, is parasitic on the red alga *Dilsea carnosa* and has a cyphelloid, gasteroid fruiting body that suggests assignment to the Cyphellaceae euagaricoid clade. Molecular sequences indicate that the species nested within *Rhizomarasmius pyrrocephalus* and *Gloiocephala phormiorum* and is close to *Xerula* and *Oudemansiella* species, in the Physalaciaceae clade (Binder *et al.*, 2006).

However, its closest terrestrial relative could not be identified with confidence (Binder *et al.*, 2006). *Gloiocephala aquatica,*
(Desjardin et al., 1995), a freshwater species, is in the same clade as *M. dilsea*, indicating that there is a second lineage of marine Agaricales (Binder et al., 2001, 2006). *Mycaureola dilsea* is seasonal in its occurrence and restricted to temperate areas occurring during late autumn in the UK when seawater temperatures are low (Stanley, 1992).

**AGARICOMYCETES incertae sedis**

**RUSSULALES**

After Hibbett et al. (2007) and equivalent to russuloid clade (Hibbett and Thorn, 2001; Binder and Hibbett, 2002).

Two genera with marine species:

1. Resupinate thallus small, basidiospores tetraradiate. .

   1. Resupinate thallus extensive, basidiospores not tetraradiate. .

   **Digitatispora** clade (Hibbett and Thorn, 2001)

   **Digitatispora** Doguet, Comptes. rendu hebd.

   Séanc. Acad. Sci., Paris, 254: 4338,1962... (2)


   Basidiomes form irregular colonies on the wood surface, mycelium with clamp connections, resupinate, hyaline to gray, soft, basidia cylindrical or subclavate, basidia elongate, no sterigmata, four-spored, hyaline, basidiospores tetraradiate, one basal arm and three radiating apical arms, hyaline, deciduous. A preliminary molecular study of this genus using mitochondrial rDNA sequence suggests this species should be placed in the russuloid clade (Hibbett, pers. comm.). However, further molecular studies are required to confirm this placement.

1. Apical branch of basidiospores up to 25 μm long, 8 μm diam.................................................. *D. lignicola*

1. Apical branch of basidiospores up to 41 μm long, 4 μm diam.................................................. *D. marina*

**Peniophoraceae**


Basidiome resupinate, irregular fruit body on wood, pinkish cream, becoming pale dull-cream to greyish-white when dry, gloeocystidia present, basidia narrowly clavate 65-75 × 9-10.5 μm, with a basal clamp
connection and four sterigmata, basidiospores ellipsoid to cylindrical, 13.5-15.5 × 8-9.5 µm, warded, thin to slightly thick-walled, amyloid and lacking appendages. *Haloaleurodiscus mangrovei* was described from decaying and decorticated branch of a living *Sonneratia alba* tree (Maekawa et al., 2005). Unlike some marine basidiomycetes, it has ellipsoid to cylindrical basidiospores 13.5-15.5 × 8-9.5 µm, warded, thin to slightly thick-walled, amyloid, and lacking appendages (Fig. 3a). Maekawa et al. (2005) suggest that the thickening of the basidiospore walls after discharge from the sterigmata could be the first acquired features to evolve and represent a unique evolutionary transition from terrestrial to marine environments. Although *H. mangrovei* resembles *Aleurodiscus sensu lato*, phylogenetically it nests in the root of the Peniophorales clade (18S, 28S rDNA sequences) (Maekawa et al., 2005).

OTHER BASIDIOMYCOTA

Clipson et al. (2001) list five other basidiomycetes in their checklist of European marine fungi, but these are maritime occurring in sand dunes and not obligate marine fungi (*Psalliota litoralis*, *Laccaria trullisata*, *Inocybe decipiens* (= *Inocybe dunensis*), *Tulostoma macrocephalum*). Other maritime basidiomycetes have been reported, but although these are undoubtedly tolerant to sea spray, they are never intertidal or submerged. Similarly, a *Coprinus* species has been collected on cut branches of *Avicennia marina* and floating in the water in Mai Po Mangrove, Hong Kong (Jones, unpublished data). Another basidiomycete found on decaying plant material (particularly *Acanthus ilicifolius*), and wood is an *Aegerita* species (Sadaba et al., 1995), whose identity has not been determined (Fig. 5).

At the time of writing we have collected 12 basidiomycetes on the intertidal bases of the palm *Nypa fruticans*, e.g. *Grammothele fuligo* (Fig. 4). Agarics have also been found on mangrove soils, especially *Coprinus*, *Cortinarius* and *Mycena* species; they are short lived, fruit during the intertidal period and shed their spores before the tide returns (Jones, personal observation). These basidiomycetes have received little attention to date and further investigation for their adaptation to semi-aquatic habitats is warranted.

Trees at Khanom mangrove, southern Thailand, were badly affected by butt rot caused by basidiomycetes. The trees were multi branched as the result of fungal attack (Fig. 6). Two species of *Phellinus* were identified by Dr. T. Hattori, Japan: *Phellinus mangrovicus* and *Ph. swieteniae*, and known to be potent wood decay species. *Phellinus mangrovicus* is of special interest as it has not been collected since it was described by Imazeki, over 70 years ago. Therefore a modern description, with illustrations, is therefore required as well as sequence data to determine its phylogenetic relationship with other species in the genus.

Although there is no documentation of butt rot of *Xylocarpus*, there is a report of butt and heart rot in another mangrove tree, *Rhizophora apiculata*. Mwangi (2001) reported that old *Rh. apiculata* trees were attacked by two pathogenic terrestrial polypores: *Phellinus pachyphloeus* and *Ph. rimosus* in Kenya.

Considerable progress has been made to resolve the taxonomic assignment of the marine basidiomycetes. The genera *Calathella*, *Halocyphina*, and *Nia* all appear to be related (euagaric clade) but have very different basidiomatal and spore morphologies. Similarly, *Physalacria* and *Mycalureola* nestle distantly in the Physalacriaceae. Many marine basidiomycetes have a reduced basidiome, regarded as an adaptation to marine conditions (Jones, 1988).

TOTAL BASIDIOMYCOTA ................. (12)
Fig. 3. Basidiospores of a. *Haloaleurodiscus mangrovei* (after Maekawa et al., 2005), b., c. *Calathella mangrovei*, Basidium, sterigmata and basidiospore (b), and basidiospores (c). Bars a, c = 5 μm; b = 10 μm.

Fig. 4. *Grammothele fuligo* saprophytic on the petiole base of the brackish water palm *Nypa fruticans* (Photo by Rattaket Choeyklin).
Fig. 5. *Aegerita* propagules on senescent stems of *Acanthus ilicifolius*, Mai Po Mangrove, Hong Kong SAR.

Fig. 6. Butt heart rot of *Xylocarpus granatum* tree in a Khanom mangrove in southern Thailand.
Section B:
PHYLUM: ASCOMYCOTA
PEZIZOMYCOTINA

1. Ascomata with bitunicate asci..........................2
2. Ascomata with unitunicate asci..........................5

2. Lichen forming ascomycetes.............................4
3. Non-lichenized ascomycetes...............................3
4. Ascomata apothecial, marine species with no known phycobiont ......................Lecanoromycetes (66)
5. Ascomata apothecial, various phycobionts..............Eurotiomycetes (56)
6. Thallus varied, sometimes poorly developed or absent ........................................Arthoniomycetes(69)
7. Ascomata perithecial........................................2
8. Ascomata apothecial, marine species with no known phycobiont.........................Leotiomycetes (68)
9. Ascomata with bitunicate asci..........................2
10. Ascomata with unitunicate asci..........................5

1. Ascomata variable in morphology and structure, formed by lysigenous locules within stromatic tissue, interascal tissue lacking, ascii variable morphology, develop in basal fascicle, thick-walled, generally fissitunicate, rarely with apical apparatus, ascospores hyaline to brown, septate constricted at the central septum, occasionally muriform..............Dothideales
2. Ascomata small, immersed in host tissue, single or superficial, or imbedded in a pseudoparenchymatal stroma, ascii ovoid to saccate to subcylindrical, ascospores hyaline to slightly pigmented, 1-septate occasionally 3-septate, sometimes enclosed in a sheath, anamorphs hyphomycetes or Coelomycetes..................Capnodiales (Mycosphaerellaceae)

PLEOSPOROMYCETIDAE

One order with marine taxa

Ascomata perithecial, multiloculate, thyrothecial-or cleistothecial-like, globose, thick-walled, immersed or erumpent, well-developed ostiole, interascal tissue cellular or trabeculate pseudoparaphyses, ascii cylindrical, fissitunicate, apical apparatus, ascospores brown, septate, muriform, often with a gelatinous sheath. Anamorphs hyphomycetes..........................Pleosporales

Key to marine taxa in the Dothideomycetes

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4. Ascospores lacking a lenticular appendage...........10
5. Ascospores lacking appendages............................6
6. Ascospores with central septum............................5
7. Ascospores with eccentric septum........................14
8. Ascospores with mural appendages........................8
9. Ascospores with bipolar cilia-like appendages, ascospores 16.5-24 × 5.5-7 µm, on Juncus.......................Heleiosa barbatula
10. Ascospores with a fine halo of fine hairs, 18-27 × 8-14 µm..............................................Capillataspora corticola
11. Ascospores with mucilaginous appendages..............9
12. Ascospores with lenticular appendage on side, 17-28 × 8-12 µm..............................................Paraliomyces lentifer
13. Ascospores lacking a lenticular appendage...............10
15. Ascospores not tuberculate.................................11
16. Ascospores with a sheath, 17-25 × 10-15 µm.........................Scirrhia annulata

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12. Ostiole not slit-like............................................. 13
13. Ascomata lenticular, ascospores 18.5-27 × 4-6 µm, on Nypa ............... Astrosphaeriella nypae
13. Ascomata subglobose, on mangrove wood ...........................
14. Ascospores with a sheath ...................................... Didymella
14. Ascospores without a sheath ............. Mycosphaerella
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16. Ascospores with bipolar germ tubes, no sheath, ascospores 59-72 × 24-30 µm......................... Salsuginnea ramicola
17. Ascomata in a loose stroma, ascospores 37-60 × 16-26 µm, on Posidonia........ Halothia positonidia
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18. Ascomata mammiform, ascospores with bipolar germ tubes, 22-30 × 10-12 µm.............................. Caryospora rhizophorae
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.............................................. Julella herbatilis
55. Ascomata with hyphal mycelium, ascospores with a faint sheath, 20-28.5 × 8-11 µm
...................................................... Leptosphaerulina mangrovei
55. Ascomata lacking ascomatal hyphae, ascospores 28-36 × 12-16 µm ............. Julella avicenniae
56. Ascospores with polar setae, hyaline to pale brown, 15-27 × 6-10 µm ............. Banheggia setispora
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57. Ascospores hyaline, 4-9-septate, 24-48 × 6-24 µm.
...................................................... Patellaria atrata

*The two marine Paraphaeosphaeria species are not obligately marine.

DOTHISDEOMYCETES
DOTHISDEOMYCETIDAE
CAPNODIALES
Mycosphaerellaceae

M. salicorniae (Auersw.) Lindau, Hilfsb. Sammeln Ascomyc.: 103, 1903.
.............................................. Sphaeria salicorniae Auersw., Bot.
.............................................. Trauschveerein, 1863.
.............................................. Lizonia salicorniae (Auersw.) Auersw.,
.............................................. Trauschveerein, 1869.
.............................................. Sphaerella salicorniae (Auersw.) Auersw.,
.............................................. Argent. 12: 115, 1881.
.............................................. Sphaerella staticolica Pat., Cat. Raisonné Plantes
cellulaires Tunésie, Paris p. 104, 1897.
Ascomata globose, subglobose, ellipsoidal, immersed in the host, conical, membranous, ostiolate, epapillate or a short papilla, pale coloured, solitary or gregarious, pseudoparaphyses absent, asci elongate-cylindrical to short clavate, short pedunculate, thick-walled, bitunicate, no apical apparatus, ascospores ellipsoidal to elongate, 1-septate, hyaline, with a mucilaginous sheath. Pycnidia or spermatogonia may be present. A well characterized genus, primarily of circa 500 terrestrial species causing leaf spot disease of a wide range of hosts. Marine taxa are generally on the salt marsh plants *Armeria*, *Limonium*, *Salicornia* and *Suaeda*. Ascomata immersed, generally lacking pseudoparaphyses, asci short clavate and ascospores hyaline, one septate often with a gelatinous sheath, e.g. *M. salicorniae*. *Mycosphaerella pneumatophorae* occurs on the “bark” of pneumatophores of *Avicennia* species, with recent records from Asian mangroves (Jones, unpublished data). *Mycosphaerella* species occurring on algae are now referred to *Mycophycias*.

1. Mainly on mangrove pneumatophores (*Avicennia*), ascospores 14-21 × 6-8.5 µm. 
   \*M. pneumatophorae\*

2. On other marine or marsh plants, ascospores narrower than 6 µm.
   \*1.\*

3. Ascospores longer than 18 µm, saprobic on *Suaeda australis*.
   \*2.\*

4. Ascospores shorter than 18 µm.
   \*3.\*

Sphaerulina Sacc., *Michelia* 1: 399, 1878. (2)

* S. *orae-maris* Linder, *Farlowia* 1: 413, 1944.


Ascomata globose, subglobose, immersed, ostiolate, papillate, membranous, hyaline to light brown, periphyses present or absent, paraphyses present or absent, filiform, simple, septate, asci clavate to cylindrical, short pedunculate, unitunicate?, apically thickened, without an apical apparatus, ascospores 3-6-septate, slightly constricted at the septa, hyaline, smooth-walled, no sheath or appendages (Fig. 7). These species are in need of modern taxonomic treatment. Although *S. orae-maris* is accepted as an obligate marine fungus (Kohlmeyer and Volkman-Kohlmeyer, 1991a), the marine niche of *S. albispiculata* has been queried (Kohlmeyer and Kohlmeyer, 1979). The latter was described by Tubaki (1957) from driftwood on Tane Island, Kyushu, Japan and does not appear to have been reported in the literature since. However, Jones (unpublished data) has collected it on driftwood in Friday Harbour, USA. It can be distinguished from *S. orae-maris* by its well-developed, bushy, white, thick and hairy neck.

Kohlmeyer and Kohlmeyer (1979) query if these species belong in *Sphaerulina* as pseudoparaphyses and bitunicate asci were not conclusively demonstrated in the type material.

Fig. 7. *Sphaerulina albispiculata*. Ascospore 5-septate, not constricted at the septa. Bar = 10 µm

1. Ascomata with a prominent bushy, white hairy neck, ascospores 25-30 × 5-6 µm, 5-6-septate.

2. Ascomata with a short papillate neck, ascospores 26-32 × 5-8 µm, 3-septate.

Pharcidia Körber., *Parerga Lichenologica*, Breslau, p. 469-470, 1865. (3)


Ascomata globose to ellipsoidal, small, solitary, ostiolate, epapillate, periphysate, dark brown to black, paraphyses septate, reticulate, in a gelatinous matrix, asci clavate to cylindrical, no apical apparatus, persistent, ascospores ellipsoidal to obovoid, 1-septate, slightly constricted at the septum, hyaline, with or without appendages (gelatinous cap-like and at both ends). Pharcidia contains some 90 names, but many are referred to Stigmidium, or lichen genera such as Arthopyrenia, and Lichenodiplis. They occur on brown algae, Laminaria digitata (Zuccaro and Mitchell, 2005) or shells of marine animals, e.g. molluscs (Kohlmeyer and Kohlmeyer, 1979).

1. Ascomata on barnacles and other marine shells..............
   .............................................................. P. balani
1. Ascomata on algae ............................................. 2

2. Ascosporcs 18-25 × 6-8 µm, with polar cap-like appendages.......... P. laminariicola
2. Ascosporcs 12-20 × 4-5 µm, without appendages ..... P. rhachiana

1. DOTHIDEALES
   Dothideaceae


Described from senescent culms of Juncus roemerianus, it occurs 28-121 cm above the rhizome within the range regarded as obligate to facultative is present throughout the year and grows well on saltwater agar (Kohlmeyer et al., 1996). Diagnostic features are the linear stromata, 1-3 mm long, generally superficial, multiloculate with ascomata in longitudinal rows, asci clavate, ascospores 3-septate, brown, with a thin sheath, and 46-60 × 9-11.5 µm. Taxonomic position needs verification at the molecular level to resolve its phylogenetic position.

DOTHIDEALES incertae sedis

BOTRYOSPHAERIALES

Botryosphaeriaceae

Sphaeria ammophilae Lasch, Flora, Jena 8: 282, 1850.

Leptosphaeria littoralis Sacc., Michelia 1: 38, 1877.
Leptosphaeria littoralis Sacc., Michelia 1: 38, 1877.

Leptosphaeria littoralis Sacc., Michelia 1: 38, 1877.
Leptosphaeria littoralis Sacc., Michelia 1: 38, 1877.

Leptosphaeria littoralis Sacc., Michelia 1: 38, 1877.
Leptosphaeria littoralis Sacc., Michelia 1: 38, 1877.
at the generic level is subject to debate. The genus was erected based on this species (Eriksson, 1981) but Leuchtmann (1984) and Kohlmeyer and Kohlmeyer (1965) placed it in *Phaeosphaeria*.


Ascomata subglobose to ampulliform, immersed to erumpent, ostiolate, epapillate or with a short papilla, carbonaceous, black, solitary or gregarious, hyaline cells filling ostiolar canal, pseudoparaphyses simple, rarely branching or anastomosing, asci cylindrical, short pedunculate, thick-walled, fissitunicate, 1-septate, constricted at the septum, hyaline, thick-walled, two-layered, tuberculate ornamentations between the two layers, the outer gelatinizing and forming a sheath (Kohlmeyer and Volkmann-Kohlmeyer, 1987c). Although tentatively referred to the Pleosporaceae, Pleosporales by Kohlmeyer and Volkmann-Kohlmeyer (1987c), we prefer to leave it in the Dothideales *incertae sedis*, until a more suitable family suggests itself. The ascospores of *B. tuberculata* are unusual in having a verrucose wall surrounded by a sheath, which becomes sticky in water. A similar species has been collected in Malaysia but further collections are necessary to determine if it is a new species.


An inconspicuous species occurring on the bark of the prop roots of *Rhizophora apiculata*, with globose to ovoid ascomata, hyaline to pale brown, coriaceous, periphysate, solitary and hairy around the ostiole (Hyde, 1989a). Asci are thick walled, saccate to clavate without an apical apparatus. Ascospores 18-27 × 8-13.5 µm, 1-septate, constricted at the septum, hyaline surrounded by small fine, hair-like appendages. Its taxonomic position needs verification at the molecular level, but few collections of this ascomycete have been made, and may escape detection because of its inconspicuous perithecia.

**Passeriniella** Berl., Icon. Fung. (Abellini) 1: 51, 1891................................................... (2)


Ascomata globose to subglobose, immersed, ostiolate, papillate, dark brown to black, coriaceous, solitary or gregarious, periphysate, pseudoparaphyses hyaline, branched, septate, asci cylindrical, pedunculate, bitunicate, with an ocular chamber, ascospores ellipsoidal, versicolour, smooth-walled, 3-septate, constricted at the septa, central cell larger and brown, end cells small and hyaline, lacking a sheath or appendages (Fig. 8). Perplexing species that require to be studied at the molecular level, since *P. obiones* has been transferred to *Byssothecium* (Barr, 2002), however this has not been universally accepted (Index Fungorum).

Currently there is confusion over the placement of *P. obiones* (= *Leptosphaeria discors*). Molecular studies show that *L. discors* does not belong in *Leptosphaeria* or *Phaeosphaeria* (Khashnobish and Shearer, 1996a, b), while the type species of *Passeriniella* has a chequered history (Kohlmeyer and Volkmann-Kohlmeyer, 1991a). Barr (2002) regards *P. obiones* as best placed in *Byssothecium* and we accept that view in this monograph. *Passeriniella savoryellopsis* and *P. mangrovei* conform neither to the generic characteristics of *Byssothecium* or *Passeriniella* (Maria and Sridhar, 2002). In *P. savoryellopsis* the hamathecium tissue, asci, 3-septate ascospores (Barr, 2002 regards them as uniseptate with a short terminal papilla), that are large, deeply constricted at the central septum are not features of either *Byssothecium* or *Passeriniella*. Further collections and a molecular study are warranted before the two species can be referred to a new genus.
1. Asci with 8 ascospores, 44-62 × 17-24 μm.............. P. mangrovei
1. Asci with 4 ascospores, 64-88 × 24-28 μm.............. P. savoryellopsis

**Fig. 8. Passeriniella mangrovei.** Versicolorous ascospore. Bar = 10 μm.

**Thallassosascus** Oll., C.R. Hebd. Séances Acad. Sci. 182: 1348-1349, 1926 ......................... (3)


Ascomata subglobose to ellipsoidal, superficial, subcutulate, ostiolate, epapillate, periphysate, subcarbonaceous to leathery, black, gregarious, pseudoparaphyses filiform, asci cylindrical to clavate, pedunculate, thick-walled, ascospores ellipsoidal, 1-septate, constricted at the septum, hyaline, thick-walled. A little known genus with 1-septate ascospores, differentiated primarily by ascospore measurements and their algal hosts and warrants further study.

1. On *Cystoseira* spp., ascomata stalked .................. T. cystoseirae
1. On other none Fucales, ascomata sessile .............. 2

2. Ascospores less than 28 μm in diam., on *Lessonia* (Laminariales) ...................................... T. lessoniae
2. Ascospores wider than 28 μm, on *Aglaozonia* spp. and *Zanardinia* (Cutleriales) .................. T. tregoubovii

**Fig. 9. Lautospora gigantea.** Ascospores hyaline, muriform and thick-walled. Bars = 20 μm.

Ascomata immersed under a stroma, subglobose, ostiolate, papillate, clypeate, coriaceous, light-coloured, single or gregarious, pale brown, periphysate, pseudoparaphyses trabeculate, anastomosing filaments in a gelatinous matrix, asci cylindrical, long pedunculate, thick-walled, fissitunicate, J-, without an apical apparatus, with an ocular chamber, ascospores ellipsoidal, 1-3-septate, constricted at the central septum, thick-walled and two layered, no sheath or appendages (Kohlmeyer and Volkmann-Kohlmeyer, 1990a). The peridium is hyaline and soft, ascospores are not ornamented and lack a sheath, characters that separate it from Caryospora. Originally described by Hyde (1989c) as a Caryospora species, but it lacks the characteristic features of that genus: erumpent to superficial ascomata, peridium carbonaceous, and ascospores surrounded by a gelatinous sheath (Kohlmeyer and Volkmann-Kohlmeyer, 1993c).

Loratospora Kohlm. & Volkm.-Kohlm., Syst. Ascomycetum 12: 10, 1993 (Type species). This species occurs on Juncus roemermannus culms in an intermediate position (10-61 cm above the rhizome) between that regarded as obligately and facultatively marine (Kohlmeyer and Volkman-Kohlmeyer, 1993c). Ascomata black immersed in the culms, carbonaceous, ostiolate, neck with periphyses, asci clavate, thick-walled, fissitunicate without an apical apparatus, with an ocular chamber, J-, while ascospores are hyaline, 3-septate surrounded by a thin mucilaginous sheath. Loratospora can be compared with Leptosphaerulina, Monascostroma and Wettsteinina but they differ in the lack of periphyses, their small ascomata, their thin walled ascomatal wall and asci that are ovoid to saccate.

Barr (1996) erected the family Planistromellaceae for six genera in the Dothideales, including Loratospora, because their locules open schizogenously by a periphysate ostiole.

Zopfiaceae


Ascomata immersed under a stroma, subglobose, ostiolate, papillate, clypeate, coriaceous, light-coloured, single or gregarious, pale brown, periphysate, pseudoparaphyses trabeculate, anastomosing filaments in a gelatinous matrix, asci cylindrical, long pedunculate, thick-walled, fissitunicate, J-, without an apical apparatus, with an ocular chamber, ascospores ellipsoidal, 1-3-septate, constricted at the central septum, thick-walled and two layered, no sheath or appendages (Kohlmeyer and Volkmann-Kohlmeyer, 1990a). The peridium is hyaline and soft, ascospores are not ornamented and lack a sheath, characters that separate it from Caryospora. Originally described by Hyde (1989c) as a Caryospora species, but it lacks the characteristic features of that genus: erumpent to superficial ascomata, peridium carbonaceous, and ascospores surrounded by a gelatinous sheath (Kohlmeyer and Volkmann-Kohlmeyer, 1993c). Coronopapilla was initially referred to the Didymosphaeriaceae (Kohlmeyer and Volkmann-Kohlmeyer, 1990a).


The only marine species assigned to this genus and collected on wood associated with sand in Australia (Abdel-Wahab and Jones, 2000). Ascomata large 870-1000 μm, conical to subglobose, immersed to erumpent, carbonaceous, papillate, periphysate, solitary or gregarious, pseudoparaphyses trabeculate anastomosing above the asci, asci cylindrical to subcylindrical with a wide opercular chamber, ascospores dark brown to black, the end-cells paler, thick-walled, 3-eu-septate and lacking a sheath (Fig. 11a). It differs from Caryospora species in possessing cylindrical asci and ascospores lacking a sheath. In Caryospora asci are usually saccate and not cylindrical as in C. australiensis.
assigning it to Zopfiaceae, with Barr (1979a) and Hawksworth (1979) referring it to the Massarinaceae and Testudinaceae, respectively.

We prefer at this stage to retain P. biturbinata in the Zopfiaceae because of ascus and ascospore morphology, however we do not consider it well placed in Zopfia. Malloch and Cain (1972) offer few details as to why the species should be transferred to Zopfia. Recent collections of the species have enabled a better understanding of its phylogenetic relationship (Suetrong et al., unpublished data).

**Fig. 11.** a. Caryospora australiensis. Three-septate ascospore. b. Platystomum scabridisporum. Muriform ascospores. Bars a = 10 μm; b = 20 μm.

**Pontoporeia** Kohlm., Nova Hedw. 6: 5-6, 1963................................. (1)

**P. biturbinata** (Durieu & Mont.) Kohlm., Nova Hedw. 6: 5, 1963 (*Type species*).


Ascomata large 805-1375 μm high, 805-1120 μm diam., globose, dark brown to black, thick-walled, pseudoparaphysate, asci bitunicate, clavate with no apical apparatus, long tapering pedicel and ascospores thick-walled, dark to blackish brown, 1-septate with a prominent hyaline germ pore, 66-90 × 32-44 μm (Fig. 12). Described from the rhizomes of *Posidonia oceanica* (Kohlmeyer, 1963), and appears to be host specific as is *Halothia posidoniae*. Cuomo et al. (1985) found both *P. biturbinata* and *H. posidoniae* common on *Posidonia oceanica* rhizomes with a frequency of occurrence of 52% and 78%, respectively, but not on *Cymodocea nodosa*, another seagrass growing in the same locality. Our examination of *P. oceanica* from Cyprus (collections in December, 2007 and February, 2008) noted that *H. posidoniae* was quite common, but that *P. biturbinata* was rare.

Currently some 16 Zopfia names are known, but many of these have been transferred to other genera and families: *Ulospora*, *Neotestudina*, *Lepidosphaeria*, *Testudina* (Testudinaceae), *Zopfiocoveola* (Zopfiaceae). Taxonomic assignment of Zopfia is problematic with Von Arx and Müller (1975) assigning it to Zopfiaceae, with Barr (1979a) and Hawksworth (1979) referring it to the Massarinaceae and Testudinaceae, respectively.

**DOTHIDIOMYCETES**

**PLEOSPOROMYCETIDAE**

**PLEOSPORALES**

The number of families in the Pleosporales is unresolved with Schoch et al. (2006) referring to only six (Leptosphaeriaceae, Lophiostomataceae, Phaeosphaeriaceae, Pleosporaceae, Sporormiaceae, Testudinaceae), while Myconet (2007) and Kirk et al. (2001) list 17 and 19, respectively. Other families have been proposed and are cited in Kirk et al. (2001) as Pleosporales incertae sedis. We refer marine taxa to nine families within the order. Greater resolution of the familial position of these taxa requires greater taxon sampling and a multigene approach.

1. Didymosphaeriaceae

**Didymosphaeria** Fuckel, Jahrb. Nassau.Ver. Naturkd. 23-24: 140, 1870................................. (1)


A doubtful *Didymosphaeria* species infrequently collected and requires further investigation (Strongman et al., 1985; Peña and Arambbarri, 1998a). Aptroot (1995) monographed the genus *Didymosphaeria* with 550 described names, accepted 7 species and transferred 100 species to other genera. He regarded *D. lignomaris* miss-placed in *Didymosphaeria* and suggested placement in *Lojkania cf enalia* (Barr, 1990a). However, this has not been universally accepted.
2. Testudinaceae


Ascomata subglobose, ampulliform or ellipsoidal, immersed, ostiolate, papillate, clypeate, carbonaceous, black solitary or gregarious, pseudoparaphyses trabeculate, anastomosing, in a gelatinous matrix, asci cylindrical, short pedunculate, J-, without an apical apparatus, with an ocular chamber, thick-walled, fissitunicate, ascospores ellipsoidal, 1-septate, slightly constricted at the septum, dark-brown, verrucose, lacking a sheath or appendage (Fig. 13).

A species originally described as a Didymosphaeria species, but transferred to Lojkania (Barr, 1990a) and subsequently to Verruculina (Kohlmeier, and Volkmann-Kohlmeier, 1990a) with its immersed clypeate ascomata with a dark peridium, a gelatinous matrix around the pseudoparaphyses, asci that are stipitate with an ocular chamber and verrucose dark brown ascospores (Kohlmeier and Volkmann-Kohlmeier, 1990a). Sequence data place it in the Testudinaceae as the most basal clade of the Pleosporales along with Lepidosphaeria nicotiae and Ulospora bilgramii (Schoch et al., 2006).

3. Leptosphaeriaceae


Ascomata conical, subglobose, obpyriform, immersed, ostiolate, papillate, clypeate, carbonaceous, light brown to brown to black, solitary or gregarious, periphysate, pseudoparaphyses septate, branched with gelatinous walls, asci cylindrical or subclavate-clavate-fusiform, short pedunculate, thick-walled, lacking or with an apical apparatus, ascospores ellipsoidal, fusiform or cylindrical, 3 or more-septa, slightly constricted at the septum, dark-brown, verrucose, lacking a sheath or appendage (Fig. 13).

A species originally described as a Didymosphaeria species, but transferred to Lojkania (Barr, 1990a) and subsequently to Verruculina (Kohlmeier, and Volkmann-Kohlmeier, 1990a) with its immersed clypeate ascomata with a dark peridium, a gelatinous matrix around the pseudoparaphyses, asci that are stipitate with an ocular chamber and verrucose dark brown ascospores (Kohlmeier and Volkmann-Kohlmeier, 1990a). The genus is polyphyletic and in need of a thorough study of wider range of taxa (Cannon and Kirk, 2007).

Currently five species are marine occurring on mangrove substrata, generally wood and maritime plants. Shoemaker and Babcock (1989) and Kohlmeyer and Volkmann-Kohlmeier (1991a) retain Leptosphaeria orae-maris in Leptosphaeria, while Khashnobish and Shearer (1996a, b), have transferred it to Phaeosphaeria.

Morphologically Leptosphaeria and Phaeosphaeria are difficult to delineate with confidence as is evidenced by the frequent transfer of species from one genus to the other. Khashnobish and Shearer (1996a) opined that the only useful characters in the delineation of these two genera were: “shape of ascoma, ascomal position relative to the substrate and the type of cells making up the peridium”. However, phylogenetically the two genera cannot be separated, with Phaeosphaeria forming a natural group, while Leptosphaeria did not form a monophyletic group (Khashnobish and Shearer, 1996b).
Fig. 12. Pontoporeia biturbinata. a. Front view of mature ascomata (cleistothecial) of Pontoporeia biturbinata on rhizomes of the sea grass Posidonia oceanica. b. Pseudoparaphyses and immature ascus. c-d. Thick-walled, ascus with long tapering pedicel. e-i. Ascospores bicelled and thick-walled. Bars a = 100 µm; b-i = 10 µm.
Fig. 13. *Verruculina enalia*. a. Ascomata submerged in mangrove wood. b. Thin-walled pseudoparaphyses. c. Cylindrical asci and pseudoparaphyses. d. Ascus cylindrical with an apical pore. e-i. Ascospores bicelled and constricted at the septum. Bars a = 100 µm; b-i = 10 µm.
The families Leptosphaeriaceae and Phaeosphaeriaceae are closely related as is evident from recent sequence data (Khashnobish and Shearer, 1996a; Cámara et al., 2002; Kod sueb et al., 2006; Schoch et al., 2006; Suetrong et al., unpublished data). Hibbett et al. (2007) refrained from classification below ordinal level therefore offer no solution as to the validity of retaining the two families in their present form. Molecular data from Cámara et al. (2002) support the separation of Leptosphaeria and Phaeosphaeria, and consider that the significant morphological characters phylogenetically are: peridial characters, anamorphs and plant hosts. Kod sueb et al. (2006) question whether the Phaeosphaeriaceae is a synonym for the Leptosphaeriaceae and advocate a re-evaluation based on wider sampling and multigene sequence analyses. Cannon and Kirk (2007) accept both families.

1. Ascospores with a wide sheath ........................................ 2
2. Ascospores with an indistinct sheath or lacking a sheath ........................................................................ 3
3. Ascospores 18-25 × 6-8 μm, on mangrove wood, tropical ........................................................ L. avicenniae
4. Ascospores 28-44 × 8-12 μm, on wood, temperate ........... L. pelagica
5. Ascospores with 3 septa .............................................. 4
6. Ascospores with 3-5 septa, 30-37.5 × 7.5-11.5 μm, indistinct sheath, on Nypa .......................................... L. nypicola
7. Ascospores 12-16 × 4-5.5 μm, olive brown, on Salicornia ........................................................................ L. peruviana
8. Ascospores 19-27 × 6-9 μm, hyaline, on wood .......... L. australiensis

4. Lophiostomataceae


Ascomata subglobose, immersed, clypeate, ostiolate, coriaceous, black, solitary or gregarious, periphysate, pseudoparaphyses trabeculate, unbranched at the base, anastomosing above the asci, in a gelatinous matrix, asci cylindrical, pedunculate, fissitunicate, with a refractive ring in the endoascus, ascospores fusiform to elongate, muriform, distoseptate, 8-13 transverse septa, 1-6 longitudinal septa, slightly constricted at the septa, golden-brown, smooth-walled, no sheath or appendages (Abdel-Wahab and Jones, 2003) (Fig. 14). Known only from the type locality Mornington Peninsula, Australia, on driftwood associated with sand, where it was common (Abdel-Wahab and Jones, 2003). It conforms to the generic charac-teristics of large ascomata, wide peridium, refractive apical ring surrounding an ocular chamber in the ascus and distosep-tation in immature ascospores that are brown and smooth-walled. Molecular data shows that D. formosa is well placed in the Lophio-stomataceae with high bootstrap support, forming a sister group comprising Massarina and Lophiostoma species (Fig. 17) (Suetrong et al., 2009 in press).

Herpotrichia Fuckel, Fungi rhenani exsic. No. 2171, 1868.............................. (1)


Ascomata globose, superficial, ostiolate, short papillate, gregarious, black, pseudo-paraphyses filiform, numerous, septate, anastomosing above the asci, in a gelatinous matrix, asci cylindrical-clavate, pedunculate, thick-walled, bitunicate, with an ocular chamber, ascospores fusiform, 1-septate becoming 3-septate, constricted at the central septum, basal part longer and narrower than the apical part, hyaline becoming pale brown, with cellular apical appendages (Hyde et al., 1999b).

The only species known from a marine habitat, it has black, globose, superficial papillate ascomata often clustered together, pseudoparaphyses filiform, numerous, septate and anastomosing above the asci, asci bitunicate, cylindric-clavate with an ocular chamber, ascospores 1-3-septate, hyaline to pale brown becoming dark brown at maturity, with apical cellular appendages (Hyde et al., 1999b).
Fig. 14. Decaisnella formosa. a-b. Asci and thin-walled pseudoparaphyses. c. Apical region of ascus with a pore. d-i. Muriform brown ascospores. Bars a-i = 10 µm.
Described from the intertidal petiole of *Nypa fruticans*. The genus *Herpotrichia* groups in Lophiostomataceae group 2 of a multigene analyses by Schoch *et al.* (2006) and further resolution at the family level requires greater species sampling.

**Lophiostoma** Ces. & De Not., Comm. Soc. Crittog. Ital. 1: 219, 1863.......................(3)

The taxonomic position of marine *Astrosphaeriella*, *Lophiostoma* and *Massarina* species has been re-evaluated at the ultrastructural and molecular level (Read *et al.*, 1997a, b; Aptroot, 1998; Hyde and Aptroot, 1998; Hyde *et al.*, 2002; Liew *et al.*, 2002; Schoch *et al.*, 2006). Earlier delineation of the genera based on slit-like versus rounded ostioles was found not to be consistent within a genus at the molecular level (Hyde *et al.*, 2002). Marine species have been transferred between these genera and the current assignment is based on the sequence data of Liew *et al.* (2002).


Ascomata subglobose to elongate, immersed to erumpent, often strongly flattened, carbonaceous, papillate with a round or slit-like ostiole, black, solitary to gregarious, pseudoparaphyses cellular, in a gelatinous matrix, asci cylindrical, thick-walled, bitunicate, short pedunculate, with an ocular chamber and faint ring, ascospores broad fusiform, 1-septate, hyaline, with or without a sheath that may be drawn out terminally.

These species have been transferred from *Massarina* based on morphological and molecular evidence (Liew *et al.*, 2002). *Lophiostoma asiana* and *L. mangrovei* have been transferred to *Astrosphaeriella* (Hyde *et al.*, 2000).

1. Ascospores 24-33 \( \times \) 6-10 \( \mu \)m, on the fern *Acrostichum* .........................*L. acrostichi*
2. Ascomycetes on mangrove wood.................................2
3. Ascospores 28-39 \( \times \) 7-10 \( \mu \)m........*L. armatisporum*
4. Ascospores 22-28 (-33) \( \times \) 4.5-6.5 \( \mu \)m..............................*L. rhizophorae*

**Massarina** Sacc., Syll. Fung. (Abellini) 2: 153, 1883.................................(10)


Ascomata subglobose to obpyriform, immersed in the substratum under a pseudostroma, or erumpent, ostiolate, epapillate, clypeate, coriaceous, dark brown to black, solitary or gregarious, periphysate, pseudoparaphyses trabeculate, anastomosing filaments, in a gelatinous matrix, asci obclavate, clavate, cylindrical, short
pedunculate, thick-walled, J-, ocular chamber without or with an apical apparatus, ascospores ellipsoidal, 1-3-septate, slightly constricted at the septa, with a mucilaginous sheath sometime drawn out to form apical appendages e.g. M. ramunculicola (Kohlmeier and Kohlmeier, 1979; Read et al., 1992b).

Species assigned to Massarina have undergone extensive revision as the result of morphological and molecular evaluation (Liew et al., 2002). Of 160 Massarina names in the literature, Aptroot (1998) only retained 43 taxa, while others have been transferred to Lophiostoma as the result of molecular evidence (Hyde and Aptroot, 1998; Hyde et al., 2002; Liew et al., 2002). Aptroot (1989) considers that M. ricifera may be better placed in Wettsteinina, and that M. lacertensis does not belong in Massarina because ascomata are immersed in an extensive thick, black stroma. We retain these species here until further molecular studies are undertaken.

Ascospores in marine Massarina species generally have a mucilaginous sheath, often elaborated into appendages (Read et al., 1994, 1997a, b; Au and Vrijmoed, 2002; Hyde et al., 2002). In M. acrostichi, M. lacertensis, M. ramunculicola, M. thalassiae and M. velataspora there are well developed sheaths, which is multilayered in M. ricifera. Polar caps to the ascospores are found in M. phragmiticola, while in M. cystophorae polar appendages are present. In M. ramunculicola, the exosporial mucilaginous sheath contains a fibrillar component. Prior to the release of ascospores, the fibrillar component penetrates the delimiting membrane at the spore poles to form a polar cap (Read et al., 1997b), a unique feature in the genus. Ascospores of Massarina thalassiae possess a well-developed exosporial mucilaginous sheath and at the spore poles, a polar chamber is formed within the episporium, which projects into the sheath. However, this does not penetrate through the sheath or the delimiting membrane (Read et al., 1994). Massarina ricifera also has two types of sheaths, one cap-like around one end of the ascospore, and a more extensive diffuse sheath around the entire spore. It differs from other marine Massarina species and requires further investigation at the TEM and molecular level.

Further ecological studies are required to determine if species marked ? are truly marine.

1. Ascospores 1-septate.................................................. 2
2. Ascospores 3-septate.................................................. 5
3. Ascospores with polar appendages or cupulate mucilaginous pad.............................................. 3
4. Ascospores with a sheath........................................... 4
5. Ascospores 45-56 × 14-19 µm.......................... M. velataspora
6. Ascospores length shorter than 45 µm.................. 6
7. Ascospores 28-44 (-47) × 10-15 µm, sheath entire ... M. lacertensis
8. Ascospores 35-42.5 × 12.5-18 µm, polar cap extends into the enveloping sheath .............. M. ramunculicola
9. Ascospores 22-28 (-33) × 4.5-6.5 µm, sheath confined to ascospore tip, extending 2-6 µm, ending bluntly........................... M. rhizophorae
10. Ascospores 28-44 (-47) × 10-15 µm, on wood........................ M. ramunculicola
11. Ascospores 19-25 × 5.5-7 µm, on Juncus................. M. ricifera
12. Ascospores 28-44 (-47) × 10-15 µm .......................... M. thalassiae
13. Ascospores narrower than 10 µm ....................... 8
14. Ascospores 26-34 × 8-9.5 µm, on Bruguiera gymnorhiza wood.......................... M. mauritiana
15. Ascospores 18-21 × 6-8 µm, on Hibiscus tiliaeus ... M. beaurivagea

Paraliomyces Kohlm., Nova Hedw. 1: 81, 1959.............................................................. (1)

P. lentifer Kohlm., Nova Hedw. 1: 81, 1959 (Type species).

Stromata black immersed in the substratum, ascomata subglobose to pyriform, immersed, ostiolate, papillate or epapillate, carbonaceous, black, solitary, periphysate, pseudoparaphyses filiform, numerous, asci cylindrical, short pedunculate, thick-walled, bitunicate, without an apical apparatus, ascospores ellipsoidal to subfusiform, 1-septate, constricted at the septum, hyaline becoming brown, with a mucilaginous sheath and a lenticular appendage at the central septum.
A monotypic genus, occurring on submerged wood and geographically well distributed in the tropics (Tam et al., 2003). The genus can be assigned to the Pleosporales, Lophiostomataceae with confidence as it forms a clade with Lophiostoma crenatum and L. caulium (Tam et al., 2003). Liew et al. (2002) have evaluated the monophyly of the genus Massarina and transferred a number of taxa to Lophiostoma. Included in their analysis was L. caulium, also used by Tam et al. (2003), and this falls into a well characterized Lophiostoma group with narrow, fusiform ascospores. Although P. lentiferus has many features in common with other marine Lophiostoma and Massarina species they are not congeneric.

Ultrastructurally, the ascospores of P. lentifer differ significantly from those of other marine Lophiostoma and Massarina species (Read et al., 1992). The mucilaginous sheath in Paraliomyces is thick (340-380 nm) with numerous electron-opaque granules. The lateral lentiform appendage is located at the central septum and comprises longitudinally oriented fibrils in an amorphous matrix and attached to the episporium by electron-dense strands that pass through the sheath, features not observed in Massarina and Lophiostoma species.

**Platystomum** Trevis., Bull. Soc. R. Bot. Belg. 16: 16, 1877 ................................................. (1)


A newly described marine species from Australian driftwood associated with sand. Ascomata subglobose, immersed, erumpent, papillate, ostiolate, periphysate, black and coriaceous, peridium two-layered, trabeculate pseudoparaphyses, ascii cylindrical with an ocular chamber, ascospores fusiform, muriform, 5-8-transverse septate and 1-3-longitudinal septate, constricted at the septa, brown with rough or verrucose spore wall surface (Figs. 11a, 15). Sequence data place it in the Lophiostomataceae as a sister group to Lophiostoma species (Fig. 17) (Suetrong et al., 2009 in press). However it is not congeneric with Lophiostoma, as evidenced by the weak bootstrap support. Barr (1990a) referred Platystomum to the Platystomataceae, Melanommatales, however, Platystomum compressum has been treated as a Lophiostoma species by Holm and Holm (1988) and this was supported by Eriksson and Hawksworth (1991). However, ascospore morphology is significantly different from Lophiostoma and we retain it as a separate genus.

**Quintaria** Kohlm. & Volkm.-Kohlm., Bot. Mar. 34: 34, 1991................................. (1)


Ascomata obpyriform, immersed, ostiolate, papillate, carbonaceous, black, solitary or gregarious, pseudoparaphyses septate, branching and anastomosing, ascii cylindrical, pedunculate, bitunicate, with an apical plate, ascospores fusiform, 5-septate, constricted at the septa, hyaline, no sheath or appendage (Fig. 16). The genus is differentiated 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.

5. **Melanommataceae**

**Acrocordiopsis** Borse & K.D. Hyde, Mycotaxon 34: 536, 1989 ............................ (2)

- **A. patilii** Borse & K.D. Hyde, Mycotaxon 34: 536, 1989 (Type species).

Both Acrocordiopsis species were reported on mangrove wood with large, black, carbonaceous, conical ascomata seated on a black stroma, epapillate, peridium thick composed of 2-3 layers, pseudoparaphyses abundant, ascii cylindrical, bitunicate with an apical thickening and an ocular chamber, with hyaline to yellowish, 1-septate ascospores, lacking a sheath or appendages (Fig. 18) (Borse and Hyde, 1989; Alias et al., 1999). Preliminary data confirms its assignment to the Pleosporales.
Fig. 16. Quintaria lignatilis. a. Black ascomata immersed in mangrove wood. b. Thin-walled pseudoparaphyses. c. Bitunicate ascus with short pedicel. d. Ascus cylindrical with uniseriate ascospores. e-g. Hyaline 5-septate ascospores. Bars a = 100 µm; b-g = 10 µm.
Fig. 17. Phylogram generated from step matrix parsimony analysis from combined SSU, LSU rDNA, RPB2 and EF-1-alpha sequences. Parsimony bootstrap value greater than 50% and Bayesian Posterior Probabilities greater than 0.95 are given above and below each clade, respectively.
Astrosphaeriella species are most similar to Trematosphaeria and Caryospora species in ascomatal features. Astrosphaeriella species generally occur on monocotyledons while Trematosphaeria occur on a wide range of plants. Ascospore length-width ratios are higher in Astrosphaeriella species than Trematosphaeria. Astrosphaeriella differs from Lophiostoma species in the narrower trabeculate pseudoparaphyses and with carbonaceous ascomata (Hyde and Fröhlich, 1999). Astrosphaeriella asiana and A. mangrovei were transferred from Lophiostoma on the basis of ascomatal structural morphology, narrower pseudoparaphyses and molecular sequencing data (Hyde et al., 2002).

1. Ascomata immersed and subepidermal, becoming superficial, conical or hemispherical, brown to black, solitary or gregarious, ostiole central, papillate, pseudoparaphyses trabeculate in a gelatinous matrix, asci cylindrical, cylindrical-clavate, pedunculate, thick-walled, bitunicate, with an ocular chamber and faint ring, ascospores elongate-fusiform, often tapering at their apices, 1 to multisepitate, slightly constricted at the septa, hyaline, brown to reddish-brown, often with mucilaginous sheaths or appendages.

Fungal Diversity

Astrosphaeriella species are most similar to Trematosphaeria and Caryospora species in ascomatal features. Astrosphaeriella species generally occur on monocotyledons while Trematosphaeria occur on a wide range of plants, ascospore length-width ratios are higher in Astrosphaeriella species than Trematosphaeria. Astrosphaeriella differs from Lophiostoma species in the narrower trabeculate pseudoparaphyses and with carbonaceous ascomata (Hyde and Fröhlich, 1999). Astrosphaeriella asiana and A. mangrovei were transferred from Lophiostoma on the basis of ascomatal structural morphology, narrower pseudoparaphyses and molecular sequencing data (Hyde et al., 2002).

1. Ascomata immersed and subepidermal, becoming superficial, conical or hemispherical, brown to black, solitary or gregarious, ostiole central, papillate, pseudoparaphyses trabeculate in a gelatinous matrix, asci cylindrical, cylindrical-clavate, pedunculate, thick-walled, bitunicate, with an ocular chamber and faint ring, ascospores elongate-fusiform, often tapering at their apices, 1 to multisepitate, slightly constricted at the septa, hyaline, brown to reddish-brown, often with mucilaginous sheaths or appendages.


Ascomata superficial, lacking a clypeus, subglobose to ellipsoidal, ostiolate, periphysate, short papillate, subcarbonaceous, blackish brown, pseudoparaphyses present, asci cylindrical, short pedunculate, without an ocular chamber or apical apparatus, ascospores ellipsoidal, 1-septate, constricted at the septum, reddish-brown, thick-walled and smooth (Kohlmeier and Volkmann-Kohlmeier, 1990a). It was referred to the Melanomataceae, Melanomatales by Kohlmeyer and Volkmann-Kohlmeier (1990a) but requires further study at the molecular level to confirm
its ordinal status. Originally described as a *Sphaeria* species growing on the salt marsh plant *Halimione portulacoides*, which was later transferred to *Didymosphaeria*, but it clearly does not belong in that genus because of its superficial ascomata.


A monotypic genus described from dead wood of intertidal roots and branches of mangrove trees (*Rhizophora mangle*), and probably related to *Caryospora* (Kohlmeyer, 1985). Characterized by large ascomata (750-900 µm high, 830-1050 µm wide), superficial on a thin black stroma, ostiolate, periphysate, carbonaceous, thick peridium (90-160 µm), trabeculate pseudoparaphyses, asci bitunicate, thick-walled, J-, with an apical apparatus, ascospores 1-septate, dark brown, verrucose, and thickened at their apices. Kohlmeyer (1985) referred it to the Massariaceae, Melanommatales, but if it is considered related to *Caryospora*, then an alternative taxonomic group is required. Resolution of its taxonomic position warrants study at the molecular level.


Ascomata subglobose, obpyriform, immersed, ostiolate, papillate, coriaceous to carbonaceous, black, solitary or gregarious, necks with hyaline thin hyphae, pseudoparaphyses unbranched, trabeculate, in gelatinous matrix, asci cylindrical, pedunculate, thick-walled, fissitunicate, with an eccentric apical plate, J-, ascospores fusiform multi-septate, slightly constricted to constricted at the septa, hyaline, smooth-walled, lacking a sheath or appendages (Fig. 19) (Kohlmeyer, 1984; McKeown *et al*., 2001). Three well characterized species from senescent, decaying mangrove wood (McKeown *et al*., 2001). Although Kohlmeyer (1968a) referred to 25 *Trematosphaeria* species, Bois (1985) accepted only a few.

The genus has been assigned to various families: Pleosporaceae (Kohlmeyer, 1968), and Melanommataceae (Barr, 1990a). We consider the latter the most appropriate at this time. The taxonomic position of *Trematosphaeria* is not fully resolved as the genus is polyphyletic (Schoch *et al*., 2006), with *T. heterospora* grouping with two other Lophostoma species (Lophostomataceae clade 1), while *T. pertusa* is in the Lophostomataceae clade 2, along with Herpotrichia and Pleomassaria species (Schoch *et al*., 2006). However, verified strains of *T. pertusa* form a robust cluster with Bimuria novae-zelandiae, Phaeodothis winteri, Montagnula opulenta and Massarina eburnea, a sister group with the Pleosporaceae, Phaeosphaeriaceae and Delitschiaceae with moderate bootstrap support (Zhang *et al*., 2008).

1. Ascospores with wall striation and sheath ............... 2
2. Ascospores lacking wall striation and sheath, 30-35.5-41 × 12-13 (-16.5) µm, 3-septate, brown, light brown at extreme poles ....................... *T. mangrovei*

2. Ascospores 20-25 × 4-6 µm, fusiform or ellipsoid, 3-septate, light brown, striated, with a sheath ................ *T. malaysiana*

2. Ascospores 34-48 × 7-10 µm, 5-septate, cinnamon brown, striate sheath ....................... *T. lineolatispora*

Fig. 19. *Trematosphaeria malaysiana*. Three-septate ascospore with striations along the entire spore. Bar = 5 µm.
6. Monoblastiaceae

**Ascocratera** Kohlm., Can. J. Bot. 64: 3036, 1986.............................................................. (1)

**A. manglicola** Kohlm., Can. J. Bot. 64: 3036, 1986 (Type species). Kohlmeyer (1986a) regards this as a common bitunicate ascomycete in the upper intertidal zone. Ascomata on a thin stroma on the wood surface, crater-like, large (1100-1400 µm diam.), black, carbonaceous, periphysate, trabeculate pseudoparaphyses in a gelatinous matrix, asci bitunicate, thick-walled with an apical apparatus, ascospores hyaline, 3-septate and constricted at the central septum and surrounded by a gelatinous sheath.

Ascospores of **A. manglicola** can be confused with those of **Massarina velatospora**. In our molecular study, **A. manglicola** forms a sister group to **Aigialus** species in a clade that also includes **Quintaria lignatilis** and **Decaisnella formosa**. However it shares few morphological characters (black, ostiolate ascomata, trabeculate pseudoparaphyses, pedunculate, 8-spores, uniseriate, cylindrical asci, septate, ellipsoidal to muriform ascospores) with these taxa (Suetrong et al., 2005, in press).

7. Phaeosphaeriaceae

The phylogenetic position of the families Phaeosphaeriaceae and Leptosphaeriaceae has been discussed above, and will not be repeated here.

**Carinispora** K.D. Hyde, Bot. J. Linn. Soc. 110: 97, 1992.............................................................. (2)


A genus known only from the palm **Nypa fruticans**, ascomata are large circa 0.8 mm, crust-like, with a central ostiole, occur beneath the epidermis with an overlaying clypeus. They lack periphyses and the peridium is light brown composed of thin-walled cells, pseudoparaphyses filiform numerous and in a gel. Asci are clavate to cylindrical, with an ocular chamber and ascospores 7-8-septate, central cells larger, and with a sheath (Fig. 20). The two species have yellow to pale-brown ascospores with measurements that overlap, but differ in the degree of septation and the morphology of the sheath (Hyde, 1992a, 1994b). **Carinispora** resembles **Phaeosphaeria** but differs in that it is a saprobe on the palm **Nypa**, in wall structure, the ocular chamber in the ascus and in the morphology of the ascospore gelatinous sheath. Infrequently collected despite intensive sampling of the host plant (Pilantananapak et al., 2005; Jones et al., 2005a).

1. Ascospores 42-66 × 7-10.5 µm, 8-9 celled, with a keel-shaped sheath.............................................. **C. nypae**

1. Ascospores 43-54 × 8-9 µm, 7-8 celled, with a narrow sheath.............................................. **C. velatispora**

**Lautitia** S. Schatz, Can. J. Bot. 62: 31, 1984.... ................................................................. (1)


**Leptosphaeria danica** Berl., Icones Fung. 1: 87, 1892.

**Leptosphaeria chondri** Rosenv., Bot Tidsskr. 27: 35, 1906.


**Sphaerella chondri** H.L. Jones, Oberlin Coll Kab. 9: 3, 1898.


Ascomata ampulliform to subglobose, immersed in cystocarps and tetracarps of **Chondrus crispus**, ostiolate, papillate, coriaceous, pale-coloured, clypeus black, gregarious, pseudoparaphyses thin, septate, simple or branched, asci subclavate to subcylindrical, short pedunculate, thick-walled, bitunicate, ascospores elongate fusiform, 1-septate, slightly constricted at the septum, hyaline, no sheath or appendages. **Lautitia danica** grows on the cystocarps of the red alga **Chondrus crispus** throughout the year, but is more prevalent during November in British coastal waters (Stanley, 1992). Ascomata are globose and produced in the cortex of the alga beneath the epidermis. Ascospores are 33-40 × 5-8 µm. The relationship of the species within the family and order warrants further investigation.
Phaeosphaeria I. Miyake, Bot. Mag. 23: 93, 1909 .......................................................... (11)
Sphaeria maritima Cooke & Plowr., Grevillea 5: 120, 1877. (nom. illegit.)
Ph. orae-maris (Linder) Khashn. & Shearer, Mycol. Res. 100: 1351, 1996.
Leptosphaeria orae-maris Linder, Farlowia 1: 413, 1944.
Leptosphaeria spartinae Ellis & Everh., J. Mycol. 1: 43, 1885.
Leptosphaeria sticta Ellis & Everh., J. Mycol. 1: 43, 1885.
Sphaeria scirpicola var. typharum Desm., Placentes Crypt. France ed. 2: 1778, 1849.
Sphaeria typharum (Desm.) Raben., Herb. Myc. ed 2: 731, 1858.
Pleospora typharum (Desm.) Fuckle, Symb. Mycol. 137, 1870.
Sphaeria perpusilla var. typharum Auers., Rabenhorst Fungi Europaeae: 831, 1865.

Ascomata subglobose, pyriform to ellipsoidal, immersed, ostiolate, papillate, coriaceous, dark brown, solitary or gregarious, pseudoparaphyses septe, filamentous, in a gelatinous matrix, branched, anastomosing, asci clavate to cylindrical, short pedunculate, bitunicate, fissitunicate, ocular chamber present, J-, lacking with or without an apical apparatus, ascospores fusiform to ellipsoidal, multi- septate, slightly constricted at the septa, yellowish to pale brown, with or without a gelatinous sheath, lacking appendages.

Phaeosphaeria species are generally parasites of grasses, sedges, rushes and other monocotyledons, although many of the marine species are saprophytes, with anamorphs (where known) in Stagonospora. A number of new species have recently been added to this genus, and others transferred from Leptosphaeria: Ph. albopunctata, Ph. halima, Ph. macrosoridium, Ph. neomaritima, Ph. orae-maris and Ph. spartinae (Shoemaker and Babcock, 1989; Khashnobish and Shearer, 1996a, b). Most of these transfers are made on the basis of the colour of the ascospores. The characters delineating Leptosphaeria and Phaeosphaeria are discussed under the former genus. Phaeosphaeria has ascocoma which range from small to large and are generally superficial on the substratum, with generally monocotyledonous hosts. The position of Ph. typharum is questionable with Leuchtmann (1984) rejecting its inclusion in Phaeosphaeria. Shoemaker and Babcock (1989) retain it in the genus for the present. Phaeosphaeria roemeriana is a rare species growing on Juncus roemerianus, between 6-52 cm above the rhizome, and is almost permanently inundated by seawater (Kohlmeier and Kohlmeier, 1998e) (Fig. 21).

1. Ascospores 3-septate........................................... 2
2. Ascospores more than 3-septate................................ 8
2. On Juncus .......................................................... 3
3. On other substrata................................................. 4
3. Ascospores 16-21 × 4-5 μm, fusiform ....................... Ph. olivacea
3. Ascospores 23-35 × 9-13 μm, fusiform....................... Ph. Roemeriana

44
4. On Spartina .............................................................. 5
4. On other substrata .................................................... 6

5. Ascospores 12-18 × 5-8 µm, yellow-brown, also on driftwood....................................................... Ph. halima
5. Ascospores 23-35 × 9-13 µm, yellow-brown to brown, only on Spartina...................... Ph. spartinicola

6. Ascospores less than 8 µm wide, golden-brown, echinate 17-24 × 6-8 µm................... Ph. orae-maris
6. Ascospore wider than 8 µm ......................................... 7

7. Ascospores (21-) 24-39 (-35) × 8-12 µm, reddish-brown, on Typha ....................... Ph. typharum
7. Ascospores 45-68 (-72) × 10-14 µm, hyaline to pale yellow, on wood, Juncus and Spartina ................................................... Ph. mac sporidium

8. On wood, ascospores 29-36 × 7-8 µm, 6-7-septate, clavate ........................................ Ph. capensis
8. On salt marsh grasses ...................................................... 9

9. Ascospores with no sheath, 35-40 (-52) × 9-11 (-14), 5-septate, yellow-brown, on Spartina ..................... Ph. spartinicola
9. Ascospores with a sheath ........................................... 10

10. Ascospores 68-85 × (10-) 15-20 µm, 6-7-septate, yellowish-brown, on Spartina .............. Ph. gessneri
10. Ascospores (30-) 32-45 × (6-) 8-14 µm, 3-5-septate, yellowish-brown, on Juncus............................ Ph. Neomaritima

8. Pleosporaceae

Decorospora Inderb., Kohlm. & Volkm.-Kohl., Mycologia 94: 657, 2002 ................. (1)


Pleospora gaudefroyi Pat., Tabulae Analticae Fungorum, Paris 2: 40, 1886.
Pleospora schoberiae (Sacc.) Berl., Icon. Fung. 2: 23, 1895.

Ascomata subglobose to ellipsoidal, immersed, ostiolate, epapillate or with a short papilla, carbonaceous, black, solitary to gregarious, pseudoparaphyses septate, ramose, asci clavate, short pedunculate, thick-walled, bitunicate, without an apical apparatus, ascospores ellipsoidal, muriform, brown, with a mucilaginous sheath slightly constricted at the center and drawn out at each apex into 2-3 subconical extensions (Inderbitzin et al., 2002). This genus was introduced to accommodate Pleospora gaudefroyi as it forms a sister taxon.
assigned to the Pleosporales, Pleosporaceae with confidence, as it forms a well supported clade with *Kirschsteiniothelia elaterascus* (Shearer, 1993a; Tam *et al*., 2003). Common characters for taxa in this clade include: persistent, anastomosing hyphal-like pseudoparaphyses, a coiled endoascus, which uncoils when the spores are released. The genus is monophyletic, with *H. nypae* found on the palm *Nypa fruticans* that differs from the type species in having smaller ascospores, a verrucose wall and a persistent sheath (Hyde, 1991b).

1. Ascospores 25-35 × 12-15 µm, ascospore wall verrucose with a persistent sheath, on the palm *Nypa fruticans* .................................................... *H. nypae*

1. Ascospores 30-55 × 17-25 µm, wall smooth, ascospores lacking a sheath, on mangrove wood........... ........................................................ *H. kanaloanus*

**Falciformispora** K.D. Hyde, Mycol. Res. 96: 26, 1992........................................................ (1)


A little known species described from mangrove wood from Mexico (Hyde, 1992b), characterised by ascomata that are black, soft-walled, superficial with a rounded ostiole, bitunicate asci with an ocular chamber, wide and cellular pseudoparaphyses and fusiform, hyaline, 6-8-septate ascospores, slightly constricted at the septa, surrounded by a thin mucilaginous sheath and single scythe-like appendage at its base.


Anamorph: *Stemphylium triglochinicola*

Marine *Pleospora* species occur on wide range of hosts, *Tamarix aphylla* twigs, seaweeds and salt marsh plants. Ascomata solitary or gregarious, globose, leathery to subcarbonaceous, immersed, ostiolate, papillate, pseudoparaphyses numerous, asci cylindrical to clavate, pedunculate, thick-walled, ascospores ellipsoid, clavariform or fusiform, muriform, with transverse and longitudinal septa, generally constricted at the septa, yellowish or pale brown with gelatinous sheaths.

Although *Pleospora* species frequently have anamorphs, the only marine species with an anamorph is *P. triglochinicola* (*Stemphylium triglochinicola*). The genus *Pleospora* is polyphyletic (Kodsueb et al., 2006) and as evidenced by the transfer of the marine *P. gaudefroyi* to *Decorospora*. Further studies are required to determine if marine species are correctly assigned to this genus as species such as *P. bjoerlingii* and *P. iqbalii* show no affinity with other *Pleospora* species (Kodsueb et al., 2006).

1. On algae ......................................................... 2
2. On other substrate ............................................. 3
3. Ascospores with 5 trans-septa, 1 longiseptum, 24-28 × 10-13 μm, on the marsh angiosperm *Spartina* ........... 46
   .......................................................... *Pl. spartinae*
3. Ascospores with 7 trans-septa, 1-3 longisepta, 45-66 × 16-25 μm, on the salt marsh plant *Triglochin* ........... 47
   .......................................................... *Pl. triglochinicola*
3. Ascospores with 7-9 trans-septa, 1 longiseptum, 35-52 × 10-15 μm, on *Spartina* ......................... *Pl. pelvetiae*


Anamorph: *Phoma* sp.
Ascomata immersed, no ostiole, subcarbonaceous, brown, pseudoparaphyses septate, thickened at their tips, asci clavate, short pedunculate, thick-walled, ascospores ellipsoid, yellowish-brown, muriform, with 3 transverse septa and 2-4 longitudinal septa, end cells slightly paler, with a thick gelatinous sheath (“perispore”). Forms pycnidia in culture (Kohlmeyer et al., 1995b).

This ascomycete occurs on senescent culms of *Juncus roemerianus* and is regularly immersed at high tide in salt marshes, although regarded as a facultative species by Kohlmeyer et al. (1995b). Distinguished from similar genera (*Lewia*, *Diademospora*), by the apical cap to the ascus, J-ocular chamber, ascospores with a wide mucilaginous sheath (up to 25 μm), ascomata not papillate, and with a *Phoma*-like anamorph.

9. *Teichosporaceae*

*Byssothecium* Fuckel, Bot. Ztg. 19: 251, 1861 ................................................................. (1)


*Leptosphaeria discors* Sacc. & Ellis, Michelia 2: 567, 1882.


*Didymosphaeria spartinae* Grove, J. Bot (Lond.) 71: 259, 1933.


*Passeriniella incarcerata* Berl., Icon. Fung 1: 51, 1892.

Ascomata subglobose or ellipsoidal, immersed to erumpent, ostiolate, subcarbonaceous, dark brown to black, gregarious. Pseudoparaphyses septate, ramose, asci clavate to subcylindrical, short
pedunculate, thick-walled, without an apical apparatus, ascospores versicoloured, end cell hyaline, central cells brown, 3-septate, and constricted at the septa. This common ascomycete on decaying culms has been assigned variously to the genera: Pleospora, Leptosphaeria, and Passeriniella (Hyde and Mouzouras, 1988; Barr, 2002). Khoshnobi and Shearer (1996a, b) showed that based on molecular analysis Passeriniella obiones did not belong in either Leptosphaeria or Phaeosphaeria. Barr (2002) assigned the species to Byssothecium based on its versicolorous ascospores, two dark brown central cells and hyaline terminal cells.

**PLEOSPORALES incertae sedis**


Ascomata globose, completely immersed in a black stroma, ostiolate, apappulate, carbonaceous, to coriaceous, black, gregarious, pseudoparaphyses trabeculate, unbranched and anastomosing above the asci, asci cylindrical, pedunculate, thick-walled, apical apparatus, ascospores ellipsoidal to broadly fusiform, to coriaceous, black, gregarious, in a black stroma, ostiolate, apapillate, pedunculate, thick-walled, apical apparatus, and brown, with hyaline to light brown apical cells, subapical cells covered by a gelatinous sheath.

This genus was initially assigned to the Melanommatales by Hyde and Borse (1986), but referred to the Massariaceae, Pyrenulales by Hawksworth *et al.* (1995). The genus is best accommodated in the Pleosporales, but further studies are required with a greater number of taxa, to assign them to a family with confidence (Tam *et al.*, 2003). Sequence data confirms their placement within the Pleosporales and preliminary data suggests an affinity with the Sporormiaceae (Suetrong, pers. comm.), however, the latter have brown, phragmosporous ascospores with germ slits to each cell. In *Aigialus* the ascospores are brown, muriform and lack germ slits. They also differ significantly in ascoma morphology, ascus shape, pseudoparaphyses morphology and in the substrata on which they grow. *Aigialus* species also form a sister group to Ascoceratera manglicola (Suetrong, pers. comm.). The position of *A. striatispora* in the genus needs to be re-evaluated. *Aigialus rhizophorae* is a nomen rejectum.

1. Ascospores 6 transverse-septate (rarely 8)...... 2
   2. Ascospores with more than 8 transverse-septate ..... 3
   3. Ascospores 35-55 × 10-16 µm, wall smooth ..........
      .............................................. A. mangrovei
   4. Ascospores 26-38 × 16-19.5 µm, wall with striations
      ............................................ A. striatispora

**Biatriospora** K.D. Hyde & Borse, *Mycotaxon* 26: 263, 1986. (*Type species*).

Assigned to the Melanommatales by Hyde and Borse (1986) its taxonomic position remains unresolved, characterized by its large (over 850 µm long) submerged, elongate ascomata in mangrove wood, bitunicate, branched pseudoparaphyses, cylindrical asci with an apical apparatus and a long pedicel and brown to dark-brown, 2-4 septate at each end of the ascospores that are fusiform with a globose end cell. Hyde and Borse (1986) refer to these as end chambers or appendages, but no mucilage is released from them as in *Lulworthia* species. Molecular data confirm its position in the Pleosporales, but it can not be assigned to any family in the order (Fig. 17) (Suetrong *et al.*, unpublished data).

**Didymella** Sacc., *Michelia* 2: 57, 1880. (4)


Ascomata solitary, globose, immersed or erumpent, ostiolate, papillate, dark in colour, pseudoparaphyses filiform, asci cylindrical, short pedunculate, thickened apex, ascospores ovoid to ellipsoidal, 1-septate, constricted at the septum, hyaline with no sheaths or appendages. Most species occur on the larger marine algae, with D. avicenniae the exception, growing on mangrove wood. Revision of the marine species is required.

1. On mangrove wood (Avicennia species), ascospores 25-32 × 10-15 µm, with a sheath ........D. avicenniae

2. Ascospores narrower than 4 µm, 8-16 × 2-4 µm, parasite of Rhodymenia ....................D. magnei

3. Ascospores 16-23 × 6-8 µm, saprobic on brown seaweeds, with a sheath ......................D. fucicola

4. Ascospores 14-22 × 4-6 µm, parasitic on the red alga Gloioptilis, no sheath..................D. gloiopeltidis

Halothia Kohlm., Nova Hedw. 6: 9, 1963 . (1)

H. posidoniae (Durieu & Mont.) Kohlm., Nova Hedw. 6: 9, 1963 (Type species).


Stromata thick, black, subepidermal in host cortex. Ascomata broadly conical to semiglobose, enclosed in a stroma, immersed becoming erumpent, ostiolate, epapillate, carbonaceous, pseudoparaphyses septate, ramose, persistent, asci cylindrical, attenuate at the base, short pedunculate, thick-walled, bitunicate, persistent, ascospores ellipsoidial, subcylindrical to obtuse-fusiform, 1-septate, constricted at the septum, dark brown, wall thickened at both ends, no sheath or appendages (Fig. 22) (Kohlmeyer and Kohlmeyer, 1964-1969). Known only from material on the sea grass Posidonia oceanica and sometimes confused with Pontoporeia biturbinata, but differs in that it has triangular ascomata with the asci produced in a layer at the base of the ascomata, pseudoparaphyses filiform, branching, asci cylindrical, bitunicate, and ascospores 1-septate dark brown and only slightly constricted at the septum. Along with Pontoporeia biturbinata the species was initially assigned to the Pleosporaceae and thought to be related to Caryospora, Herpotrichia and Ottia (Kohlmeyer, 1963). However, its relationship to other taxa in the family, is in need of investigation.


Ascomata globose, immersed, ostiolate, epapillate, clypeate (2-3 under a small clypeus), coriaceous, hyaline at the base, light brown at the sides, pseudoparaphyses branched and anastomosing, septate, in a gelatinous matrix, asci cylindrical, short pedunculate, thick-walled, refractive apical apparatus over the ocular chamber, ascospores ellipsoidial to fusiform, 1-septate, slightly constricted at the septum, pale brown, with 10 or more cilia-like polar appendages. The species can be considered marginally marine as it occurs 42-67 cm above the rhizomes of Juncus roemerianus. Kohlmeyer et al. (1996) were unable to assign it to any family in the Dothideomycetes although they referred to similarity to Appendispora frondicola (Hyde, 1994a). The latter species was placed in the Dothideales incertae sedis by Kirk et al. (2001).


**Fig. 22.** *Halothia posidoniae.* **a.** Ascomata conical partly immersed in rhizomes of the sea grass *Posidonia oceanica.* **b.** Surface of ascoma is rough. **c-d.** Ostiolar region of ascomata. **f.** Cylindrical ascus. **g-h.** Asci and pseudoparaphyses arising from basal ascogenous tissue. **i-k.** Apical region of asci with an apical pore. **l.** Thin walled anastomosing pseudoparaphyses. **m-p.** Thick-walled, 1-septate ascospores. Bars a = 500 µm; b, e = 200 µm; c-d, h = 100 µm; f-g, l = 20 µm; i-k, m-p = 10 µm.
Ascomata subglobose, obpyriform to ellipsoidal, immersed becoming erumpent, ostiolate, papillate to epapillate, coriaceous, clypeate, brown to dark brown, solitary or gregarious, pseudoparaphyses septate, branching and anastomosing, asci clavate to cylindrical, short pedunculate, thick-walled, bitunicate, fissitunicate, ocular chamber apical ring J-, ascospores ellipsoidal, muriform, 7-8-transseptate, 1-longiseptate, constricted at the septa, golden-brown, with a gelatinous sheath.

*Julella avicenniae* was originally described as a *Pleospora* species, but transferred to *Julella* on the basis of it possessing ascomata that develop on woody substrata, immersed beneath a clypeus, the peridium with a single layer of elongated cells, and narrow pseudoparaphyses (Hyde, 1992c). However, it is frequently found on the aerial twigs of *Avicennia marina* in Morib mangrove, Malaysia damaged by a moth larva (Jones, unpublished data).

Although clustering within the Pleosporales, its relationship with other taxa in the order cannot be inferred from data currently available (Tam et al., 2003). In a new analysis, *J. avicenniae* forms a sister clade to one comprising *Helicascus, Massarina velataspora* and *Kirschsteiniothelia elaterascus* (Su特朗 et al., unpublished data).

A second maritime species occurs on the senescent leaves of *Juncus roemerianus*, some 23-118 cm above the rhizome. Kohlmeyer et al. (1997) regarded *J. herbatilis* as facultatively marine. It is included in the key below for comparison with *J. avicenniae*.

1. On mangrove wood (*Avicennia* species), ascospores 28-36 × 12-16 µm, hyaline but generally brown........

...............................................................

1. Facultatively marine on culms of *Juncus roemerianus*, ascospores 18-22.5 × 5-6.5 µm, hyaline

...............................................................

### Kirschsteiniothelia D. Hawksw., Bot. J. Linn. Soc. 91: 183, 1985


Ascomata on driftwood, bark, or coniferous wood, ascomata small (57-128 µm high, 104-268 µm in diameter), semiglobose, superficial, ostiolate, short papillate, carbonaceous, black and gregarious. Pseudoparaphyses septate, anastomosing, asci clavate to elongate-ellipsoidal, pedunculate, thick-walled lacking an apical apparatus, and ascospores brown, 1-septate and constricted at the septum.

The genus *Kirschsteiniothelia* has been referred to the Pleosporaceae (Eriksson and Hawksworth, 1981; Kirk et al., 2001), Pleomassariaceae (Barr, 1993), and questionably the Massarinaceae (Kodsueb et al., 2006). The genus appears to be polyphyletic (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 *Massarina ramunculicola* in a sister clade to the Melanommataceae. 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).

### Leptosphaerulina Mc Alpine, Fung. Diseases Stone-Fruit Trees: 103, 1902


Ascomata erumpent on wood, dark brown, globose, papillate, ostiolate, membranous, with dark brown sepalte, hyphae anchoring ascoma to substratum, pseudoparaphyses sparse, asci elongate to saccate, clavate, few in number, persistent in nature but deliquesing in culture, ascospores light brown, muriform with 4-5 trans-septa and 1-2 longitudinal septa, thin-walled, ellipsoidal to oval, apical cell may be hyaline, with
pronounced sheath constricted at the central septum (Fig. 23).

The first marine species of *Leptosphaerulina* reported from submerged attached decaying branches of the mangrove tree *Kandelia candel* (Inderbitzin *et al*., 2000), also found on the herbaceous mangrove plant *Acanthus ilicifolius* (Jones, pers. observ.) Few *Leptosphaerulina* species occur in warmer climates, while this fungus is the only species found on wood and in the marine environment. Its occurrence in the Pearl River Estuary may be explained by the variable salinity of the water, which ranges from 5-24 ‰.

The genus includes some 50 names and is generally referred to the Pleosporaceae (Eriksson and Hawksworth, 1991; Kirk *et al*., 2001), although Kodsube *et al.* (2006) find that *Leptosphaerulina* and *Macroventuria* are phylogenetically related with no affinities with the Pleosporaceae. These two genera lack pseudoparaphyses, a taxonomic character that differentiates the Pleosporales from the Dothideales. We therefore refer the genus to Dothideomycetes incertae sedis.

**Lineolata** Kohlm. & Volkm.-Kohlm., Mycol. Res. 94: 687, 1990 ....................................... (1)


Ascomata obpyriform, immersed to superficial, ostiolate, papillate, subcarbonaceous to subcoriaceous, periphysate, and dark brown to black, pseudoparaphyses trabeculate, in a gelatinous matrix, asci cylindrical, short pedunculate and ascospores 1-septate, ellipsoidal, brown with surface sculpturing. Originally described as *Didymosphaeria rhizophorae* (Didymosphaeriaceae, Melanomatales), but transferred to this new genus because it differs in the following features: no clypeus, almost superficial ascomata, a coloured peridium, a hamathecium with a gelatinous matrix, asci with an apical ring-like structure around the ocular chamber and ornamented ascospores Kohlmeyer and Volkman-Kohlmeyer, 1990a). Molecular data confirm its position in the Pleosporales, but cannot be assigned to any family within the order (Suetrong *et al*., unpublished data). It forms a clade comprising *Massarina* species, and *Leptosphaeria bicolor*. Further taxon sampling is required to resolve its position.

**Massariosphaeria** (E. Müll.) Crivelli, Diss. Eidgenöss. Techn. Hochschule Zürich 7318: 141, 1983.................................................. (2)


Ascomata subglobose, immersed, ostiolate, epapillate to papillate, coriaceous, light to dark brown, pseudoparaphyses septate, densely packed in a gelatinous matrix, asci cylindrical to clavate, short pedunculate, thick-walled, with an ocular chamber, ascospores fusiform, hyaline to light brown, 7-14-septate with a gelatinous sheath. Both species have pycnidia with globose, ovoid to ellipsoidal hyaline conidia.

**Massariosphaeria typhicola** has been assigned to different genera with Leuchtmann (1984) considering it best placed in *Massariosphaeria*, while Barr’s (1989) more recent review places it in *Chaetomastia*. Leuchtmann (1984) referred *Massariosphaeria* to the Lophiostomataceae while Barr (1989) places it in the Dacampiaceae. Later she assigned *Chaetomastia* to the new family Teichosporaceae (Pleosporales) (Barr, 2002). A molecular study is required to resolve the phylogeny of these genera.
Fig. 23. Leptosphaerulina mangrovei. a. Ascoma superficial on substratum. b. Immature asci. c. Ascus with ectoascus ruptured (lower arrow) and extension of the endoascus (upper arrow). d. Line drawing of ascospore. Bars a-d = 10 μm.

1. Ascospores 7-11-septate, 34-62 × 7-13 μm ............ M. typhicola
1. Ascospores 10-14-septate, 50-71.5 × 9-12 μm ........ M. erucacea

Ascomata fusiform, conical or subglobose, immersed under a dark clypeus, ostiolate, short neck, pseudoparaphyses thin-walled, numerous, anastomosing, asci cylindrical, pedunculate, fissitunicate, with an apical apparatus, large ocular chamber and prominent ring, ascospores 1-septate, constricted at the septum, brown to black, smooth-walled, with hyaline apical germ pores and lacking a sheath or appendages (Hyde, 1991b). Salsuginea differs from another mangrove bitunicate ascomycete Helicascus in lacking a stroma, as the ascomata are formed under a clypeus with a distinctive ocular chamber to the ascus and ascospores with prominent apical pores and lacking a mucilaginous sheath. Fresh material was not available for a molecular study, so its relationship to Helicascus can not be determined at this stage.

Gibberidea nipae Henn., Hedw. 47: 257, 1908.
Anamorph: Phialophora cf. olivacea.
Probably one of the earliest ascomycetes described from the marine environment on the marine palm Nypa fruticans collected by Cesati (1880) in the Philippines and named Sphaeria beccariana. Hennings (1908)
collected an identical taxon *Gibberidea nipae*. This is a common species on the lower bases of *Nypa* fronds and the large, carbonaceous, immersed to superficial ascomata easily detected by touch. Pseudoparaphyses are unbranched and constricted at the septa, asci bitunicate, fissitunicate, asci with a polar appendage formed by the inversion of an apical sheath-like material (Fig. 24) (Jones *et al*., 1996). Referred to different orders including the Patellariales, it is best left as Pleosporales incertae sedis until molecular studies are undertaken to determine its phylogenetic position.

**Fig. 24.** *Tirisporella beccariana*. Light microscope micrographs. **a.** Ascus with short pedicel. **b, d.** Ascospores with pale or hyaline polar cell to which the appendage remains attached. **c.** Scanning electron micrograph, ascospore with polar appendage (Ap) formed by fragmentation of a sheath. Arrow highlight verrucose spore wall. Bars a-b = 20 µm; c = 5 µm, d = 10 µm.


**Hysteriales**

1. Ascomata scattered, immersed, ellipsoidal, ostiolate, papillate, periphyses lacking, glaborous, black, pseudoparaphyses, thin, septate, with a slime layer, asci numerous, cylindrical, short pedunculate, ascospores narrowly fusiform, straight or slightly curved 1-3-septate, constricted at the central septum, hyaline, smooth with a sheath. Shoemaker and Babcock (1989) transferred this species from *Leptosphaeria* to *Wettsteinina*, although they state “the type has hyaline ascospores that are variable in shape, long and slender and 1-septate when young, later broader and tardily appearing 3-septate forming a ring-like septa”. Kodsu et al. (2006) examined the phylogenetic relationship of three *Wettsteinina* species and showed they were monophyletic, but distinct from the Pleosporaceae. Schoch *et al.* (2006) showed that *W. lacustris* also did not group within the Pleosporaceae clustering with *Massaria platani*. Placement in the Pleomassariaceae is suggested by Kodsu *et al.* (2006) but further studies are required with wider taxon sampling.

**DOTHIDEOMYCETES incertae sedis**

1. Lirelliform ascomata, erumpent or superficial, opening by an elongate slit, interascal tissue narrow, cellular pseudoparaphyses, asci cylindrical, fissitunicate, ascospores hyaline or brown, septate, sometime with a mucilaginous sheath, anamorphs varied..............................................................

**Patellariales**

1. Stromata absent, ascomata erumpent, eventually apothecial, interascal tissue narrow anastomosing pseudoparaphyses, asci cylindrical, fissitunicate, 1-septate or muriform, usually no sheath, anamorphs. Anamorphs coelomycetes where known........................

**Jahnulales**

1. Ascomata perithecial, superficial rarely immersed, on a stalk, mycelium wide, asci clavate or cylindrical, pseudoparaphyses present, ascospores brown, generally 1-septate, with a sheath, anamorphs rare....

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HYSTERIALES
Hysteriaceae

Gloniella Sacc., Syll. Fung. (Abellini) 2: 765, 1883.............................................................. (1)

A species collected at a number of sites in South Africa (Steinke and Jones, 1993; Steinke and Hyde, 1997a) and has dark-brown, rounded or discoid to cupulate, flat hysterotheciod ascomata, that are superficial and gregarious. Pseudoparaphyses swollen at the tips, rarely branching, septate, hyaline and longer than the asci. Asci clavate, short pedicel, bitunicate, fissitunicate and with an apical opercular chamber. Ascospores hyaline, smooth 5-8-septate and clavate. This resembles a Patellaria species collected in Hong Kong on Kandelia candel, but differs in that the paraphyses are not branched. Saprobic on intertidal Avicennia marina.

PATELLARIALES
Patellariaceae

Banhegyia L. Zeller & Toth, Sydowia 14: 326, 1960.............................................................. (1)
B. setispora L. Zeller & Toth, Sydowia 14: 327, 1960 (Type species).

Ascomata arising singly, initially closed, later opening by a pore to form a flat or convex black disc, apothecioid, superficial, sessile, circular, subgelatinous when moist, 0.3-0.9 (width) × 0.6 mm (high), (x = 0.7 × 0.57 mm, n = 38). Margin entire, raised and incurved. Outer surface of stalk smooth. Hypothecium thin-walled with isodiametric colourless cells 16-40 µm (x = 29.3 µm, n = 9). Hamathecium paraphysoidal, hyaline, branched above, 96-172 × 1-2 µm (x = 132.4 × 1.4 µm, n = 50). Asci cylindric-clavate, with a stipe, bitunicate, thick-walled, with ocular chamber in apical dome, fissitunicate, 8-spored, J- in Meltzer’s reagent, 92-150 × 14-40 µm (x = 116 × 23 µm, n = 45). Ascospores irregularly biseriate, clavate, slightly curved, not constricted at the septa, 4-9-septate, hyaline, no mucilaginous sheath, 24-48 × 6-24 µm (x = 37.6 × 10.2 µm, n = 70) (Fig. 27).
No anamorph in culture.
Habitat: on badly decayed wood of Kandelia candel, Three Fathom Cove, Hong Kong SAR, China.
Distribution: Hong Kong SAR, China and Thailand.

JAHNULALES
Hypostromataceae

Fresh collections of this unique ascomycete on Nypa fruticans in Thailand has enabled a re-evaluation of its phylogenetic relationship.
relationship in the Dothideomycetes (Suetrong et al., 2009, in press). Ascomata 1100-1750 µm high, 290-640 µm around the center, obtusely clavate to fusiform, stipitate, peridium differentiated into several layers, superficial on the substratum, epapillate, coriaceous, solitary and olive brown. Pseudoparaphyses narrow, numerous, septate anastomosing, or simple, asci cylindrical, thick-walled, few in number and developing at the base of the ascomata, ascospores fusiform, apiculate, unequally 1-septate, constricted at the septum, apical cell larger, orange-brown to chestnut brown, basal cell turbinate, light brown, with a gelatinous appendage (Fig. 25).

Phylogenetically Manglicola guatemalensis is the first marine member of the Jahnulales, although the anamorphic fungus Xylomyces rhizophorae has also been reported from marine locations (Kohlmeyer and Volkmann-Kohlmeyer, 1998d). Recently a Xylomyces species has been shown to be an anamorphic species in the Jahnulales (Campbell et al., 2007). Initially M. guatemalensis was thought to be closely related to the Pleosporaceae or Venturiaceae (Kohlmeyer and Kohlmeyer, 1971) while Huhndorf (1992) and Huhndorf et al., (1994) classified it in the Hypostromataceae incertae sedis. Morphological and molecular evidence places it in the Jahnulales with strong bootstrap support with Aliquandostipite species as a sister group (Fig. 26) (Suetrong et al., 2009, in press). This is yet another marine lineage and is of particular interest as all other Jahnulales members are freshwater or peat swamp species (Pang et al., 2002; Pinruan et al., 2002). It has been hypothesised that marine fungi are derived from terrestrial or freshwater habitats that have migrated into the sea (Shearer, 1993c; Jones, 2000). The mangrove habitat of M. guatemalensis may well form a link between lignonicolous freshwater taxa and estuarine to marine environments. Vijaykrishna et al. (2006) have examined the ancestry of freshwater taxa from terrestrial species and conclude this migration occurred 390 million years ago.

EUROTIOMYCETES

EUROTIOMYCETIDAE

Two orders with marine taxa.

1. Peridium composed of thick-walled cells, ascomatal appendages present ................................ Onygenales
   1. Peridium thin, membranous, no ascomatal appendages ........................................ Eurotiales

ONYGENALES

Gymnoascaceae

G. littoralis (G.F. Orr) Currah, Mycotaxon 24: 87, 1985

Ascomata yellow to orange brown, globose, peridial hyphae, hyaline to yellow, simple or branched, smooth, slightly thick-walled, asci globose, ascospores yellow-brown to orange-brown, smooth, thick-walled, oblate with equatorial rim, 2.9-3.8 × 4.2-5.7 µm, anamorph with arthro and aleurioconidia 2.0-2.8 × 3.5-7 µm. Gymnascella has priority over Arachniotus for those with oblate ascospores. A well-characterized member of the Onygenales (Currah, 1985).
Fig. 25. Manglicola guatemalensis. a. Mature ascomata of Manglicola guatemalensis on the surface of Nypa fruticans, partially immersed in mud. b, d. Ascoma superficial seated on the substratum. c. Longitudinal section of ascoma with stalk, asci and pseudoparaphyses. e. Narrow pseudoparaphyses. f. Cylindrical ascus. g. Ascus tip with ocular chamber. h. Ascospore in ascus with apical and basal appendages (arrow). i-p. Bicelled ascospores. Bars a = 500 µm; b = 250 µm; c-d = 100 µm; e, h = 10 µm; f-g = 50 µm; i-p = 20 µm
Fig. 26. Phylogram generated from weighted parsimony analysis (step matrix) from combined SSU and LSU rDNA sequences. Parsimony bootstrap value greater than 50% and Bayesian Posterior Probabilities greater than 0.95 are given above and below each clade, respectively.
**EUROTIALES**

Trichocomaceae


Anamorph: *Penicillium limosum* Ueda

Ascomata cleistothecial, globose to subglobose, superficial, scattered, pale yellow, asci subglobose to ellipsoidal, evanescent at maturity, ascospores subglobose 3-3.5 × 2.5-3 µm, hyaline spore wall roughened (Udea, 1995b). Isolated several times from marine sediments in Nahasaki, Japan (Udea, 1995b).

**CHAETOTHYRIOMYCETIDAE**

Three orders with marine taxa (Geiser *et al*., 2001).

1. Primarily nonlichenized taxa, dark mycelium on substrata or inconspicuous immersed mycelium, ascomata erumpent to superficial, sometimes setose, short apical periphysoids, asci clavate, thickening of the apical region, ascospores hyaline to pale grey and transversely septate to muriform.......................... Chaetothyriales

... .......................................................... Pyrenulales

1. Mostly lichenized, saxicolous, ascomata superficial to immersed in the thallus, hamathecium often absent or evanescent tissue of gelatinized pseudoparaphyses, ostiole covered with periphyses, asci fissitunicate or evanescent, ascospores hyaline to brown, septate to muriform .......... Verrucariales

**CHAETOTHYRIALES**

Herpotrichellaceae

*Capronia* Sacc., Syll. Fung. (Abellini) 2: 288, 1883 ...................................................(1)


Herpotrichiella ciliomaris Kohlm., Nova Hedw. 2: 313, 1960

Fig. 27. *Patellaria* cf *atrata*. a. Superficial apothecium. b. Section through ascoma with hymenium. c, e. Pseudoparaphyses with branched club-shaped tips. d. Immature thick-walled asci and pseudoparaphyses. f-g. Clavate asci. h-i. Ascospores hyaline, clavate, curved 4-9 septate. Bars a-b = 200 µm; c-g = 25 µm; h-i = 10 µm.
Ascomata globose to ovoid, superficial rarely immersed, ostiolate, epapillate, membranous, variable in colour from hyaline to light to dark blue to black, solitary or gregarious, apical paraphysoids merging with periphyses, asci cylindrical to subclavate, short pedunculate, bitunicate, thick-walled apically, ascospores ellipsoidal to subovoid, 1-septate, constricted at the septum, hyaline, with a crown of cilia-like appendages at each pole. Initially described as a Herpotrichiella it was transferred by Muller et al. (1987) to Capronia based on morphological characteristics. An ultrastructural study (Au et al., 1999b) showed that the periphysoids arise from the upper third of the ascomal wall, extending through the ostiolar canal and merging with the apical setae. The ascus has no ocular chamber, but the endoascus is thickened at the apex. Ascospores are verrucose, while the cilia-like appendages arise sub-terminally from the mesosporium through discontinuities in the episporium. A frequently collected species on bark in Friday Harbour, USA (Jones, 1985; Au et al., 1999b).

The taxonomic position of C. ciliomaris remains in question, as it is the only marine species in the genus, with hyaline ascospores, 1-septate with a crown of sub-terminal appendages and no anamorph has been reported for it. These are not characteristic features of Capronia.

**PYRENULALES**

**Pyrenulaceae**

*Pyrenographa* Aptroot, Bibliotheca Lichenologica 44: 103, 1991........................ (1)


Ascomata developing under a dark stroma, subglobose to fusiform, ostiolate, short papilla, periphysate, pseudoparaphyses branched, septate, asci clavate to cylindrical, short pedunculate, thick-walled, bitunicate, with an apical ring, J-, ascospores ellipsoidal to fusiform, 3-septate, not constricted at the septa, yellow brown, thick-walled, smooth and lacking a sheath or appendages (Fig. 28). Originally described from mangrove wood collected in Queensland, Australia (Aptroot, 1991), it is common on various mangrove tree species, especially Rhizophora apiculata and Sonneratia species (Alias et al., 1996; Jones and Abdel-Wahab, 2005; Jones and Pugsili, 2006). Aptroot (1991) states that the fungus stains the wood purple, we have not observed this. However, we have noted that the wood around the ascomata is bleached white and may be due to enzyme action. It is easily recognizable on mangrove wood by the prominent white zones surrounding the raised ascomata. Its position high in the intertidal zone exposes it to sunlight and long periods of drying out at low tides. Found in locations not subject to routine submergence. Here placed in the Pyrenulaceae, it has also been referred to the Requienellaceae (Kirk et al., 2001).

*Xenus* Kohlm. & Volkm.-Kohl., Cryogamie Bot. 2: 367, 1992.........................(1)

*X. lithophylli* Kohlm. & Volkm.-Kohl., Cryogamie Bot. 2: 368, 1992 (*Type species*).

Ascomata subglobose, superficial, ostiolate, periphysate, epapillate, clypeate, black and gregarious, pseudoparaphyses trabeculate, branched and anastomosing, asci clavate, thick-walled, without an apical apparatus, ascospores 1-3-septate, slightly constricted at the central septum, hyaline, no appendages or sheath (Kohlmeiyer and Volkmann-Kohlmeyer, 1992).

A monotypic genus parasitic on the red alga Lithophyllum sp., attached to coral rock collected in the Caribbean (Belize). Kohlmeyer and Volkmann-Kohlmeyer (1992) referred it to the Dothideales incertae sedis, but noted similarities with the bitunicate ascomycetes Arthopyrenia halodytes, Pharcidia laminariicola and P. rhachiana. Its taxonomic position is far from clear but a consensus places it in the Pyrenulales.

**Requienellaceae**

*Mauritiana* Poonyth, K.D. Hyde, Aptroot & Peerally, Fungal Diver. 4: 102, 2000.............(1)

*M. rhizophorae* Poonyth, K.D. Hyde, Aptroot & Peerally, Fungal Diver. 4: 102, 2000 (*Type species*).
Fig. 28. *Pyrenographa xylographoides*. a. Ascoma within a black stroma. b. Longitudinal section through an ascoma on a raised cushion of wood. c. Ascus clavate with immature ascospores. d. Pseudoparaphyses branched. e-h. Ascospores brown 3-septate. Bars a-b = 200 µm; c-h = 10 µm.
Ascomata globose to ovoid, immersed, ostiolate, short neck, pale brown, gregarious, pseudoparaphyses filamentous, septate, branching, asci cylindrical to clavate, with an ocular chamber, bitunicate, thick-walled, short pedunculate, ascospores fusiform, dark brown the end cells paler, 9-13-distoseptate, septa thick, slightly constricted at the central septum, smooth walled and lacking a sheath or appendages (Fig. 29). This species has been recovered from marine habitats (Jones, unpublished data on branches of Hibiscus tiliaceus immersed in the intertidal, Thailand and Guam) although generally growing on the more terrestrial parts of mangrove trees, especially Rhizophora mucronata. Poonyth et al. (2000b) referred the genus to the Pyrenulales sensu stricto, as it has immersed ascomata, interascal tissue composed of branched pseudoparaphyses, thick-walled, fissitunicate asci and brown, septate ascospores.

Xanthopyreniaceae


Fig. 29. *Mauritiana rhizophorae*. a. Cylindrical ascus with biseriate ascospores. b. Scanning electron micrographs of ascospore. c-d. Fusiform ascospores with 12-13 distoseptate. Bars a, c-d = 10 µm; b = 5 µm. (Photos by Aisyah Alias).

1. Perithecia large (310-590 µm) on the seaweed *Pelvetia canaliculata*................................. **C. pelvetiae**
2. Thallus superficial on the substratum.................................... 3
3. Thallus with black, carbonaceous ridges... **C. elegans**
4. Involucrellum intermixed with the substratum, wide spreading.................................................. 5
5. Perithecia semi-immersed, 0.15-0.55 mm diam., involucrellum well developed and spreading laterally.............................. **C. sublitorale**
6. Perithecia immersed in pits in the substratum, 0.1-0.24 mm diam., involucrellum lid-like, not spreading........................................... **C. foveolatum**

Key after Mohr et al. (2004).

**VERRUCARIALES**

**Verrucariaceae**


*M. ascothylli* (Cotton) Kohlm. & Volkm.-Kohlm., Syst. Ascomycetum **16**: 3, 1998 (*Type species*).


*Sphaerella ascothylli* (Cotton) Sacc. & Trotter, Sacc.: Syll. Fung. **22**: 147, 1913.


Ascomata ovoid, ellipsoid to obpyriform, immersed in the host, ostiolate, epapillate, periphyseate, coriaceous, brown solitary or gregarious, periphysoid in the upper part of the ascoma, asci fusiform to clavate, pedunculate, ascospores ellipsoidal, 1-septate, hyaline, no appendages or sheaths. These two species have been transferred from Mycosphaerella because they have periphyseate ostioles with the periphysoids arising from the upper peridium. They form mycophycobioses with marine macroalgae (Kohlmeier and Volkman-Kohlmeier, 1998b).

1. Ascospores 15-20 × 4-5 μm, mycobiont of Apophysa lyallii..........................M. apophysaee
1. Ascospores 15-22 × 4-6 μm, mycobiont of Ascophyllum nodosum and Pelvetia canaliculata .......... .................................................................M. asphyllii

V. ceuthocarpa Wahlenb., in Acharius, Methodus: 22, 1803.

V. halizoa Leight., Lichen Flora of Great Britain & Ireland, 461, 1871.
V. maura Wahlenb., in Acharius Methodus: 19, 1803.
V. meridionalis P.M. McCarthy, Muelleria 8: 103, 1994.
V. mucosa Wahlenb., in Acharius Methodus: 23, 1803.
V. striatula Wahlenb., in Acharius Methodus:Methodus: 21, 1803.

Crustose pyrenocarpous lichens generally with a green unicellular photobiont (genus Dilabifilum = syn. Pseudopleurococcus), thallus discrete, scattered, immersed or superficial, black ascomata, periphyseate, asci and paraphyses deliquesce early, clavate to cylindroclavate, fissitunicate asci containing 8 hyaline, ovoid to subglobose to ellipsoidal ascospores (McCarthy, 2001) (Figs. 31-33). Many Verrucaria lichens are to be found in the littoral and supralittoral zone and are thus thought to be salt-tolerant (Fletcher, 1975, 1980) but Verrucaria serpuloides has been found on dredged-up stones from 30 m in Antarctica (Lamb, 1973).

Perithecial ascomata with an apical ostiole, with short pseudoparaphyses bordering the upper part of the perithecial cavity and
hanging into this without touching the hymenium (Gueidan et al., 2007). Bitunicate asci dehiscence often by gelification of the outer wall.

Molecular studies of the family concluded they were a sister group to the non-lichenised order Cladothryrales (Lindemuth and Lumbsch, 2001; Lumbsch et al., 2005). Current studies indicate that the generic delineations of the Verrucariaceae were not monophyletic. In fact, Verrucaria is highly polyphyletic and is spread out in eleven clades. Four lineages were identified by Gueidan et al. (2007), one constituting a marine group (V. mucosa, V. striatula). A second aquatic group was identified with V. maura (marine), V. adriatica and V. scabra (freshwater), suggesting that this genus migrated to the marine environment on at least two separate occasions.

Recently described species include V. allantoidea, V. halochlora from Japan and V. corallensis, V. meridionalis, V. subiscreta from Australia (McCarthy, 1991, 1994; Harada, 1995; McCarthy 2008) (Fig. 32). Verrucaria tavaresiae is unique in having a brown alga Petroderma maculiforme as a photobiont, while others have green algae (Coccolobry, Desmococcus, Dilabilifum, Myrmecia) or a xanthophyte (Heterococcus) photobiont (Moe, 1997). Aquatic Verrucaria species are generally cold-water species with various numbers recorded from different localities: Fidalgo Island Washington (7-9 species), New England, (7 species), Great Britain (8 species), the Antarctic Peninsula (6-8 species) and 10 from Scandinavia (Ryan, 1988; Taylor, 1982; Purvis et al., 1992; Lamb, 1948; Sartessus, 1993). There are many terrestrial Verrucaria species known from bark.

1. Photobiont a brown alga, Petroderma maculiforme ..................................................V. tavaresiae
2. Photobions from other algal groups......................2
3. Thallus epihithic and conspicuous grey-brown to green-brown, medium-green, green-black or black ..............................................4
4. Thallus not submerged.................................................5
5. Thallus white to pale-grey, often poorly developed, perithecia semi-immersed, to superficial, solitary to 2 - 3 together, 0.4 - 0.8 mm diam., involucrellum thick and well developed ..................V. halochlora
6. Thallus submerged, jet-black, involucrellum well-developed, ascosporae broadly ellipsoid 15 - 17.5 × 8-9.5 μm ..................................V. serpuloides
7. Thallus with prominent, glossy, branched and swollen ridges (jugae)..............................6
8. Thallus continuous to sparingly rimose, lower to mid-littoral species.................................8
9. Thallus strongly rimose to areolate, upper littoral to supralittoral species ..........................10
10. Margin of thallus placodioid-dissected .................11
11. Margin not dissected placodioid ....................11
12. Thallus grey-brown to olive-green or green black, not effuse or in blotches ..................13
13. Thallus grey-brown to mid-green-black, perithecia 0.22-0.45 mm diam .......................V. aucklandica
14. Thallus grey-brown to mid-green-black, perithecia 0.22-0.45 mm diam ........................14
14. Thallus dark olive-green to green-black, perithecia 0.12-0.22 mm diam .................. \( V. \) subdiscreta

15. Thallus pale-buff to grey-brown.......................... 16

15. Thallus olive-brown, greenish-grey, dark grey brown to dark greenish-black.............................. 17

16. Thallus pale-buff with conspicuous black cracks, perithecia 0.1-0.2 mm diam., not radially ridged, exciple colourless, ascospores 10-15 × 6-9 μm...... .................................................. \( V. \) tessellatula

16. Thallus buff-brown, grey-brown or green-grey, without prominent black cracks, perithecia 0.2-0.3 mm diam., often radially ridged, exciple brown to brown-black, ascospores 14.5-23.5 × 7-11 μm ...... .............................................................. \( V. \) bubalina

17. Ascospores 9-16 (17) μm long .................... 18

17. Ascospores 16-26 μm long, thallus olive brownish, green grey to dark-brown, prothallus distinct, exciple brown-black ................ \( V. \) fusconigrescens

18. Thallus eflusse, dull medium-green to green, black, areolate only around the perithecia, exciple brown-black, 25-32 μm thick, ascospores 9-12 (-16) × 6-7 (8.2) μm.................................................. \( V. \) sessilis

18. Thallus strongly rimose to areolate, dark green to greenish black, exciple 10-20 μm thick, hyaline to brown-black, ascospores 12-20 (-22) × 6-8 (-9) μm .............................................................. \( V. \) maura


LABOULBENIOMYCETES
LABOULBENIOMYCETIDAE
LABOULBENIALES:
Laboubenacea


This species has been described and illustrated by Kohlmeyer and Volkmann-Kohlmeier (2003b) on which the following summary is drawn from: Thallus 150-230 μm, receptacles 105-112 × 48-53 μm, ascomata 76-118 × 38-44 μm, elongate- ellipsoidal, sessile, ostiolate, hyaline to light-brown, solitary, appendages born on a side branch, asci 4-spored, elongate to clavate, thin-walled, unitunicate, early deliquesceing, ascospores 26-35 × 4 μm, elongate-fusiform, pointed at the apex, rounded at the base, 1-septate, lower cell smaller, and surrounded by a mucilaginous sheath. The marine status of this species needs questioning as it was found at the base of the elytra of the beetle \textit{Aepus robini}, living in the \textit{Laminaria} zone (Kohmeyer and Kohlmeyer, 1979).

LECANOROMYCETES
LECANOROMYCETIDAE
LECANORALES
Dactyloporaceae

\textit{Dactylospora} Körb., Syst. Lich. Germ. 271, 1855.................................................. (3)

Apothecia initially sub-globose, becoming subglobose or discoid, flat or convex, superficial, sessile, leathery, dark reddish-brown, becoming black, solitary, sometimes gregarious, asci clavate, short pedunculate, apically thick-walled, without an apical apparatus, ascospores ellipsoidal or obovoid, 1-septate, constricted at the septum, with longitudinal or verrucose ornamentations (Fig. 34). No appendages except in \textit{D. canariensis}. Au \textit{et al.} (1996) have illustrated the complexity of the ascospore wall in \textit{D. haliotrepha}, the wall consisting of a series of ridges derived from outgrowths of the mesosporium, and surrounded by the exosporium. The areas between the ridges are filled with mucilage and when the exosporium ruptures, the mucilage is lost. Another observation is that the pseudoparaphyses are

Fig. 32. *Verrucaria maura*. Habitat on shore in South Wales.

Fig. 33. Ascospores of: a. *Verrucaria allantoidea*. b. *V. halochlora*. Bars a-b = 5 μm.
surrounded by a hyphal sheath which stains with ruthenium red. Hafellner (1979) suggested that the ascus in *D. haliotrepha* was one layered, but the study of Au *et al.* (1996) confirms that it is bitunicate.

*Dactylospora canariensis* was originally referred by Kohlmeyer (1967) and Kohlmeyer and Kohlmeyer (1968) to *Banhegyia uralensis* and *B. setispora*, respectively, but on re-examination was found to be a different species from the original collection (Kohlmeyer and Volkmann-Kohlmeyer, 1998c; Kutorga and Hawksworth, 1997). It is the only *Dactylospora* species with appendaged ascospores and produces antheridia in culture.

1. Ascospores with appendages.............. *D. canariensis*
   1. Ascospores lacking appendages.................... 2

2. Ascospores narrow (less than 7 µm), 10.9-17.2 × 3.5-6.4 µm, verrucose spore wall ........... *D. mangrovei*
   2. Ascospores wider than 7 µm, 18-28 × 8-12 (-14.5) µm, spore wall with longitudinal striations

*LEOTIOMYCETES*

*LEOTIOMYCETIDAE*

*HELOTIALES*

*Helotiaceae*


A. *encephaloides* Curr., Proc. R. Soc. Lond. 9: 119, 1859 (Type species).


Apothecia superficial, reddish-brown, sessile, discoid, paraphyses filiform, septate, apically branching, swollen at the apex, asci cylindrical, short pedunculate, in a gelatinous matrix, ascospores fasiculate, filiform, unicellular, hyaline with inconspicuous mucilage (Hyde *et al*., 1999b). Occurs on the petiole base of *Nypa fruticans* intertidally in brackish, estuarine habitats. Hyde *et al.* (1999b) drew attention to its similarity to *Vibrissea*, sections *Apostemium* and *Microstemium*, which are difficult to distinguish at the morphological level (Iturriaga, 1997).

*Vibrisseaceae*

*Vibrissea* Fr., Syst. Mycol., Index alphab. 2: 4, 31, 1822................................................. (1)


Apothecia superficial, reddish-brown, sessile, discoid, paraphyses filiform, septate, apically branching, swollen at the apex, asci cylindrical, short pedunculate, in a gelatinous matrix, ascospores fasiculate, filiform, unicellular, hyaline with inconspicuous mucilage (Hyde *et al*., 1999b). Occurs on the petiole base of *Nypa fruticans* intertidally in brackish, estuarine habitats. Hyde *et al.* (1999b) drew attention to its similarity to *Vibrissea*, sections *Apostemium* and *Microstemium*, which are difficult to distinguish at the morphological level (Iturriaga, 1997).

*Dermateaceae*


(Calloria marina* Phillips, in Smith (1908), unpublished manuscript).

Apothecia concave, becoming convex and discoid, erumpent, superficial, sessile, light orange, becoming darker, solitary or gregarious, paraphyses filamentous, branched,
septate with swollen tips, asci cylindrical-clavate, tapering at the base, unitunicate, thin-walled, with an apical ring, ascospores ellipsoidal, 1-septate, smooth-walled, hyaline, lacking a sheath or appendages. Hosts usually cast brown seaweeds in the drift zone and strictly not an obligate marine species. Which raises the question of when are fungi truly marine? In this instance when are the seaweeds colonised by the fungus? Some 25 Laetinaevia species are listed in Index Fungorum of which L. marina is the only marine fungus.

Fungal Diversity

LICHINOMYCETES
LICHINALES
Lichinaceae

Lichina C. Agardh, Syn. Alg. Scand. Xii, 9, 1817.............................................................. (2)

L. confinis (O.F. Müll.) C. Agardh, Spec. alg. 1: 105, 1821.


Fucus pygmaeus f. minor Turner
Lichen confinis O.F. Müll., Icon. Plant. Daniae. 5: 5, 1782.

Lichina pumila sensu Gray A natural arrangement of British plants 1: 1-824, 1821.


Stereocaulon confinis (O.F. Müll.) Hoffm. Dutschl. Flora, p130, 1796.

L. pygmaea (Lightf.) C. Agardh, Flora Scotia 2: 964, 1777.

Fucus pygmaeus Lightf., Flora Scotia 2: 964,1777.

Thallus fruticose, erect, tufted, in clumps, becoming terete near the apices, 10 mm tall, and 0.1-0.2 mm thick, shiny dark brown to black or dark olive-green, gelatinous when wet, apothecia terminal, globose or flask-shaped, photobiont Calothrix (Cyanophyceae) (From http://floraseries.landcareresearch.co.nz). A genus of some 13 species of which two are marine. An important distinction between these two species is the presence of a cortex in L. pygmaea which makes it cartilaginous, while L. confinis has a loose hyphal weft containing many species of photobiont including Chlorophyceae and principally Calothrix (Fletcher, pers. comm.) (Fig. 35).

However, at least nine names are marine, mostly Antarctic, S. America. Only the above two species are known from the Northern Hemisphere (Fletcher, pers. comm.).

1. Lobes flatted, 1cm long, often prostrate, richly branched in one plane, shiny dark brown to black, apothecia terminal, globose, ascospores uniseriate.

L. pygmaea

1. Thallus terete, erect, tufted, 5 mm high, lobes dull, olive-brown to black.

L. confinis

ARTHONIOMYCETES
ARTHONIALES
Roccellaceae


Ascomata lirelliform, simple or branched, immersed in calcareous substrata, opening with a longitudinal slit, light brown, no periphyses, single or gregarious, paraphysoid, anastomosing, septate, in a gelatinous matrix, asci clavate, short pedunculate, thick-walled, with an ocular chamber, ascospores ellipsoidal to fusiform, 1-septate, not constricted at the septum, smooth, hyaline, and lacking a sheath or appendages (Kohlmeyer and Volkmann-Kohlmeyer, 1988b). A lichenoid species known from Belize, Caribbean and the Great Barrier Reef, Australia found on the lower side of subtidal coral slabs, on worm tubes and on molluscan shells. Originally placed in the Opegraphales by Kohlmeyer and Volkmann-Kohlmeyer (1988b) it is referred here to the Arthoniales (Kirk et al., 2001). However, Lumbsch and Huhndorf (2007) question this assignment.

ARTHONIOMYCETIDAE family incertae sedis
Melaspileaceae

**Fig. 34.** *Dactylospora haliotrepha.* **a.** Apothecia on mangrove wood. **b-d.** Asci, pseudoparaphyses and ascospores. **d.** Tips of the pseudoparaphyses staining with melzer. **e.** *Dactylospora mangrovei* SEM micrograph of ascospore with corrugated surface. Bars **a = 500 µm; b-d = 10 µm; e = 5µm**


Ascomata lirelliform, coriaceous, erumpent, dark coloured with an opening that runs the length of the ascoma, solitary or gregarious, pseudoparaphyses branched, anastomosing and in a gelatinous matrix, asci clavate, thick-walled, with an ocular chamber, wall staining blue in Melzer’s reagent, ascospores 1-septate, ellipsoidal, hyaline, becoming light brown, constricted at the septum, with a mucilaginous sheath (Fig. 36). The sheath ruptures at the apex to form a band or “skirt” at the septum to which it is attached (Vrijmoed *et al.*, 1996). It is found commonly on mangrove wood and can be confused with *Massarina* species with its 1-septate, hyaline ascospores, surrounded by a mucilaginous sheath. However, in *M. mangrovei*, the sheath ruptures apically to form a skirt-like appendage around the spore. Currently some 132 species are assigned to the genus, and includes lichenized, lichenicolous and saprobic taxa (Coppins, 1989). The genus is in need of revision and placement of this species remains unresolved.
Fig. 35. Habitat of a-b. *Lichina confinis*. c-d. *L. pygmaea* (Photos by Anthony Fletcher).

Fig. 36. *Melaspidea mangrovei*. a. Lirelliform ascomata on mangrove wood. b, d. Ascospores 1-septate markedly constricted at the septum with a skirt-like equatorial appendage. c. Thick-walled ascus and pseudoparaphyses. Bars a = 100 µm; b, d = 5 µm; c = 10 µm.
Three subclasses with marine taxa

Perithecial or derived cleistothecial ascomata, unitunicate asci, basal or peripheral in ascoma with a wide range of anamorphs.

1. Ascomata in a pseudostroma or coloured stroma or absent, lacking germ pores ........................................ 2

2. Ascomata perithecial, rarely cleistothecial, rarely stromatic, with well developed, interascal tissue poorly developed, asci cylindrical with J+ apical apparatus, ascospores brown to black, with germ pores ........................................... Xylariomycetidae

1. Ascospores with wing-like appendages ........................................... Hypocreales

1. Ascospores oval or globose ........................................................ 4

2. Ascomata in wood, asci apically thickened, ascospores with anamorph, ascomata yellow to pale brown, interascal tissue poorly developed, generally J-, ascospores septate, variable morphology, hyaline to brown, anamorphs may be present ........................................................... Hypocreomycetidae

2. Ascomata perithecial rarely cleistothecial, rarely stromatic or in a pseudostroma, necks well developed, interascal tissue poorly developed or absent, asci cylindrical or clavate often thick-walled but not fissitunicate, ascospores 0-1-septate, varied anamorphs ........................................... Sordariomycetidae

HYPOCREOMYCETIDAE

Three orders with marine taxa

1. Ascospores in a stroma, perithecial, papillate or short necks, generally coloured, asci clavate to cylindrical, ascospores 1-septate, hyaline to pale brown, prominent anamorph ........................................... Hypocreales

1. Ascospores 1-3-septate .......................................................... 9

2. Ascomata in wood, asci apically thickened, ascospores 1-3-septate ........................................... Swampomyces

2. Ascomata dark, thick-walled, opening by an irregular lysigenous pore, ascii clavate, long peduncle, ascospores hyaline to brown, allantoid ............................................ Coronophorales

HYPOCREALES

Key to the marine Hypocreales and Hypocreales incertae sedis

1. Ascospores with wing-like appendages ........................................... Emericellopsis

1. Ascospores 4-5 × 7-8 µm, 2-3 wings, up to 10 µm long ........................................... E. maritima

2. Ascospores 5-9 × 3-4.2 µm, 3 triangular wing-like appendages with an attenuated tips, projecting 5.6-10 µm ........................................... E. stolkiae

3. Ascospores 6-11 × 4-7 µm .................................................... Payosphaeria

5. Ascomata perithecial, rarely cleistothecial, sometimes stromatic and coloured, ostiole weakly to well developed, interascal tissue apical paraphyses or catenophyses or absent, asci thin-walled often deliquescing, ascus apical apparatus poorly developed, generally J-, ascospores septate, variable morphology, hyaline to brown, anamorphs may be present ........................................................... Hypocreomycetidae

2. Ascomata perithecial rarely cleistothecial, sometimes stromatic or in a pseudostroma, necks well developed, interascal tissue poorly developed or absent, asci cylindrical or clavate often thick-walled but not fissitunicate, ascospores 0-1-septate, varied anamorphs ........................................... Sordariomycetidae

HYPOCREALES

Three subclasses with marine taxa

1. Ascomata rarely in a stroma ................................................... 2

2. Ascomata perithecial, rarely cleistothecial, sometimes stromatic and coloured, ostiole weakly to well developed, interascal tissue apical paraphyses or catenophyses or absent, asci thin-walled often deliquescing, ascus apical apparatus poorly developed, generally J-, ascospores septate, variable morphology, hyaline to brown, anamorphs may be present ........................................................... Hypocreomycetidae

3. Ascospores 1-septate .......................................................... 2

4. Ascospores 3-septate .................................................... Torpedospora

6. Ascospores 1-3-septate ........................................................ 9

7. On seaweed (Laminaria), ascospores, pale brown verruculose, 13-20 × 7-9 µm ........................................... Pronectria

3. Ascospores 3-septate .................................................... 5

4. Ascospores needle-shaped .................................................... Halonecridia

6. Ascospores 1-septate .................................................... 7

8. Ascospores 17-26 × 8-13 µm, no known anamorph, ascocoma orange ................................................... Kallichroma

9. Ascocoma immersed in senescent leaves of Juncus roemerianus, asci with an apical ring, ascospores 3-septate, fusiform to elongate ellipsoidal 26.5-34.5 × 6-7 µm ........................................... Juncigena

Bionectriaceae

The assignment of marine Nectria-like taxa to this family is debatable and sequences of other genera are required before their true placement can be made. With the exception of Emericellopsis, they lack anamorphs, while the often submerged ascomata with long necks are not typical of the Hypocreales, e.g. Halonecridia.

Emericellopsis J.F.H. Beyma, Antonie van Leeuwenhoek Ned. Tijdschr. Hyg. 6: 264, 1940. ........................................................... (2)


Anamorph: Acremonium species.

Ascomata cleistothecial, globose, glaborous, superficial, asci scattered, globose to subglobose, thin-walled, hyaline, moderately persistent, ascospores ellipsoid to oval unicellular, dark green to pale brown, surrounded by subhyaline wings, triangular with an attenuated tip, finely spinulose (Davidson and Christensen, 1971). Emericellopsis species have been reported from marine habitats (Udea, 1980, 1995a) but are generally regarded as facultatively marine. This aspect requires to be challenged, as they are isolated from marine sediments, and often ruled out as truly marine.

This genus is assigned to the Bionectriaceae, forming a third marine lineage within the family (Rossman et al., 2001). Udea (1995a) isolated E. microspora from marine sediments and found that optimum growth was in 80% seawater. Artemczuk (1980) lists Emericellopsis maritima (Fig. 37) from sediments in the Black Sea, with ascospore measurements of 4-5 × 7-8 µm. Acremonium species are also frequently encountered on incubated wood from marine habitats (Jones, unpublished data).

Fig. 37. a. Emericellopsis maritima. Ascospore. b. Conidium. Bars a-b = 5 µm.


Ascomata solitary or gregarious, globose or subglobose, usually immersed, ostiolate, papillate, coriaceous, orange-coloured to pale brown, lacking paraphyses, asci clavate, short pedunculate, unitunicate, thin-walled, deliquescent, ascospores elongate, fusiform or cylindrical, unicellular, and hyaline. No appendages or sheath. A genus accepted by Rossman et al. (1999) for the present as a member of the Bionectriaceae, but they point out that the immersed ascomata with long necks and the elongate asceptate ascospores are not typical of the Hypocreales. Sequence data are required to resolve its taxonomic position.


Anamorph: Trichothecium-like

Ascomata gregarious, globose, superficial, no ostiole, cleistothecial, membranous, white becoming orange or pale brown, lacking paraphyses, asci globose or subglobose, sessile, unitunicate, thin-walled, deliquescing, ascospores broad ellipsoid or ovoidal, 1-septate, not constricted at the septum, hyaline, lacking appendages or a sheath. Molecular studies confirm the assignment of the genus to the Bionectriaceae, with affinities to Roumegueriella rufula, another cleistothecial member of the Bionectriaceae (Rehner and Samuels, 1995).


Ascomata solitary or gregarious, subglobose, immersed sometimes erumpent, ostiolate, periphysate, lacking a papilla, orange-brownish to orange-yellowish, peridium thick, lacking paraphyses, asci clavate, unitunicate, thin-walled, deliquescing, ascospores ellipsoid or ovoid, 1-septate, constricted at the septum, hyaline lacking appendages or a sheath. Originally described as Hydronectria but transferred by Kohlmeyer and Volkmann-Kohlmeier (1993a) to Kallichroma because the type species of Hydronectria is a lichen, with the alga Trentepohlia, occurs on rocks in freshwater.
and is temperate in its distribution. *Kallichroma* species are saprobic, marine (primarily on mangrove wood) and sub-tropical to tropical. They also differ in ascoma, paraphyses, ascus and ascospore morphology from *Hydronectria*. Kohlmeyer and Volkman-Kohlmeier (1993a) state the asci are persistent, but we frequently observe ascii deliquescing. Molecular data supports placement in the Bionectriaceae, but is the most distant genus in the family (Rossman *et al*., 2001; Schroers, 2001). SEM studies show longitudinal ridges running the length of the ascospores of *K. tethys* (Hyde, 1986).

1. Ascospore wall smooth ......................... *K. glabrum*
1. Ascospore wall with longitudinal ridges ...... *K. tethys*

**Hypocreaceae**


Ascomata ovoid to pyriform, superficial, scattered or aggregated, pale coloured becoming pink or orange-red, glabrous with hyaline to pale-yellow, unbranched, septate, smooth-walled short, hyphal-like hairs, short neck, periphysate, asci cylindrical, short pedunculate, hyaline, no apical apparatus, ascospores broadly ellipsoid to ellipsoid, uniseriate, yellowish brown, thick-walled, no germ pore, surface ornamented (Fig. 38).

The only species known from marine habitats, isolated from marine sludge at Oomura Bay, Japan (Udea and Udagawa, 1983). Characterized by its striated ascospores and a polyphialidic anamorph.


Ascomata globose to pyriform, superficial, ostiolate, papillate, lacking periphyses, membranous, hyaline, solitary or gregarious, paraphyses few, branched, septate, hyaline, asci long cylindrical, short pedunculate, persistent, uniseriate, thin-walled, no apical apparatus, ascospores round to oval, unicellular, hyaline, thin-walled, smooth and lacking a sheath or appendages. A poorly known species described from mangrove wood samples from Malaysia and Singapore, but common on submerged test blocks at these locations with 61 collections (Leong *et al*., 1990). Tentatively assigned by Leong *et al.* (1990) to the Hypocreales (as Nectriaceae) its taxonomic position needs further study at the molecular level.

![Fig. 38. *Neocosmospora tenuicristata*. a. Ascospore. b. Conidium. Bars a-b = 5 \( \mu \text{m} \).](image)
HYPOCREALES incertae sedis

**Torpedospora** Meyers, Mycologia 49: 496, 1957

- **T. radiata** Meyers, Mycologia 49: 496, 1957 (Type species).

Ascomata solitary, subglobose to ellipsoidal, immersed or superficial, ostiolate, papillate or epipapillate, subcarbonaceous to coriaceous, dark brown, paraphyses ramose, deliquescing or persistent, asci clavate to ellipsoidal, unitunicate, thin-walled, early deliquescing, ascospores cylindrical to elongate-ellipsoidal, 3-septate, constricted at the septum, hyaline but pale orange in a mass, with appendages at one or both poles (Fig. 39). Although these species have appendaged ascospores and deliquescing asci, and tentatively assigned to the Halosphaeriales, they were later excluded from the order (Kohlmeyer, 1972a). The morphology of the ascomata is very different from those of the Halosphaeriaceae and molecular data show they are a sister group to the Bionectriaceae, Hypocreales from LSU rDNA, or the clades comprising the Phyllachorales, Halosphaeriales, Microascales from SSU rDNA and combined data set (Sakayaroj et al., 2005b).

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1. Ascospores with appendages at one end, longer than 30 µm.......................................................... **T. radiata**
2. Ascospores with appendages at both ends, shorter than 25 µm.................................................. **T. ambispinosa**


Ascomata subglobose to pyriform, immersed, ostiolate, papillate, coriaceous, fuscous, solitary, periphysate, pseudo-paraphyses thin, branched, septate, asci fusiform to cylindrical, short pedunculate, thin-walled, unitunicate, apical apparatus with an apical ring, J-, ascospores fusiform to elongate-ellipsoid, 3-septate, constricted at the septa, hyaline, no sheath or appendages. A salt marsh fungus, with a *Cirrenalia adarca* anamorph, which grows on the submerged bases of leaves (between 12-25 cm above the rhizomes) of *Juncus roemerianus*, and thus regarded as obligately marine. Originally Eriksson (1999) considered it to belong in the Magnaporthaceae. Thongkantha et al. (2009) found no support for this. Using DNA sequences from protein coding and ribosomal nuclear loci, Schoch et al. (2006) noted three subclades (1. Torpedospora spp., 2. Swampomyces spp. and Etheirophora spp. and 3. Swampomyces sp. and Juncigena adarca) were associated with the Coronophorales with good support. The data suggests that the 3-septate Swampomyces species may be congeneric with **Juncigena adarca** but further clarification of the molecular data of *S. triseptatus* is required.


Ascomata pyriform, subglobose, globose, coriaceous, centrum apricot coloured, solitary, immersed, ostiolate, necks with periphyses, dark brown to black, paraphyses numerous, simple, hyaline, in a gel, asci cylindrical-oblong, unitunicate, thin-walled, short pedunculate, apically thickened, J-, persistent, ascospores clavate, ellipsoidal, 1-3-septate, hyaline, slightly to constricted at the septa, no appendages or sheaths. All species found predominantly on mangrove wood (Fig. 40).
(Abdel-Wahab et al., 2001a). The genus was tentatively assigned to the Polystigmataceae (Kohlmeyer and Volkman-Kohlmeyer, 1987c), but was left unclassified pending sequence data. At the ultrastructure level, the ascus apex consists of a large amorphous apical thickening, but no central pore was observed, although serial sections were made (Read et al., 1995). Molecular data has not helped in resolving the higher level taxonomic position of this genus, which groups with Torpedospora species (Sakayaroj et al., 2005b). Swampomyces armeniacus shows closer affinity with Etheirophora species, but further strains of S. triseptatus need to be sequenced to resolve the status of the genus (Schoch et al., 2006).

Fig. 39. Ascospores of a-b. Torpedospora radiata. c. Torpedospora ambispinosa. Bars a-b = 10 µm, c = 5 µm.

Fig. 40. Ascospores of a. Swampomyces clavatispora. b. S. aegyptiacus. Bars a-b = 5 µm.


(12-18 µm), bristle-like, rigid, slightly curved and of undetermined origin. Molecular data places them in the TBM clade with affinities to the Coronophorales in the Hypocreomycetidae (Schoch et al., 2006).

1. Ascospores with appendages at both ends, 16-21.5 × 6-8 µm .................................................... *E. bijubata*
1. Ascospores with appendages at one end .............. 2

2. Ascospores up to 21 µm, on bark of *Rhizophora mangle*, up to 7 appendages ........... *E. blepharospora*
2. Ascospores up to 29 µm, on other hosts, with more than 7 appendages ............................ *E. unijubata*

CORONOPHORALES

Nitschkiaceae


*G. bivestia* Jørg. Koch, E.B.G. Jones & S.T. Moss, Bot. Mar. 26: 265, 1983 (*Type species*). Ascomata hemispherical-oblong tuberiform, cleistothecial, superficial, leathery to carbonaceous, brown to black, with a weak subiculum, paraphyses numerous, septate, constricted at the septa, simple or branched, asci broadly clavate, long pedunculate, unisporic thin-walled at maturity, no apical apparatus, generally persistent, ascospores broadly fusiform, 1-septate, slightly constricted at the septum, hyaline later brown, with appendages. Appendages formed by fragmentation of a sheath forming apical and equatorial appendages (Koch et al., 1983).

Hibbett et al. (2007) refer the Nitschkiaceae to the Coronophorales, the order to which Koch et al. (1983) originally assigned *Groenhiella*. However, a molecular study is required to validate its assignment to the Nitschkiaceae and to the Coronophorales. The most recent study is that of Petersen (1997) on the ultrastructure of the ascospores and confirms the exosporic origin of the appendages, comprising fibrillar electron-dense material in an electron-transparent matrix and circa 360 nm thick. As the ascus deliquesces the exosporic sheath separates from the episporium and then fragments to form the polar and equatorial appendages.

HALOSPHAERIALES

Halosphaeriaceae

The Halosphaeriales is one of the most intensively studied marine ascomycete order at the morphological, ultrastructural and molecular level with 53 genera (of which 35 are monotypic) and 126 species. Nearly 50% of the genera have been sequenced and found to form a monophyletic group within the Ascomycota (Fig. 41). Hibbett et al. (2007) places the Halosphaeriales within the Microascales. However, Zhang et al. (2006) and Tang et al. (2007a) retain the order, and this is followed in this volume. Tang et al. (2007a) undertook a multigene analysis of the systematics of the Sordariomycetes. Three subclasses were defined: Hypocreomycetidae, Sordariomycetidae and Xylariomycetidae as employed in this monograph. They noted that the Microascales is paraphyletic with *Ceratocystis* phylogenetically associated with *Fauvelina*, while *Microascus* and *Petriella* formed a separate clade and were basal to other members of the Halosphaeriales (Tang et al., 2007a). In the LSU dataset the Halosphaeriales and Microascales form subclasses, with the latter in a basal position. In the SSU dataset the Microascales splits the Halosphaeriales into two separate clades, but with weak support. The Microascales are basal to the Halosphaeriales in the RPB2 and combined datasets, but with too few taxa to satisfactorily resolve their taxonomic position (Tang et al., 2007a).

Key to the genera

1. Ascospores aseptate ................................................. 2
1. Ascospores septate ................................................. 8

2. Ascospores appendaged .......................................... 3
2. Ascospores lacking appendages .................................. 4

3. Ascospores with polar and 4 groups of equatorial hair-like appendages ............................ *Nautospaeria*
3. Ascospores with a single, uncoiling polar appendage ......................................................... *Moana*

4. Ascospores longer than 50 µm, filiform, range 50-300 × 4-15 µm ........................................ *Bathyascus*
Fig. 41. One of three MPTs inferred from LSU rDNA sequences of all halosphaeralean taxa, generated with maximum parsimony analysis. Bootstrap values higher than 50% are given above branches. Scale bar indicates 10 character state changes.
4. Ascospores shorter than 50 µm, spherical or ellipsoidal..........................5
5. Ascospores spherical to round..............................6
6. Ascospores ellipsoidal, range 9-38 × 4-24 µm...........6
7. Ascomata brown, necks short, ascospores spherical......5
8.Ascospore appendages with a different morphology........24
9. Ascospores with polar and/or equatorial appendages..11
10. Ascis deliquescent early ..................................7
11. Ascis persistent..........................................10
12. Ascus tip thimble-shaped, or slightly thickened......12
13. Ascospores without unfolding bipolar appendages...13
14. Ascospores with a faint sheath .........................15
15. Ascospores with a single polar appendage .............17
16. Ascospores with a bipolar hamate appendix, or polar and equatorial appendages ..........18
17. Ascospores with a hamate polar appendix .............19
18. Ascospores with an ephemeral drop of polar mucilage, becoming 2-4-septate on germination.....19
19. Ascospores 1-septate.................................9
20. Ascospores 1 to many-septate .........................44
21. Ascospores with no appendages .......................10
22. Ascospores with polar and/or equatorial appendages or with sheaths .................14
23. Ascospores with sheaths ....................................26
24. Ascospores with an exosporic sheath..................41
25. Ascospores with polar or subpolar appendages......28
26. Ascospores with polar hair-like and lateral sheath-like appendage ...................29
27. Ascospores with only one type of appendage........22
28. Ascospores with two types of appendages.........25
29. Ascospores with a single polar appendage...........15
30. Ascospores with a bipolar hamate appendix, or polar and equatorial appendages ..........18
31. Ascospores with subpolar appendages.................32
32. Ascospores with a fragmenting sheath, and polar unfurling appendages..............36
33. Ascospores with a fragmenting sheath, and polar unfurling appendages..............36
34. Ascospores with an exosporic sheath..................41
35. Ascospores with a subapical appendage.................37
36. Ascospores with a sheath and polar and lateral or subpolar appendages ..........36
37. Polar strap-like mucilaginous and subpolar hair-like appendages.........................39
38. Polar appendages emerging from a hood-like structure..........................Cucullosporella
39. Polar appendages not formed through a hood........20
40. Ascospores shorter and narrower than 35 µm and 20 µm, respectively..................22
41. Ascospores longer than 35 µm and wider than 20 µm..................................................22
42. Ascospores with subpolar appendages...............32
43. Ascospores with a fragmenting sheath, and polar unfurling appendages..............36
44. Ascospores with two types of appendages.........25
45. Ascospores with only one type of appendage........28
46. Ascomata formed beneath a stroma, ascospores 6-21 × 6-8 µm..............................16
47. Ascomata not stromatic.....................................17
48. Ascospores oval, 24-32 × 8-12 µm.....................17
49. Ascospores filiform, 60-80 × 4-6 µm ascomata thick-walled ................................Oceantitis
50. Ascospores with polar unfurling appendages......9
51. Ascospores with a different morphology ............24
52. Ascospores with polar and equatorial appendages..11
53. Ascospores with a single polar appendage...........15
54. Ascospores with only one type of appendage........22
55. Ascospores with two types of appendages.........25
56. Ascospores with a bipolar hamate appendix, or polar and equatorial appendages ..........18
57. Ascospores with a fragmenting sheath, and polar unfurling appendages..............36
58. Ascospores with subpolar appendages.................32
59. Ascospores with a sheath and polar and lateral or subpolar appendages ..........36
60. Ascospores with a subapical appendage.................37
61. Polar appendages emerging from a hood-like structure..........................Cucullosporella
62. Ascospores longer than 35 µm and wider than 20 µm..................................................22
63. Ascospores shorter and narrower than 35 µm and 20 µm, respectively..................22
64. Ascospores with subpolar appendages...............32
65. Ascospores with a fragmenting sheath, and polar unfurling appendages..............36
66. Ascospores with two types of appendages.........25
67. Ascospores with only one type of appendage........28
68. Ascomata formed beneath a stroma, ascospores 6-21 × 6-8 µm..............................16
69. Ascomata not stromatic.....................................17
70. Ascospores oval, 24-32 × 8-12 µm.....................17
71. Ascospores filiform, 60-80 × 4-6 µm ascomata thick-walled ................................Oceantitis
72. Ascospores with polar unfurling appendages......9
73. Ascospores with a different morphology ............24
74. Polar appendages emerging from a hood-like structure..........................Cucullosporella
75. Polar appendages not formed through a hood........20
76. Ascospores longer than 35 µm and wider than 20 µm..................................................22
77. Ascospores shorter and narrower than 35 µm and 20 µm, respectively..................22
78. Ascospores with subpolar appendages...............32
79. Ascospores with a fragmenting sheath, and polar unfurling appendages..............36
80. Ascospores with two types of appendages.........25
81. Ascospores with only one type of appendage........28
82. Ascomata formed beneath a stroma, ascospores 6-21 × 6-8 µm..............................16
83. Ascomata not stromatic.....................................17
84. Ascospores oval, 24-32 × 8-12 µm.....................17
85. Ascospores filiform, 60-80 × 4-6 µm ascomata thick-walled ................................Oceantitis
86. Ascospores with polar unfurling appendages......9
87. Ascospores with a different morphology ............24
88. Polar appendages emerging from a hood-like structure..........................Cucullosporella
89. Polar appendages not formed through a hood........20
90. Ascospores longer than 35 µm and wider than 20 µm..................................................22
91. Ascospores shorter and narrower than 35 µm and 20 µm, respectively..................22
92. Ascospores with subpolar appendages...............32
93. Ascospores with a fragmenting sheath, and polar unfurling appendages..............36
94. Ascospores with two types of appendages.........25
95. Ascospores with only one type of appendage........28
96. Ascomata formed beneath a stroma, ascospores 6-21 × 6-8 µm..............................16
97. Ascomata not stromatic.....................................17
98. Ascospores oval, 24-32 × 8-12 µm.....................17
99. Ascospores filiform, 60-80 × 4-6 µm ascomata thick-walled ................................Oceantitis
100. Ascospores with polar unfurling appendages.....9
101. Ascospores with a different morphology ..........24
Fungal Diversity
32. Ascospore appendages with a spade-like tip.........
   ........................................................................ Arenariomyces
32 Ascospores appendages lacking a spade-like tip.33
33. Ascospores with 2 sub-polar appendages...........
   ........................................................................ Antennospora
33. Ascospores with more than 2 sub-polar appendages
   ........................................................................
34. Ascospores with 3-4 sub-polar spoon-shaped
   appendages ....................................................... Haiyangia
34. Ascospores with 5-7 appendages ...............Corallicola
35. Equatorial appendage ring- or annulus-like ......
35. Equatorial appendages distinct .....................
36. Chamber-like polar appendage from which
   mucilage is released .......... Ceriosporopsis tubulifera
36. Polar appendages do not release mucilage ......37
37. Equatorial appendage annulus-like ..........Ondinella
37. Equatorial appendage ring-like ........Lautisporopsis
38. Equatorial appendages lunate, with a cup-like
   polar appendage ................ Halosphaeriopsis
38. Appendages spoon-like or obclavate .............
39. Appendages spoon-like, do not fragment...........
   ........................................................................ Halosphaeria
39. Appendages become fibrillar at maturity ........
40. Polar appendage longer than equatorial
   appendages ....................................................... Ocicosuspora
40. Appendages equal in length ................ Sablecota
41. Appendages with a cup-like exosporic fragments
   at their tips ..................................................... Marinospora
41. Appendages lacking cup-like fragments at their
   tips ....................................................................
42. Ascomata grayish-white, exosporic sheath
   envelopes the spore and horn-like polar appendage
   ........................................................................ Bovicornua
42. Ascomata brown to dark coloured, appendages not
   horn-like ................................................................
43. Exosporic sheath highly fibrillar (mucilaginous),
   circa 5 µm wide, appendage slug-like..............
   ........................................................................ Limacospora
43. Exosporic sheath compact, not fibrillar, polar
   appendage uncoiling in water ..................... Ceriosporopsis
44. Ascospores with no appendages...............45
44. Ascospores with appendages ..................47
45. Ascospores filamentous, broad at one end, tapering
   at the other ...................................................... Trailia
45. Ascospores not tapering at one end ..........46
46. Ascospores 5-septate (rarely 9), asci with 4
   ascospores ...................................................... Luttrellia
46. Ascospores 3-septate, asci with 8 ascospores........

........................................................................... Pseudolignicincola
47. Ascospores hyaline or brown with polar and
   equatorial appendages.................................48
47. Ascospores hyaline, with only polar appendages...
   ........................................................................ 50
47. Ascospores with sheath, lacking polar and
   equatorial appendages .................................56
48. Appendages hair-like tufts, one polar and four
   equatorial............................................................... 49
48. Polar appendages spine-like, equatorial
   appendages formed by fragmentation of an
   exosporic sheath ........................................... Corollospora
49. Catenophyses present, ascospores hyaline,
   appendages string-like, lacking an equatorial pad...
   ........................................................................ Haivispora
49. Catenophyses lacking, ascospores with hyaline end
   cells and brown central cells, equatorial pad
   present .............................................................. Nereiospora
50. Ascospores with a single polar appendage........51
50. Ascospores with bipolar appendages ...........
51. Appendage an ephemeral drop of mucilage........
   ........................................................................ Okeanomyces
51. Tetraradiate appendages formed after release from
   the ascoma ....................................................... Thalespora
52. Ascospores appendages hamate, unfurling in water
   ........................................................................ 53
52. Ascospore appendages not hamate ..............55
53. Ascospores narrower than 7 µm .............. Oceaniitis
53. Ascospores wider than 7 µm ..........................54
54. Ascospores verrucose, wider than 40 µm...........
   ........................................................................ Magnisphaera
54. Ascospor not verrucose, narrower than 40 µm....
   ........................................................................ Halosarphaea sensu lato
55. Ascospores appendages sub-polar, spine-like......
   ........................................................................ Arenariomyces
55. Ascospores appendages broad strap-like .Haligena
55. Ascospores appendages round ........ Trichomaris
56. Ascospores 12-20 µm wide, central cells dark,
   appendages a fragmenting sheath net-like........
   ........................................................................... Carbosphaerella
56. Ascospores hyaline, 7-11 µm wide ..................
   ........................................................................ Appendichordella


Ascomata globose to obpyriform, ostiolate, papillate, coriaceous, black, superficial, solitary or gregarious, with a long cylindrical to conical neck circa 250 µm, periphysate, asci clavate, long pedunculate,
thin-walled, unitunicate, persistent, ascospores fusiform, slightly curved, 1-septate, thick-walled, hyaline but distinct appendages not reported. Molecular and morphological data confirm the position of this genus within the Halosphaeriales (Dupont et al., 2009). On trawled sunken wood fragments collected at 1,000 m depth in the Pacific Ocean off Vanuatu Islands, the ascomata are large (600-650 µm), with a thick peridial wall, no paraphyses or catenophyses, asci unitunicate, clavate with a long pedicel, persistent, ascospores 32-35 × 3.2-3.6 µm, hyaline, fusiform, 1-septate and with no appendages (Fig. 42). Ultrastructural data suggest there is an exosporium which may form a thin mucilaginous layer around the ascospore.

Fig. 42. Alisea longicola. Ascospore. Bar = 10 µm.

**Aniptodera** Shearer & M.A. Mill., Mycologia 69: 893, 1977 ............................................... (9)

■ **A. chesapeakensis** Shearer & M.A. Mill., Mycologia 69: 894, 1977 (*Type species*).


**A. limnetica** Shearer, Mycologia 81: 140, 1989.


Ascomata globose to subglobose, immersed or superficial, ostiolate, papillate, membranous, hyaline to light brown to dark brown, neck variable in length cylindrical, periphysate, catenophyses present but deliquescing, asci clavate, short pedunculate, unitunicate, thin-walled, but with an apical pore and a retracting plasmalemma subapically, persistent or deliquescing, ascospores ellipsoidal, 1-septate, hyaline, thick-walled, with or without apical appendages which unfurl when mounted in water (Hyde and Jones, 1989c; Campbell et al., 2003).

Initially this genus was well circumscribed (Shearer and Miller, 1977), but with the addition of further species the situation has become confused. Originally ascospores were characterized as thick-walled, 1-septate, lacking bipolar appendages, with persistent asci, with a retracting plasmalemma, and an apical pore. Since the assignment of species with bipolar, unfurling appendages, the differences between it and *Halosarphaea* have become confused (Kong et al., 2000) (Fig. 41). Any taxonomic changes proposed for *Halosarphaea* must take into account the genus *Aniptodera*. Marine *Aniptodera* species occur on a wide range of substrata: mangrove and driftwood, *Nypa fruticans*, *Juncus roemerianus*. Some freshwater *Aniptodera* species may also occur in saline habitats, for example *A. limnetica* was reported by Nakagiri (1993b) on *Bruguiera gymnorrhiza* wood collected in the Shiira River mangrove, Japan. Ascospores in *A. limnetica* are thin-walled and released through a fissure in the apical plate which splits at the pore. We regard *Aniptodera indica* as a synonym of *Tirispora unicaudata* (Ananda and Sridhar, 2002). Assignment of *A. juncicola* and *A. mangrovei* to the genus needs to be tested at the molecular level as they may be better placed in other genera.

The stability of ascospore appendages as a character in the delineation of genera might be questioned in view of the behaviour of those of *Aniptodera salsuginosa* when mounted in water of different salinity. In freshwater the appendages immediately detach but uncoil when mounted in salinities of 3-10 ‰ (Nakagiri and Ito, 1994). The issue of appended/non-appendaged ascospores in *A. chesapeakensis* also needs resolution, before the taxonomy of this genus can be resolved.
1. Ascospores with bipolar appendages .......................... 2
2. Ascospores 37-45 × 12-14 µm, on mangrove wood .... 3
3. Ascospores 14-20 × 4-7 µm, on mangrove bark ...... 4
4. Ascospores 10.5-13 × 7-8 µm .......................... 5
5. Ascospores thick-walled ............................................ 6
6. Ascospores 20-25 × 8-10 µm .......................... 7

**Anisostagma** K.R.L. Petersen & Jørg. Koch, 
Mycol. Res. 100: 211, 1996 ..........................  (1)

**A. rotundatum** K.R.L. Petersen & Jørg. Koch, 
Mycol. Res. 100: 211, 1996 (Type species).

Ascomata globose to broadly ellipsoidal, immersed to erumpent, coriaceous, ostiolar, papillate, cream-coloured to pale brown, solitary or gregarious, neck long (140-420 µm), periphysate, catenophyses present, asci clavate, pedunculate, unitunicate, thin-walled, lacking an apical apparatus, early deliquescing, ascospores globose to ellipsoidal, unilocular, hyaline, thin-walled without appendages or a sheath (Petersen and Koch, 1996). **Anisostagma rotundatum** resembles *Thalassogena sphaerica*, both possessing sphaerical-ellipsoidal hyaline ascospores and with no appendages or sheaths. Two distinguishing characters are: peridium structure and ascus morphology. In *Thalassogena* the peridial wall is undifferentiated, while in *Anisostagma* it is two layered (inner layer of flattened thin-walled cells and an outer layer forming a textura angularis). An apical pore is present in *Thalassogena*, but lacking in *Anisostagma* (Petersen and Koch, 1996). Whether these characters are sufficient to separate these two genera remains to be resolved.

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**Antennospora** Meyers, Mycologia 49: 501, 1957 ..........................  (1)

* A. quadricornuta (Cribb & J.W. Cribb) T.W. 

**Halosphaeria quadricornuta** Cribb & J.W. Cribb, 


Ascomata subglobose or ellipsoidal, immersed, superficial when growing on the calcareous tubes of mollusks, ostiolar, papillate, coriaceous or subcarbonaceous, dark brown, solitary or gregarious, catenophyses deliquescing, periphysate, ascii clavate, pedunculate, unitunicate, thin-walled, no apical apparatus, deliquescing early, ascospores ellipsoidal, 1-septate, slightly constricted at the septum, hyaline with polar appendages. Appendages subterminal, at each end of the spore, at right angles to each other, cylindrical, and attenuate (Figs 41, 43h). Their ultrastructure has been examined by Yusoff *et al.* (1994c). Ascospores of *A. salina* and *A. quadricornuta* are morphologically different with two round, sub-polar appendages in the latter species, while the former has 4-5 sub-terminal wing-like appendages (Yusoff *et al.*, 1994c). Consequently, and supported by molecular data, *A. salina* was transferred to *Haiyangia* (Pang *et al.*, 2008b).


**Sphaerulina amicta** Kohlm., Nova Hedw. 4: 414, 1962.

**Haligena amicta** (Kohlm.) Kohl., Marine 

Ascomata globose to subglobose, immersed, ostiolar, papillate, coriaceous, light brown to reddish-brown, solitary, periphysate, catenophyses deliquescing, asci clavate, pedunculate, unitunicate, thin-walled, without an apical apparatus, deliquescing, ascospores cylindrical or ellipsoidal, 3-septate, constricted at the septa, hyaline and with a pronounced sheath. A monotypic genus (previously assigned to *Sphaerulina* and *Haligena*) characterized by a gelatinous sheath to the
ascospore, which is composed of thread-like appendages arising from the episporium (Johnson et al., 1987). Well placed in the Halosphaeriales.


*Peritrichospora trifurcata* (Höhnk) Kohlm., Nova Hedw. 3: 89, 1961


Ascomata globose or subglobose, immersed generally superficial, attached to substrata by subicula, with or without ostioles, papillate or epapillate, carbonaceous, dark brown, solitary, catenophyses deliquescent, asci fusiform to clavate, unitunicate, thin-walled, early deliquescent, ascospores filiform, 0-1-septate, hyaline and lacking appendages. This genus differs from those of *Corollospora*, and re-established the genus. In *Arenariomyces* the subpolar appendages are outgrowths from the mesosporium, while in *Corollospora* they comprise both the mesosporium and episporium (Jones et al., 1983a). Furthermore, the base of the appendage is swollen with electron-dense fibres on one side.

1. Ascospores 1-septate. .................................................. 2
2. Ascospores 3-septate, 27–34 × 6–8 μm. *A. triseptatus*
3. Ascospores consistently with 3 appendages, mainly on sand, 24–38 × 7–16 μm. *A. trifurcatus*
4. Ascospores with 3–4 appendages, mainly on wood, 28–39 × 10–14 μm. *A. majusculus*

**Fungal Diversity**

*Bathyascus* Kohlm., Rev. Mycol. 41: 190, 1977............................................................. (4)


Ascomata subglobose or ellipsoidal, immersed, ostiolate, papillate, coriaceous, dark brown, solitary, neck lacking periphyses, ascophyses deliquescent, asci fusiform to clavate, unitunicate, thin-walled, early deliquescent, ascospores filiform, 0-1-septate, hyaline and lacking appendages. This genus was initially assigned to the Halosphaeriales because of the deliquescent nature of the asci, but preliminary molecular studies show that it has little affinity with that order. Furthermore, *B. tropicalis* may be incorrectly placed in the genus because of the thin-walled nature of the ascoma, not a feature of the genus. *Bathyascus* superficially resembles *Pseudohalonectria* in ascospore morphology, but differ in the degree of spore septation, and cylindrical asci with a well developed apical apparatus (Shearer, 1993b). A molecular study is required to confirm whether *B. tropicalis* would be better assigned to *Thalespora* (Jones et al., 2006).

1. Ascospores with no septum, ascomata many layered peridium.................................................. 2
2. Ascospores 3-septate, 70–100 × 8–10 μm, ascomata thin-walled ............................ 2
3. Ascospores thick-walled, a deep sea species, 50–72 × 4–6 μm. *B. vermisorus*
4. Ascospores thin-walled, a mangrove species............................................. 3
5. Ascospores 90–145 × 2.5–4 μm. *B. avicenniae*
6. Ascospores 205–300 × 9–15 μm. *B. grandisporus*


Ascomata globose to subglobose, ostiolate with short conical necks, greyish white, erumpent, membranous, gregarious, centrum pseudoparenchyma breaks down, no catenophyses, asci broadly clavate, pedunculate, unitunicate, thin-walled, early deliquescing, no apical pore, ascospores unequally 1-septate, slightly curved, constricted at the septum, hyaline and appendaged. At each pole there is a single appendage enclosed within an outer sheath which swells when mounted in sea water. A genus that shares many features with *Ceriosporopsis* but differs in the degree of elaboration of the ascospore appendages as seen at the TEM level (Yusoff et al., 1993). The exosporic wall layer enrobes both the spore and polar appendages, which arise as outgrowths of the spore. The exosporium is bipartite, the inner region has regular, parallel electron-dense lamellations that radiate from the episporium while the outer region consists of electron-dense fibrillar material. Molecular results confirm the placement of *Bovicornua* in the Halosphaeriales. It clusters with *Ceriosporopsis halima* with strong support within the same clade as *Marinospora*, *Ceriosporopsis tubulifera* and *Ondiniella* (Fig. 41).

**Carbosphaerella** I. Schmidt, Feddes Repert. 80: 108, 1969. (2)


**C. pleosporoides** I. Schmidt, Feddes Repert. 80: 108, 1969 (Type species).

Ascomata globose or subglobose, superficial, subiculate, ostiolute, papillate or epapillate, carbonaceous, black, lacking paraphyses, asci obpyriform, subglobose, ovoid, short pedunculate, lacking an apical apparatus, unitunicate, deliquescing early, ascospores ellipsoidal or ovoid, 3-septate or muriform, brown, apical cell paler, with a pronounced gelatinous sheath (Johnson et al., 1984). A well delineated genus with its inclusion in the order supported by molecular and morphological evidence. The phylogeny of *C. leptosphaerioides* is confirmed by molecular analysis. It is well delineated in the Halosphaeriales and has affinities with *Remispora pilleata* and *R. maritima* (Fig. 41).

1. Ascospores with transverse septa only..........................
   ............................... *C. leptosphaerioides*
1. Ascospores with both transverse and longitudinal septa.........................*C. pleosporoides*

**Ceriosporopsis** Linder Farlowia 1: 408, 1944. (5)


**C. halima** Linder, Farlowia 1: 408, 1944 (Type species).


Ascomata subglobose to cylindrical, immersed, ostiolute, papillate, coriaceous or subcarbonaceous, light brown to black, solitary or gregarious, catenophyses deliquescing, asci clavate, pedunculate, unitunicate, thin-walled, deliquescing early, ascospores ellipsoidal, 1-septate, hyaline, with appendages. Appendage morphology variable depending on the species (Johnson et al., 1987). *Ceriosporopsis cambrensis* may have been described on the basis of more than one species, as the original description is confused in certain details (Jones et al., 1995), consequently can be designated a doubtful species.

*Ceriosporopsis tubulifera* differs in many details from the type species *C. halima*, but primarily in the origin and nature of the ascospore appendage (Figs. 41, 43a, 44a) (Johnson et al., 1987). It possesses a polar end-chamber from which mucilage is released, but this does not arise from the mesosporium. However, its phylogenetic position is placed within the *Marinospora* clade with good support (Fig. 41). However, it is not monophyletic with the type species, *Ceriosporopsis halima*. In other *Ceriosporopsis* species the polar appendages arise from the mesosporium (Johnson et al., 1987). *Ceriosporopsis circumvestita* and *C. sundica* have been transferred to new genera:
Lautisporopsis and Limacospora, respectively (Yusoff et al., 1994a; Jones et al., 1995).

1. Ascospores with equatorial appendages
2. Ascospores lacking equatorial appendages
3. Ascospore appendages $>750$ nm

**Fig. 43.** Ascospores of various halosphaeriaceous ascomycetes. a. Ceriosporopsis tubulifera. (mucilage arrowed) b. Lautisporopsis circumvestita. c, d. Cucullosporella mangrovei, apical collar arrowed. e. Halosarpheia trullifera. f. Saagaromyces glitra. g. Haiyanga salina. h. Antennospora quadricornuta. Bars a, b, e, g = 10 µm, d, f = 25 µm, h = 20 µm.

2. Polar ascospore appendage an end chamber containing mucilage

3. Polar ascospore appendage arising from the mesosporium, without an end chamber

C. capillacea
3. Ascospore appendages <750 nm.......................... 4

4. Ascospores 22.5-26 × 8-10 µm.................. C. halina

4. Ascospores 29-31.5 × 10.5-14.5 µm ... C. cambreensis


Ascomata subglobose, superficial or immersed, ostiolate, papillate or epipapillate, coriaceous to carbonaceous, dark brown, solitary or gregarious, paraphyses absent, catenophyses deliquescing, asci subglobose to clavate, unitunicate, thin-walled, deliquescing early, ascospores ellipsoidal, 0-septate, hyaline, slightly constricted at the septum, with 5-7 polar appendages at each pole. This species is very similar to Arenariomyces and differs in that the centrum pseudoparenchyma has no pit connections; ascospore appendages do not terminate in a spade-like structure; and it can be found on dead coral rocks (Volkman-Kohlmayr and Kohlmeyer, 1992). The genus should be examined at the molecular level to determine if it is distinct from Arenariomyces (Jones et al., 1983a).

Corallicola Volkm.-Kohl. & Kohlm., Mycotaxon 44: 418, 1992............................ (1)

C. nana Volkm.-Kohl. & Kohlm., Mycotaxon 44: 418, 1992 (Type species).

Ascomata subglobose, superficial, ostiolate, short papillate or epipapillate, subulate, coriaceous, dark brown, solitary or gregarious, catenophyses deliquescing, asci deliquescing early, unitunicate, thin-walled, ascospores ellipsoidal, 1-septate, hyaline, slightly constricted at the septum, with 5-7 polar appendages at each pole. This species is very similar to Arenariomyces and differs in that the centrum pseudoparenchyma has no pit connections; ascospore appendages do not terminate in a spade-like structure; and it can be found on dead coral rocks (Volkman-Kohlmayr and Kohlmeyer, 1992). The genus should be examined at the molecular level to determine if it is distinct from Arenariomyces (Jones et al., 1983a).


Anamorph: Varicosporina angulosa Abdel-Wahab & Nagah.


Fig. 44. Scanning electron micrographs of halosphaeriaceous ascomycetes. a. Ceriosporopsis tubulifera. b. Remispora crispa. c. Saagaromyces abonnis (Photo by Theresa Baker). d. Tirispora unicaudata. Bars a-c = 5 µm, d = 10 µm.

Anamorph: *Varicosporina prolifera* Nakagiri

*Peritrichospora lacera* Linder, Farlowia 1: 415, 1944.
Anamorph: *Halosigmoidea luteola* Nakagiri & Tubaki.
*Peritrichospora integra* Linder, Farlowia 1: 414, 1944.


Ascomata globose or subglobose, superficial, erumpent, subiculate, ostiolate or lacking ostioles, papillate or epapillate, carbonaceous, pale brown to black, catenophyses deliquescing, asci fusiform or subclavate, apiculate, short pedunculate, unitunicate, thin-walled, lacking an apical apparatus, deliquescing, ascospores various fusiform, subellipsoidal, constricted at the septum, 1-14-septate, muriform with longitudinal and trans-septa, hyaline to pale brown to dark brown, with appendages. Two types of appendages: polar spine-like appendages arising as outgrowths of the mesosporium and episporeium and secondary fine hair-like appendages formed by fragmentation of the exosporium (Jones et al., 1983a) (Figs. 45a-d). Delineation of species has been largely based on ascospore measurements, possession of polar spines and nature of the appendages (Prasannarai et al., 2000). However, Nakagiri and Tubaki (1986) also demonstrated significant differences in ascomatal wall structure, number of cell wall layers and especially the columnar-like cells in the outer layer (Sundari et al., 1996; Hsieh et al., 2007).

Species are common sand dwelling fungi, forming a cohesive morphological group, and well supported by molecular data (Campbell et al., 2002). No distinct taxonomic groups can be discerned within the genus, which is probably paraphyletic, and continuously evolving. However, recent analysis of molecular data suggests the genus may comprise two well-defined groups (Jones et al., 2009; unpublished data). Corollospora species have anamorphs from three different genera: Clavatospora, Halosigoidea and Varicosporina.

Campbell et al. (2002) provided a sequence of Corollospora sp. isolated from material collected in South Africa (Steinke and Jones, 1993). This is sufficiently different from other Corollospora species to warrant the erection of a new species, which is proposed here.

Corollospora baravispora  Steinke & E.B.G. Jones, sp. nov. ..........................Fig. 45d. Mycobank:MB513019

Ascomata globose or subglobose, superficial, nigra, carbonacia, solitaria vel gregaria, ostiulata, papillata, subiculata. Subiculum texturam angularem formans. Centrum ascomatica immutari cellulis pseudoparenchymaticis, hyalinis, leptodermis, foveolatis, deliquescentibus. Paraphyses nullae. Ascii octospori, ellipsoides, unitunicati, mox deliquescentes. Ascosporeae 36-40 × 18-22 μm, fusiformes, 1-septatae, ad septa leviter constriictae, brunei. Appendices bigeneres: (i) appendices polares, spiniformes, 10-15 μm longae, 1-2 μm diam. (ii) appendices circa septum centralem 10-12 μm longae, peritrichiatae, per fragmenta exospororum effectae et appendices apicales 4-6 μm longae.


Holotype: culture PP6266, Sequence AF 491263, Fig. 45d.

Etymology: from the Polynesian “baravi” = beach, and spora, in reference to its habitat.


1. Ascospores light to dark brown ............................ 2
   1. Ascospores hyaline ....................................... 7

2. Ascospores 1-or more-septate, no trans-septa........ 3
   2. Ascospores with trans-sept.............................. 6

3. Ascospores with polar spines.............................. 4
   4. Ascospores wider than 10 μm, 1-septate, 36-40 × 18-22 μm, pale brown ......................... C. baravispora
   5. Ascospores narrower than 10 μm ....................... 5

   4. Ascospores 1-septate, 18-25 × 6-9 μm, dark ........
      ........................................................................ C. cinnamomea
5. Ascospores 1-septate, 27-32 × 8-9 μm, brown........... C. portaisica
6. Ascospores 63-220 × 20-38 μm, 12-21 trans-septa, polar appendages 25-75 μm .......... C. fusca
6. Ascospores 74-99 × 24-34 μm, 13 trans-septa, polar appendages 52-86 μm .......... C. novofusca
7. Ascospores 1-septate..................................... 8
7. Ascospores with more than 1-septate.................. 10
8. Ascospores wider than 8 μm, 22-33 × 8-10 μm, polar appendages................................. C. marinim
8. Ascospores narrower than 8 μm........................ 9
9. Ascospores 18-30 × 3-4 (-5), polar appendages 4-7 μm with Varicosporina anamorph .......... C. angulsa
9. Ascospores 26-45 × 3-7 μm, polar appendages 6-5-12 μm................................. C. gracilis
10. Ascospores with 3-septate.............................. 11
10. Ascospores with more than 3-septate............... 13
11. Ascospores wider than 7 μm............................ 12
11. Ascospores narrower than 7 μm wide, 35-57 × 3-7.5 μm, polar appendages 3-8 μm .......... C. angusta
12. Ascospores 29-44 × 6-5-8.5 μm, polar appendages 9-13 μm ........................................ C. armoricanana
12. Ascospores 25-34 × 7-12 μm, polar appendages 10-14 μm ........................................ C. intermedia
13. Ascospores with polar appendage ...................... 18
13. Ascospores without polar appendages .............. 14
14. Ascospores 5-septate, 50-85 × 5-8 μm .......... C. luteola
14. Ascospores with more than 5-septate............... 15
15. Ascospores predominately 7-septate................. 16
15. Ascospores with more than 7-septate............... 17
16. Ascospores 60-108 × 13-26 μm ..................... C. colossa
16. Ascospores 52-112 × 7-16 μm ...................... C. pulchella
17. Ascospores 7-11-septate, 65-98 × 8-12 μm ............... C. pseudopulchella
17. Ascospores 13-septate, 73-120 × 5-8 μm .............. C. filiformis
18. Ascospores 3-5-septate................................. 19
18. Ascospores over 5-septate.......................... 20
19. Ascospores 39-63 × 10-19 μm, polar appendages 10-14 μm ................................. C. lacera
19. Ascospores 38-59 × 8-10 μm, polar appendages 5-12 μm ................................. C. quinqueseptata
20. Ascospores 7-8-septate, 100-163 × 25-38 μm, polar appendages 10-38 μm .................. C. besarispora
20. Ascospores 3-12-septate, 45-102.5 × 7.5-17.5 μm, polar appendages 12-25 μm .......... C. indica

*Cuculosporella* K.D. Hyde & E.B.G. Jones, Mycotaxon 37: 200, 1990 ......................... (1)


Ascomata subglobose, ovoid or ellipsoidal, immersed, ostiolate, papillate, greyish brown to black, solitary or gregarious, periphysate, catenophyses present, asci clavate, pedunculate, uniloculate, thin-walled, thickened at the apex with a lens-shaped refractive region, persistent, ascospores fusoid to ellipsoidal, 1-septate, not constricted at the septum, hyaline with polar appendages (Hyde and Jones, 1986a). This genus, along with *Halosarphiea*, has bipolar unfurling appendages, but differs from it in that the appendages comprise two components, bundles of fibrillar material in an amorphous matrix (Figs. 43c, d). Molecular sequences and morphological observations confirm that this genus is distinct from other ascomycetes with bipolar unfurling appendages (Alias et al., 2001) (Fig. 41).

Haligena Kohlm., Nova Hedw. 3: 87, 1961 (1)

■ *H. elaterophora* Kohlm., Nova Hedw. 3: 87, 1961 (Type species).

Ascomata globose or ovoid, immersed or superficial, ostiolate, papillate or epapillate, coriaceous or subcarbonaceous, black, solitary or gregarious, periphysate, catenophyses deliquescing, asci clavate, apiculate, pedunculate, uniloculate, thin-walled, lacking an apical apparatus, early deliquescing, ascospores oblong ellipsoidal, 3-5-septate, constricted at the septa, hyaline, with polar appendages (Figs. 49a-e). Appendages initially wrapped around the ascospores but separates to form long strap-like appendages (Johnson et al., 1987).

This is a genus that has undergone several revisions with species referred to other genera: *Appendichordella* (Johnson et al., 1987), *Magnisphaera* and *Ascosalsum* (Oceanitis), largely based on the morphology and ultrastructure of the ascospore appendages (Campbell et al., 2003; Dupont et al., 2009). Molecular data indicate *H. elaterophora* is
well placed in the Halosphaeriales but it is not monophyletic. *Haligena salina* has therefore been transferred to a new genus *Morakotiella* (Sakayaroj et al., 2005a) (Fig. 41).


Ascocoma globose, subglobose, obpyriform, ellipsoidal, immersed to superficial, ostiolate, papillate, coriaceous, pale brown to black, catenophyses deliquescent, necks variable in length, periphysate, asci clavate, pedunculate, unitunicate, thin-walled, retraction of the plasmalemma apically in some species, no apical apparatus, persistent, ascospores broad-ellipsoidal, 1-septate, not constricted at the septum, with apical appendages, initially closely adpressed to the spore wall (hamate) later separating and uncoiling to form long polar thread-like, sticky appendages (Kohlmeyer and Kohlmeyer, 1977) (Figs. 43e, 46). Kong et al. (2000) were the first to draw attention to the polyphyletic nature of this genus, and this has been subsequently supported by other studies (Anderson et al., 2001).

Although all species have bipolar unfurling appendages they differ greatly in other characters. For example, degree of ascospore septation; wall ornamentation (Jones and Moss, 1978, reported a highly verrucose wall for *H. spartinae*); shape of the ascus; length of the ascus pedicle; deliquescent or persistent asci; asci with or lacking an apical pore; presence of catenophyses, and thickness of the ascoma wall (Jones, 1995). Molecular data suggest that the genus was in need of division but care must be exercised as the genus has many overlapping features with *Aniptodera*, but few species of that genus have been sequenced to date. Paraphyly of the genus must also not be ignored (Mitchell, pers. comm.). As the result of molecular studies (Abdel-Wahab et al., 1999, 2001b; Campbell et al., 2003; Pang et al., 2003a,b; Pang and Jones, 2004) a number of *Halosarpehia* species have already been transferred to new genera. No anamorphs have been reported for the marine *Halosarpehia* species, however Anderson and Shearer (2002) report a *Trichocladium* anamorph for the freshwater species *Halosarpehia heteroguttulata.*
Halosarpheia sensu stricto


1. Ascospores unisegmented. 
   1. Ascospores 1-septate. 
   2. Ascospores 25-32 μm. .......... **H. fibrosa**

Halosarpheia sensu lato


The position of **H. bentotensis**, **H. culmiperda**, **H. kandeliae**, **H. marina**, **H. minuta** and **H. phragmiticola** remains unresolved. In a number of cases cultures of these species are not available for a molecular study. Until such data is available, it is pointless to speculate as to their future assignment at the generic level.

1. Ascospores 3-septate, 28-36 × 6-8 μm. ............. **H. bentotensis**
2. Ascospores less than 15 μm long (10-14 × 4-6 μm)........... **H. minuta**
3. Species on wood .............................................. 4
4. Species on other substrata................................. 5

4. Ascospores 18-23 (-26) × 9-12 μm, ascus with short pedicel, appendages cap-like, then filamentous...........
5. Ascospores 12-21 × 4-7.5 μm, ascus with a long pedicel, appendages well developed...... **H. marina**
6. Ascospores 25-32 μm on Juncus......................... **H. culmiperda**
7. Ascospores 25-35 × 7.5-10.5 μm, on Phragmites...... **H. phragmiticola**
8. Ascospores 18-23 (-26) × 9-12 μm, ascus with short pedicel, appendages cap-like, then filamentous...........

We accept the species keyed out above as **Halosarpheia sensu stricto** species, however, the remaining must await further studies at the molecular level. **Halosarpheia kandeliae** differs from many of the **Halosarpheia** species in having asci with long drawn out stalks (tail-like). Species with similar ascospore measurements have asci with short pedicels. Another unusual feature of **H. kandeliae** is the polar appendages initially appears amorphous and only later forms the characteristic thread-like bipolar appendages (Abdel-Wahab et al., 1999). Although ascospore measurements of **Halosphaeria culmiperda** are similar to those of **H. viscosa**, it differs in ascus morphology. Asci of **H. culmiperda** are similar with those of the **H. fibrosa** group in that they are persistent, clavate to oval, with a pore, and a stalk one third of the ascus length.

Species transferred to other genera:

- **H. abonnis**, **H. ratnagiriensis** to Saagaromyces
  - K.L. Pang & E.B.G. Jones
- **H. spartinae** to Magnisphaera J. Campb., J.L. Anderson & Shearer
- **H. cincinnatula**, **H. unicaudata** and **H. viscidula** to Oceantitis J. Kohlm (Ascosalsum J. Campb., J.L. Anderson & Shearer)
- **H. retorquens** and **H. lotica** to Natantispora J. Campb., J.L. Anderson & Shearer
- **H. viscosa** to Panorbis J. Campb., J.L. Anderson & Shearer
- **H. aquatica** and **H. heteroguttulata** to Ascosaccus J. Campb., J.L. Anderson & Shearer, both freshwater species.
H. appendiculata Linder, Farlowia 1: 412, 1944 (Type species).

Ascomata globose or subglobose, ellipsoidal, immersed erumpent, ostiolate, papillate, coriaceous or membranous, pale to dark brown to black, solitary or gregarious, catenophyses deliquescing, asci clavate or subfusiform, pedunculate, unitunicate, thin-walled, deliquescing early, ascospores ellipsoidal, 1-septate, hyaline, with 3-4 spoon-shaped equatorial appendages and one at each end of the spore. Ultrastructure of the appendages have been elucidated by Jones et al. (1984).

Kohmeyer (1972a) referred 12 species to this genus but subsequent studies have assigned them to other genera:

H. cucullata to Okeanomyces K.L. Pang & E.B.G. Jones
H. quadricornuta to Antennospora Meyers
H. salina to Haiyanga K.L. Pang & E.B.G. Jones
H. mediosetigera to Halosphaeriopsis T.W. Johnson
H. maritima, H. pilleata, H. quadri-remis, H. stellata to Remispora Linder
H. trullifera to Halosarpheia Kohlm. & E. Kohlm.
H. circumvestita to Lautisporopsis E.B.G. Jones, Yusoff & S.T. Moss
H. torquata to Ondiniella E.B.G. Jones, R.G. Johnson & S.T. Moss

Currently only one species is accepted in the genus (Pang et al., 2004b; Sakayaroj et al., 2005a).


Anamorph: Trichocladium achrasporum (Meyers & R.T. Moore) Dixon

Ascomata subglobose or ellipsoidal, immersed or erumpent, ostiolate, papillate, subcarbonaceous, dark brown to black, solitary or gregarious, asci clavate, pedunculate, unitunicate, thin-walled, lacking an apical apparatus, deliquescing early, ascospores ellipsoidal or subfusiform, 1-septate, slightly constricted at the septum, hyaline with a small apical appendage and 3-4 crescent-shaped equatorial appendages. Appendages formed by the fragmentation of an exosporic sheath (Moss and Jones, 1977; Jones et al., 1984). A monotypic genus well placed in the Halosphaeriales and supported by both morphological and molecular evidence (Spatafora and Blackwell, 1994; Sakayaroj et al., 2005a) (Fig. 41).


Ascomata globose to subcylindrical, immersed, ostiolate, papillate, membranous or coriaceous, dark brown to black, periphysate, catenophyses, asci clavate to ellipsoidal, short pedunculate, thin-walled, unitunicate, no apical apparatus, deliquescing early, ascospores ellipsoidal, 1-septate, slightly constricted at the septum, hyaline with appendages at both ends of the spore. Appendages are obclavate, curved, attenuate and observed to release a drop of mucilage from their tips (Fig. 43g) (Zainal and Jones, 1984). In H. salina the appendages are outgrowths of the spore and attached to the mesosporium by an isthmus of electron-dense material. At the TEM level electron-dense striations run the entire length of the appendage, these are confined to the outer layer of the spore while the core appears amorphous (Yusoff et al., 1994c).

Haiyanga salina is distantly related to Antennospora quadricornuta and Halosphaeria appendiculata, but well placed in the Halosphaeriales (Figs 41, 47). Haiyanga salina, instead of clustering with Antennospora quadricornuta (a genus it was most recently assigned to), forms a moderately-supported group with two isolates of Arenariomyces trifurcatus (Fig. 47). However, the two genera differ in their habitat, nature of the ascomata and most strickling in the origin and
ultrastructural detail of the appendages. Morphological data also support the erection of a new genus for this species, especially the ultrastructure and ontogeny of the ascospore appendages (Pang et al., 2008b). Ascospore appendages of Haiyanga salina are also similar to those of Remispora species, especially R. stellata and R. quadriremis.

**Havispora** K.L. Pang & Vrijmoed, Mycologia 100: 293, 2008 ............................................. (1)


Ascomata subglobose to ellipsoidal, immersed, coriaceous, solitary or gregarious, lacking paraphyses, catenophyses present deliquescing, long necks, asci clavate, pedunculate, unirnicate, thin-walled, persistent, ascospores ellipsoidal, hyaline, thin-walled, 3-septate, constricted at the septa, with tufts of appendages (Pang et al., 2008a).

Appendages polar and four at the central septum, string-like composed of intertwining strands (Fig. 53b). A new genus described from material collected at Longyearbyen, Norway on driftwood and characterized by the ellipsoidal thin-walled ascospores, 24-(30)-36 × 8-(11)-14 μm with tufts of polar and equatorial appendages initially string-like and composed of intertwining strands that separate in seawater (Pang et al., 2008a). The tufts of polar and equatorial appendages in Havispora resembles those of the genera Nautosphaeria and Nereiospora. However the ascospores of *N. cristaminuta* are unicellular while Nereiospora species have ascospore with brown central cells. *Nereiospora cristata* has Monodictys pelagica as its anamorph (Mouzouras and Jones, 1985). The molecular result indicates clearly that this genus is well placed in the Halosphaeriales. It is phylogenetically nestled in the *Nereiospora* and Monodictys clade, although with low bootstrap support (Fig. 41).

**Iwilsoniella** E.B.G. Jones, Syst. Ascomycetum 10: 8, 1991 ................................................... (1)

🔺 **I. rotunda** E.B.G. Jones, Syst. Ascomycetum 10: 8, 1991 (Type species).

Ascomata subglobose, immersed to superficial, ostiolate, papillate, membranous, dark brown, solitary or gregarious, no catenophyses, asci clavate, short pedunculate, lacking an apical pore, unirnicate, thin-walled, deliquescing early, ascospores round, unicellular, hyaline without a visible sheath.

However, at the scanning electron microscope level a sheath is apparent peeling away from the spore wall. It sporulates in culture on cornmeal seawater agar. It was described from a test block exposed in a water cooling tower with brackish water circulating...
hyaline, round, one-celled ascospores lacking appendages and deliquescing asci. This genus requires further study to determine if it is correctly assigned to the Halosphaeriales (Jones, 1991).


Ascomata subglobose, ovoid, ostiolate, papillate, immersed to superficial, light to dark brown, coriaceous, solitary or gregarious, catenophyses, asci clavate, pedunculate, unitunicate, thin-walled, no apical apparatus, deliquescing early, ascospores ellipsoidal, 1-septate, slightly constricted at the septum, hyaline with a mucilaginous sheath extended to form equatorial and polar appendages (Fig. 43b). A monotypic genus with the transfer of *Ceriosporopsis circumvestita* to this genus based on a scanning and transmission electron microscope studies of ascospore appendage ontogeny (Yusoff et al., 1994a).


Ascomata subglobose to ellipsoidal, immersed to superficial, ostiolate, papillate, coriaceous, light brown to black, catenophyses deliquescing, asci clavate or subfusiform, pedunculate, unitunicate, thin-walled, persistent, apiculate, asci released from the ascoma through the neck, ascospores ellipsoidal, 1-septate, hyaline, lacking appendages (Pang et al., 2003a). The genus *Lignincola* has only one unifying character, the hyaline, 1-septate ascospores, lacking appendages. *Lignincola longirostris* with an ascus with an apical pore and retraction of the plasmalemma has been transferred to the new genus *Neptunella* (Pang et al., 2003a). Clearly *L. tropica* does not belong in the genus either, but lack of a consensus on the morphology of its ascus prevents its transfer to a new genus (Kohlmeyer, 1984; Kohlmeyer and Volkmann-Kohlmeyer, 1988a) (Fig. 41). Originally the ascus was described as possessing an apical pore (Kohlmeyer, 1984), but subsequently Kohlmeyer and Volkmann-Kohlmeyer (1988a) revised the description to exclude taxa with an apical ascus pore from the genus. Molecular data show no affinity between *L. tropica* (ascus with an apical pore) and the type species, consequently it should be transferred to a new genus (Pang et al., 2003a). We have been unable to obtain fresh material of *L. tropica* (with no apical pore), therefore reassignment must await further molecular studies. *Lignincola nypae* clearly does not belong in this genus but is left here for the present until fresh material is collected, isolated and sequenced.

1. Ascospores ellipsoidal .................................................. 2
2. Ascospores 1. Ascospores cylindrical .................................. *L. nypae*
   22-36 × 12-16 μm, thick-walled. .................. 2
   1. Ascospores 12-24 × 5-8 μm, thin-walled..... *L. laevis*


Ascomata deeply immersed in wood, pale brown, ostiolate, long necks, no periphyses, asci clavate, tapering, pedunculate, unitunicate, thin-walled, deliquescing early, interthecial filaments present, ascospores 1-0-septate, hyaline, with a mucilaginous sheath.

Originally described as *Ceriosporopsis sundica*, but segregated to a new genus based on ultrastructural characters, primarily the ontogeny of the ascospore appendages (Jones et al., 1995).

The polar appendages are extensions of the sheath and not discrete mesosporal outgrowths characteristic of the genus *Ceriosporopsis*. Its relationship with *Ceriosporopsis, Marinospora* and *Bovicornua*, requires evaluation at the molecular level.
**Luttrellia** Shearer, Mycologia 70: 692, 1978 ...

...................................................................... (1)

**L. estuarina** Shearer, Mycologia 70: 693, 1978 (Type species).

Ascomata superficial, globose to sub-globose, membranous, becoming pale brown, ostiolate, neck long, cylindrical hyaline and periphysate. Asci clavate to cylindrical, thin-walled and deliquesce. Cataphyses present. Ascospores hyaline, multiseptate and lacking appendages. There is no known ana-morph. The only genus in the Halosphaeriales.
with tetraspore asci. Saprophytic on wood. An infrequently collected species and its position in the Halosphaeriales requires verification.

**Magnisphaera** J. Campb., J.L. Anderson & Shearer, Mycologia 95: 546, 2003 ............. (1)

- **M. spartinae** (E.B.G. Jones) J. Campb., J.L. Anderson & Shearer, Mycologia 95: 547, 2003 (*Type species*).


Ascomata globose to subglobose, immersed, ostiolate, papillate, dark brown to black, thick-walled, periphysate, solitary or gregarious, asci clavate, pedunculate, unitunicate, thin-walled, deliquescent early, ascospores ellipsoidal to fusiform, hyaline, 4-9-septate (generally 5), constricted at the septa, with polar appendages, initially closely adpressed to the spore wall, then separating and uncoiling to form long thread-like appendages (Fig. 48c). A new genus erected as the result of a re-evaluation of the genus *Halosarpheia*

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**Fig. 48.** Scanning electron micrographs of selected ascomycetes with polar unfurling appendages. a, b. *Oceanitis cincinnatula*. c. *Magnisphaera spartinae*. e. *Natantispora retorquens*. d, f. *Oceanitis unicaudata*. Bars a, c = 10 µm, b, d-f = 2 µm.
distinguished by its broadly acerose, septate ascospores, constricted at the septa, with a verrucose spore wall, polar appendages arising from a pore and supported by 18S rDNA sequence data (Campbell et al., 2003) (Fig. 41).

**Marinospora** A.R. Caval., Nova Hedw. 11: 548, 1966...................................................... (2)

- **M. calyptrata** (Kohlm.) A.R. Caval., Nova Hedw. 11: 548, 1966 (Type species).

Ascomata ellipsoidal, subglobose, immersed, ostiolate, papillate, subcarbonaceous or subcoriaceous, light brown to black, periphysate, solitary or gregarious, catenophyses deliquescing, asci clavate, unitunicate, thin-walled, no apical apparatus, deliquescing early, ascospores broadly ellipsoidal, 1-septate, constricted at the septum, hyaline, with equatorial and polar appendages: a single appendage at each pole, and 4 radiating appendages at the central septum. Primary appendage an outgrowth of the mesosporium and episporium, with a fragmenting exosporic sheath forming tiny caps to the tips of the primary appendages (Johnson et al., 1984).

These species were initially referred to *Ceriosporopsis*, but subsequently transferred to *Ceriosporella* and finally *Marinospora*. Sequence data confirm that the genus is distinct from *Ceriosporopsis*, although closely related (Sakayaroj et al., 2004) (Fig. 41). Morphologically its polar and equatorial appendages are distinctive with the cup-like exosporic remnants at their tips (Johnson et al., 1984). *Marinospora longissima* has been regarded as a synonym of *M. calyptrata* (Kohlmeyer and Kohlmeyer, 1979), but molecular data indicate they are distinct species (Fig. 41).

1. Ascospores 20-34 × 8-18 μm, with longer polar appendages to equatorial appendages. *M. longissima*...
the degree of ascospore septation, the ontogeny of the polar appendages and ascoma structure (Sakayararo et al., 2005a).

**Nais** Kohlm., Nova Hedw. 4: 409, 1962. (1)

- **N. inornata** Kohlm., Nova Hedw. 4: 409, 1962 (Type species).

Ascomata subglobose, immersed to superficial, ostiolate, papillate, coriaceous, dark brown to black, gregarious, long necks (100-620 µm), periphysate, catenophyses present, asci clavate, short pedunculate, unitunicate, thin-walled, no apical apparatus, deliquescing early, ascospores broadly ellipsoidal, 1-septate, slightly constricted at the septum, hyaline, lacking appendages or a sheath. A genus characterized by hyaline bicelled ascospores with a characteristic arrangement of the internal wall ornamentation along the septum where small oil globules aggregate and lacking appendages. It is inferred from phylogenetic analysis of the partial large subunit ribosomal DNA sequences to be closely related to *Aniptodera*, forming a moderately supported monophyletic group with a bootstrap value of 89% (Pang et al., 2003a) (Figs. 41, 47, 55). Two further species have been described: *N. glitra* now transferred to *Saagaromyces* and a freshwater species *N. aquatica*. The latter differs from *N. inornata* in that ascospores develop appendages on release from the ascomata (Hyde, 1992d).

**Natantispora** J. Campb., J.L. Anderson & Shearer, Mycologia 95: 543, 2003. (2)


- **N. retrorquens** (Shearer & J.L. Crane) J. Campb., J.L. Anderson & Shearer, Mycologia 95: 543, 2003 (Type species).

**Halosarpehia lotica** Shearer, Mycotaxon 20: 505, 1984.

**N. retrorquens** (Shearer & J.L. Crane) J. Campb., J.L. Anderson & Shearer, Mycologia 95: 543, 2003 (Type species).


Ascomata globose, immersed to superficial, ostiolate, papillate, membranous, black, long neck, periphysate, catenophyses present deliquescing, asci clavate, short pedunculate, unitunicate, thin-walled, with an apical pore and retraction of the plasmalemma at the tip of the ascus, deliquescing early, ascospores fusiform to ellipsoidal, 1-septate, hyaline with a hamate appendage initially closely adpressed to the spore wall, separating and unraveling to form long drawn out thread-like polar appendages (Fig. 48e). Campbell et al. (2003) segregated these two species from *Halosarpehia* based on sequence data, although distinguishing morphological features at the generic level are not well established. From combined 18S and 28S sequences *Natantispora* species are distinctly placed from *Halosarpehia sensu stricto* (Figs. 41, 47) (Abdel-Wahab et al., 2001b).

1. Ascospores 26-38 × 10-14 µm, appendages not extending to the middle septum ............... *N. lotica*

1. Ascospores 20-33 × 7-11 µm, appendages extend beyond the middle septum .................... *N. retrorquens*


Ascomata subglobose, immersed or superficial, ostiolate, papillate, coriaceous, cream-coloured, solitary or gregarious, neck periphysate, catenophyses, asci clavate, pedunculate, unitunicate, thin-walled, early deliquescing, no apical apparatus, ascospores ellipsoidal, 1-septate, not constricted at the septum, hyaline, with two types of appendages.

Polar gelatinous appendages covering the apical region and along one side of the spore, becoming strap-like or forming a wide band; second type subpolar, a fragmenting gelatinous sheath forming a crown of hair-like filaments born on flat cushions. *Naufragella* species are frequently difficult to distinguish from *Remispora*. Mounted in seawater, two types of appendages can be discerned: 1) Gelatinous strap-like polar appendages with faint striations, initially covering the apices and one side of the ascospores but swelling in water and separating from the side of the spore and extending to 90 µm long; and 2) Sub-polar hair-like appendages arising from a small flat cushion and spreading out in water (Koch, 1989).
The origin of these appendages has not been elucidated. The appended ascospores of *Nohea umiumi* superficially resemble those of *Naufragella*, but differ in that in the former ascospores have two thick gelatinous appendages attached to one side of the spore and two tufts of subapical fibres on the other side (Kohlmeyer and Volkmann-Kohlmeyer, 1998a). Molecular data show that *Naufragella* is distantly related to *Remispora* (Fig. 41).

Morphologically the two *Naufragella* species are very similar and differ only slightly in ascospore measurements, which overlap, and in the nature of the apical appendages. *Naufragella delmarensis* is probably a synonym of *N. spinibarbata*, but sequence data are required for these two rare species before this is formally proposed (Koch, pers. comm.).

1. Ascospores 18.5-21 × 8-9.5 μm, with striated apical appendages..............................................*N. delmarensis*

1. Ascospores 18-26 × 8-12 μm, with smooth apical appendages..............................................*N. spinibarbata*


Ascomata globose to subglobose, immersed, ostiolate, papillate, coriaceous, hyaline to pale brown, solitary or gregarious, catenophyses deliquescing, asci clavate to ellipsoidal, short pedunculate, unitunicate, thin-walled, lacking an apical apparatus, deliquescing early, ascospores ellipsoidal, unicellular, hyaline, with tufts of bristle-like appendages apically at the spore equator. Sakayaruj et al. (2004) confirmed the assignment of this genus within the Halosphaeriales based on partial 28S rDNA sequences which grouped with *Haligena elaterophora* and *Remispora galerita* (Fig. 41).
However, there is no homology between appendage ontogeny in these genera. The hair-like appendages in *Nereiospora* are similar to those of *Nereiospora* species, however the latter are 3-5-septate, central cells brown with hyaline to pale ends cells. Phylogenetically they are not related (Sakayaroj et al., 2004).


  Ascomata subglobose, immersed to erumpent, ostiolate, with long necks (80-1125 μm), membranous, hyaline, pale to brown, solitary or gregarious, no periphyses or paraphyses, asci cylindrical-clavate, ellipsoidal-clavate, short pedunculate, unitunicate, thick-walled apically, with retraction of the plasmalemma at the apex, apical pore, persistent to deliquescing, 1-septate, asci with retraction of the plasmalemma at the apex, apical pore, persistent to deliquescing, 1-septate, slightly constricted at the septum, no sheath or appendages (Figs 41, 55).

  Assignment of this species with its hyaline, bicelled ascospores lacking appendages has proved difficult, initially referred to *Gnomonia*, then *Lignincola*, but differing from the type species *L. laevis* in ascus morphology. Sequences of the large subunit rRNA gene, indicates that *Lignincola laevis* and *L. longirostris* have a close relationship, but they are not monophyletic. *Neptunella* has therefore been erected for *L. longirostris* as it differs from *L. laevis* as follows: 1). asci with retraction of the plasmalemma, an apical thickening and pore; 2). an extra ascospore wall layer (the exosporium) is present; and 3). asci are persistent and do not get released through the ostiole, as in *L. laevis*. Thus there is morphological and molecular evidence to separate these two taxa (Pang et al., 2003a).


  Anamorph: *Monodictys pelagica* (T.W. Johnson) E.B.G. Jones

  Ascomata subglobose or ellipsoidal, immersed or superficial, with or without ostioles, papillate or epapillate, carbonaceous, black, solitary or gregarious, centrum cells deliquescing, asci broadly fusiform or clavate, pedunculate, unitunicate, thin-walled, lacking an apical apparatus, deliquescing early, ascospores 3-5-septate. Constricted at the septa, central cells brown, end cells hyaline, with tufts of hair-like appendages apically and at the central septum. Jones et al. (1983a) erected the genus to accommodate species with polar and equatorial appendages that are ontogenetically distinct from those of *Corollospora*.

In the study by Campbell et al. (2002) *Nereiospora* nests within the *Corollospora* clade. However, in a more extensive treatment of the Halosphaeriales, *Nereiospora* is distantly placed from *Corollospora* (Fig. 41). In *Nereiospora* appendages arise from the mesosporium, while in *Corollospora* they are spine-like and formed by outgrowths of the epi- and mesosporium, while the secondary appendages are formed by fragmentation of an exosporial layer (Jones et al., 1983a).

1. Ascospores 32-54 × 12-17 μm, with 5 septa...........................................N. comata

1. Ascospores 24-41 × 8-16 μm, with 3 septa...........................................N. cristata

**Nimbospora** Jørg. Koch, Nordic J. Bot. 2: 166, 1982.............................................................. (3)


Ascotamata globose to subglobose, ostiolate, papillate, membranous, hyaline, immersed, solitary or gregarious, necks periphysate, no paraphyses, asci clavate, short pedunculate, ununitec, thin-walled, deliquescent early, ascospores ellipsoidal, 1-septate, not constricted at the septum, hyaline, and appenedaged. Ascospores in Nimbospora have two types of appendages: a well developed exosporic mucilaginous sheath, and secondary fibrillar appenedaged at the spore equator that are formed as outgrowths of the mesosporium. These fibrillar appendages initially are contained within the sheath, but on spore release into water, the outer region ruptures and the appenedaged break through (Read et al., 1993a). Sequence data places the genus in the Halosphaeriales in a sister group to Aniptodera chesapeakensis and Nimbospora effusa (Campbell et al., 2002), while in a larger data set it nests in a sister group to Neptunella longirostris and is basal to a clade comprising a range of taxa (Fig. 41).

Kohlmeeyer and Volkmann-Kohlmeeyer (1991c) compare N. umiumi with the genera Halosarpeia (does not possess tufts of hair-like appendages), Nautospora (probably mean Nautosphaeria), Nimbospora and Nereiospora (all having tufts of hair-like appendages, but these lack the long unfurling appendages forming sticky filaments), and any resemblance is therefore superficial. Molecular data show no affinity between these genera (Fig. 41).

Oceanitis Kohlm., Rev. Mycol. 41: 193, 1977 ................................................................. (4)


Ascomata subglobose to ellipsoidal, on a thin hypostroma, ostiolate, epapillate, coriaceous, brown to dull orange, gregarious, paraphyses absent, asci clavate, unitunicate, thin-walled, without an apical apparatus, deliquescing, ascospores filiform to elongate fusiform, 1-11-septate, hyaline, with bipolar appendages or at one end of the spore (Figs. 48a, d, f). Appendages initially closely adpressed to the spore wall, separating, and uncoiling to form long thin narrow sticky threads. A genus initially described with needle-shaped, falcate, ascospores, 1-septate, hyaline with an appendage at one end and not collected since its description on trawled submerged wood at 3,975 m, in the Gulf of Angola, Atlantic Ocean (Kohlmeier, 1977).

A recent collection from submerged wood at 1,000 m in the Pacific Ocean off Vanuatu Islands has enabled further characterization of the genus (Dupont et al., 2009). Ascomata aggregated into a stroma, with a thick peridium, 200 μm wide, composed of polygonal cells with large lumina forming a textura angularis, merging towards the center into flattened cells. Ascii deliquesce early. The cavity of the ascomata are filled with fusiform ascospores, more or less grouped, 1-septate, hyaline with an appendage at one end and not collected since its description on trawled submerged wood at 3,975 m, in the Gulf of Angola, Atlantic Ocean (Kohlmeier, 1977).

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**Fungal Diversity**


Anamorph: *Periconia prolifica*

Anastasiou

Ascomata subglobose, ostiolate, papillate, coriaceous, immersed, brownish-black or brownish-red, solitary or gregarious, catenophyses deliquescing, asci clavate, short pedunculate, unitunicate, thin-walled, without an apical apparatus, deliquescing early, ascospores cylindrical, 1-septate, slightly constricted at the septum, hyaline, with a single cap-like or globose gelatinous appendage at one spore apex, and deciduous. Frequently, appendages not observed. A genus proposed by Pang et al. (2004b) to accommodate *Halosphaeria cucullata* based on a recent collection of the fungus in Malaysia. No ascospore appendage was observed in any of the material examined but the characteristic reddish ascomata and the production of the anamorph *Periconia prolifica* from single ascospore isolates confirmed its identity. LSU rDNA phylogeny revealed that this fungus is not related to *Halosphaeria appendiculata*, but is not monophyletic with it. They form a sister group to *Ascosacculus* (Fig. 55).


*Halosphaeria torquata* Kohlm., Nova Hedw. **2**: 311, 1060.

Ascomata elongate-cylindrical or subglobose, immersed or superficial, ostiolate, papillate, membranous, ranges from hyaline to pale brown, necks short and cylindrical, no periphyses, catenophyses deliquescing, asci clavate to subfusiform, apiculate, pedunculate, unitunicate, thin-walled, no apical apparatus, deliquescing, ascospores broadly ellipsoidal, 1-septate, slightly constricted at the septum, hyaline with appendages. Two types of appendages: spine-like polar appendages and an annulus-like equatorial appendage, arising as outgrowths of the episporium, with amorphous material within the appendages and lacking an exosporium (Jones et al., 1984). A cold water species. Isolates were examined for their phylogenetic relationship. The LSU rDNA phylogeny revealed that this genus is not related to *Halosphaeria* (Kohlmeyer, 1972a), but closely related to *Ceriosporopsis tubulifera* and *Marinospora* species (Fig. 41).


Ascomata ellipsoidal, immersed under a thin black stroma, ostiolate, papillate, light brown, solitary or gregarious, necks long (60-300 µm long) and periphysate, asci clavate, pedunculate, unitunicate, thin-walled, deliquescing early, lacking an apical apparatus, ascospores ellipsoidal, 1-septate, not constricted at the septum, hyaline, with a single polar appendage, initially hamate, separating from the spore wall and eventually uncoiling to form long, sticky filaments. *Ophiodeira* is a monotypic genus that is reminiscent of *Halosarpheia* species with its single polar appendage uncoiling to form sticky filaments. It differs from the genera with unfurling polar appendages in that the ascomata are formed beneath a thin stroma, has deliquescing asci, absence of catenophyses and with only a single polar appendage (Kohlmeyer and Volkmann-Kohlmeyer, 1988a). At the molecular level it forms a sister clade with *Halosarpheia*-like species with a single polar appendage: *O. scuticella*, *O. cincinnatula*, *O. unicaudata* and *O. viscidula* with bipolar appended ascospores (Dupont et al., 2009) (Figs 47, 55).

The only feature separating it from these taxa is that the ascomata are formed beneath a thin stroma (applies also to *O. scuticella*). Tang et al. (2007) have highlighted the congruence between morphological and molecular classification schemes and this is becoming a common observation in phylogenetic studies (Binder et al., 2006).

Appendages such as those of *O. scuticella* and *Ophiodeira monosemeia* that do not appear to readily uncoil in water, have been observed for other taxa and may be attributed to their degree of maturation or the media they are mounted in. In *Aniptodera salsuginosa*, the
salinity of the water markedly affects the unfurling of the polar appendages (Nakagiri and Ito, 1994), while in a freshwater *Halosarphoeia* species, amorphous material was released, and connected to the spore by a fine thread, prior to its organization into filaments (Jones, 2006).

**Panorbis** J. Campb., J.L. Anderson & Shearer, Mycologia 95: 544, 2003 .............................. (1)  


Ascomata globose, ostiolate, papillate, membranous, immersed or superficial, black, neck with periphyses, catenophyses deliquescent, asci clavate, unitunicate, thin-walled, deliquescent, with an apical pore, ascospores cylindrical to fusiform, 1-septate, hyaline, with bipolar appendages. Appendages closely adpressed to the spore wall, separating, and uncoiling to form long sticky thread-like filaments. *Panorbis viscosus* resembles *Natantispora* reto'riquens morphologically although they are not related phylogenetically (Campbell et al., 2003) (Fig. 47). However it is morphologically not well delineated from *Natantispora*, the key provided merely separating them on ascospore shape and measurements: ellipsoid (less than 25 µm) in the former and dufoid-ellipsoid (over 25 µm) in the latter. More genera with polar unfurling appendages need to be sequenced to determine the validity of this genus.

**Pseudolignincola** Chatmala & E.B.G. Jones, Nova Hedw. 83: 225, 2006. ............................. (1)  

Anamorph: *Humicola siamensis* Chatmala & E.B.G. Jones

Ascomata globose, dark brown, deeply immersed in the wood, coriaceous, with a long (710-1100 µm) periphysate neck, solitary, catenophyses present, asci clavate to slightly cylindrical, long pedicellate, unitunicate, thin-walled, truncate at the apex with a refractive thickening and retraction of the plasmalemma at the apex, ascospores cylindrical, 1-4-septate, hyaline, smooth-walled, lacking a sheath or appendages. Described from wood collected in Thailand, it has clavate asci with a truncated thickened apex, a pore, the ascus plasmalemma is retracted and ascospores are 1-4-septate, hyaline, cylindrical and lacking appendages (Fig. 50) (Jones et al., 2006). This ascomycete is morphologically similar to *Lignincola* *nypae*, but differs in the dimensions of ascomata, asci, 1-4-septate ascospores and with a *Humicola* anamorph. Phylogenetically LSU sequences place it in an unsupported clade with *Antennospora*, *Cucullosporella*, *Halosarphoeia* and *Lignincola* *tropical* (Figs 41, 47, 55).

**Remispora** Linder, Farlowia 1: 409, 1944... (8)  
- *R. maritima* Linder, Farlowia 1: 410, 1944 (Type species).


*Arenariomyces* *quadri-remis* (Höhnk) Meyers, Mycologia 49: 505, 1957.  


Ascomata globose, subglobose, ovoid, immersed or superficial, ostiolate, papillate, coriaceous, hyaline to dark brown, solitary or gregarious, catenophysate, necks periphysate, asci clavate broadly fusoid, pedunculate, apiculate, unitunicate, thin-walled, without an apical apparatus, deliquescent, ascospores 1-septate, ellipsoid to rhomboidal, hyaline, with polar appendages. Appendages morpho-
logically variable depending on the species (Figs. 51, 52a–c, e, 53a).

Molecular sequences indicate that *Remispora* is polyphylectic with *R. spitsbergenensis*, *R. pilleata*, *R. quadri-remis* and *R. stellata* forming a well supported clade, while the type species, *R. maritima* (Fig. 41) forms sister group with *R. pilleata* and *Carbosphaerella leptosphaerioides*. *Remispora crispa* and *R. galerita* are distantly placed (Fig. 41), the former grouping with *Ocostaspora apilongissima* and *Morakotiella salina*, while the latter forms a basal clade to the order with *Nautosphaeria cristaminuta* and *Haligena elaterophora*. *Remispora minuta* is a new species described from unidentified wood collected in Singapore and for which no molecular data is available (Pang et al., 2004a). The erection of new genera for *R. crispa* and *R. galerita* are warranted, but further isolates are required to prove their monophyly.

*Remispora* was described by Barghoorn and Linder (1944) but all species were transferred to *Halosphaeria* by Kohlmeyer (1972a). The genus is characterised by hyaline to brown ascomata, with the peridium composed of one cell type, asci clavate that deliquesce early, and ascospores with polar appendages of variable morphology (Johnson et al., 1984; Manimohan et al., 1993a). Initial ultrastructural studies of *R. maritima* and *R. pilleata* showed that the appendages were exosporic in origin and consisting of a fibrous component in an amorphous matrix. Fragmentation of the sheath giving rise to the wing-like polar appendages (Jones and Moss, 1978; Johnson et al., 1984). However, radiating appendages are found in *R. quadri-remis* and *R. stellata* but the substructure was the same as in *R. maritima* and *R. pilleata* (Manimohan et al., 1993a). In *R. crispa*, the appendages are closely adpressed to the spore wall and not wing-like or radiating, but ultrastructurally are similar to *R. stellata* and *R. quadri-remis*. In these two species, appendages arise in a polar position with radiating bundles of electron-dense stands exuded through pores in the episporium and embedded in an amorphous matrix. Similar observations were made for *R. galerita*, but differs from other species in that the polar appendage is more discrete (Manimohan et al., 1993b).

1. Ascospores ellipsoidal ........................................ 2
2. Ascospores rhomboid, 24-36 × 12-20 µm..................... *R. pilleata*
3. Ascospores with four or more appendages at each pole ......................................................... 6
2. Ascospores with a single polar appendage................. 3
4. Ascospores 18-30 (-32) × 8-13 µm, with wing-like appendages................................................. *R. maritima*
3. Ascospore appendages variously shaped.................... 4
5. Cap-like ascospore appendages with radiating strands, 20-28 × 7-12 µm ........................................ *R. galerita*
4. Ascospore appendages moustache-like..................... 5
6. Ascospores with 4 appendages at each apex............... 7
5. Ascospores constricted at the septum, 17-26 × 6-10 µm.................................................. *R. minuta*
6. Ascospores with 6 appendages at each apex, 24-30 × 8-12 µm.......................... *R. stellata*
7. Ascospores 20-28 × 7-13 µm, appendages long, ribbon-like 19-24 × 3-6 µm long *R. spitsbergenensis*
6. Ascospores 18-20 (-34) × 8-12 µm, appendages radiating, obclavate 12-21.5 × 2.5-4 µm.......................... *R. quadri-remis*


Ascomata ellipsoidal, immersed, ostiolate, papillate, coriaceous, hyaline to brown, necks long (up to 1 mm), periphysate, catenophyses present, asci clavate, long pedunculate, unitunicate, thin-walled, with or without apical pore, persistent, retraction of the plasmalemma at the apex, ascospores ellipsoidal, 1-septate, slightly constricted at the septum, hyaline, with or without polar appendages. Appendages large if present, initially closely appressed to the spore wall, separating, uncoiling to form long sticky filamentous threads (Fig. 44c). The genus was erected to accommodate two species of Halosarpeia and Nais glitra (Fig. 43f), as they did not group within the Halosarpeia sensu stricto clade, the type species of the genus (Pang et al., 2003b) (Fig. 55). Morphologically they differ in the following respects from Halosarpeia species: 1). Asci persistent, cylindrical-clavate, with a long stalk up to one third of the length of the ascus; 2). Apical pore present in S. ratagirienisis and S. glitra; and 3). Ascospores large, oval and heavily guttulated. Therefore there is molecular and morphological evidence for their segregation from the genus Halosarpeia. (Pang and Jones, 2004).

   .......................................................... S. glitra
2. Ascospore with bipolar appendages......................... 2
3. Ascospores greater than 48 μm: 48-64 (-72) × 22-28 μm........................................... S. ratagirienisis
4. Ascospores shorter than 48 μm: 33-47 × 14-22 μm .................................................... S. abonnis


Ascomata ellipsoidal to subglobose, immersed to partly immersed, yellow to brown, ostiolate, papillate, necks short and periphysate, lacking catenophyses, asci clavate, pedunculate, unitunicate, thin-walled, no apical apparatus, persistent to deliquescing, ascospores ellipsoidal, hyaline, thin-walled, 1-septate. With one appendage at each pole and four at the equatorial septum (Fig. 53c). Appendages flattened, attenuate and strap-like, with parallel striations, later splitting into fine threads (Pang et al., 2004a). A new taxon described from material collected on wood from a sandy beach in southern China. This genus is characterized by its unique bipolar and quadri-equatorial appendages, which disintegrate when mounted in seawater. The appendages are obclavate, tapered to a fine point, appear striated when released from the ascus but later become fibrillar (Pang et al., 2004a). The ascospores resemble those of Halosphaeria appendiculata and Ocostaspora apilongissima with polar and four equatorial appendages. In O. apilongissima appendages are striate, fragment into threads, but the polar appendages are much longer than the equatorial ones. In H. appendiculata the appendages do not breakdown but maintain their spoon-like morphology (Jones et al., 1984). The LSU rDNA data confirms its placement in the Halosphaeriales and is distantly related to Halosphaeria appendiculata and Ocostaspora apilongissima (Fig. 41).


A monotypic genus with cream-coloured ascomata, globose, immersed to superficial, ostiolate, papillate, coriaceous, with long necks (230-570 μm), periphysate, with catenophyses, asci clavate, unitunicate, papillate, pedunculate, J-, flattened at the apex with an apical pore and hyaline subglobose ascospores without sheaths or appendages (Kohlmeiyer and Volkmann-Kohlsmeyer, 1987a). This species has not been extensively collected and further studies are required to determine if it is correctly referred to the Halosphaeriales. Ascospores superficially resemble Iwilsoniella rotunda, but the species differs in ascomatal characteristics, the latter with dark coloured ascomata, with short necks, asci lacking an apical pore and deliquescing early.


Ascomata ellipsoidal, immersed in wood, ostiolate, papillate, coriaceous, unitunicate,

**Fig 51. Remispora spitsbergenensis.** Bar = 10 µm.

thin-walled, light brown, solitary, paraphyses absent, asci ellipsoidal, short pedunculate, clavate, unitunicate, thin-walled, deliquescing early, ascospores elongate-fusiform, rounded at the pole, tapering toward the base, straight or slightly curved, 1-septate, not constricted at the septum, hyaline, with 2-4 terminal radial appendages formed after release from the ascus (Fig. 54). This species is phylogenetically close to *Okeanomyces cucullatus* (Fig. 55), but they differ in ascospore appendage morphology: a single ephemeral mucilaginous drop/pad in the latter but tetraradiate in *Th. appendiculata* and formed after release from the ascomata (Fig. 54) (Jones et al., 2006). Marine ascomycetes with ascospores over 100 µm include *Bathyascus*, *Lindra* and *Lulworthia*, the latter two genera are members of the Lulworthiales.
while Bathysacus may not be correctly assigned to the Halosphaeriales (Jones, unpublished data).


Ascomata globose to subglobose, superficial, ostiolate, papillate, periphysate, pale to dark brown, catenophyses present, ascus clavate, short pedunculate, with a ring and an apical plate, unitunicate, thick-walled apically with retraction of the plasmalemma at the tip, persistent, ascospores 1-septate, constricted at the septum, ellipsoid, hyaline with a single appendage at one pole (Fig. 44d). Initially adressed to the spore wall but unfurls to form a long filamentous thread. _Aniptodera indica_, described by Ananda and Sridhar (2001), is reduced to synonymy with _T. unicaudata_.

_Tirispora mandoviana_ was originally described from freshwater habitats (Sarma and Hyde, 2000) but has recently been collected in Indian mangroves where salinity ranges from 1.1-34.1 ‰ (Maria and Sridhar, pers. comm.).

Phylogenetically _T. unicaudata_ forms a sister group to _Halosarpeia marina_ and _Panorbis viscousus_, but with weak support (Fig. 55).

1. Asci with retracted plasmalemma, an apical ring and pore, catenophyses present, ascospores 24-32 × 8-12 μm.................................................... _T. unicaudata_ 1. No retraction of the plasmalemma but with an indistinct apical pore, no catenophyses, ascospores 15-22 × 8-12 μm .................................................... _T. mandoviana_


Ascomata subglobose, immersed in blackened area of algal host, ostiolate, papillate with long necks (140-450 μm long), hyaline, thin-walled, solitary or gregarious, no paraphyses, ascus cylindrical to clavate, unitunicate, thin-walled, no apical apparatus, deliquescing early, ascospores filamentous, tapering, thick-walled, 1-4-septate, not constricted at the septa, hyaline, bent double and coiled within the ascus, no appendages or sheath. An infrequently collected species known from brown seaweeds, and further studies are required to establish its position in the Halosphaeriales, as Sutherland (1915) referred it to the Hyponecetriaceae. However, Rossman _et al._ (1999) excluded it from the Hypocreales because of the long-necked ascomata, lack of apical paraphyses and blackening of the host thallus. We do not consider its placement in the Halosphaeriales as satisfactory, but is left here until collections are available for a molecular study.


Ascomata superficial on an extensive subiculum on crab carapace, thick-walled, coriaceous, papilla lacking or short, aparaphysate, periphysate, asci elongate clavate, thin-walled, unitunicate, ascospores oblong to ellipsoidal, 15-22 × 4.6-5 μm, 1-3- septate, bipolar uncoiling appendages. Appendages initially coiled around the ascospore, later uncoil and consist of two parts: a short proximal region is stiffer and a distal region which is flexible, sticky and stretching to a great length (Hibbits _et al._, 1981). It differs from those of the _Halosarpeia_ complex in that appendages are not hamate, adhering to the ascospore wall, and later unfurling. A genus requiring further study, at the molecular level, to determine whether it is correctly assigned to the Halosphaeriales.


Ascomata globose to subglobose, immersed or semi-immersed, hyaline below to light brown above, ostiolate, papillate, membranous, solitary or gregarious, necks periphysate, catenophyses present deliquescing, asci ovoid to clavate, unitunicate, thin-walled, pedunculate, no apical apparatus,

deliquescent early, ascospores ellipsoidal, 1-septate, slightly constricted at the septum, hyaline, with appendages. Two types of appendages: a thin skin-like sheath with a pore at the apex from which a viscous cap emerges. This cap-like appendage slowly unfurls to form thread like appendages.

We regard *Buxetroldia bisaccata* as a synonym of this species as the features separating them are not sufficient for a new genus. This species differs from other genera with unfurling polar appendages in that the ascospore wall comprises three layers: mesosporium, episporium and exosporium. The latter has been shown by McKeown *et al.* (1996) to be loosely attached to the episporium, except at the central septum. The appendages comprise electron-dense fibrillar material, within which there are tripartite strands similar to the episporium. The basal part of the appendage is stout and arises through a discontinuity in the exosporium. This differs from the porefields reported for *Halosarpheia* species (Alias *et al.*, 2001).

Ascospore measurements of *T. australiensis* overlap with those of *Buxetroldia bisaccata*, although the asci are greater in length (125-162 × 32-45 µm) as opposed to 70-102 × 22-26 µm in *T. australiensis* (Hyde, 1990). Thus the differences between the two genera/species, revolve around the degree of separation of the sheath from the ascospore wall. Petersen and Koch (1997) show the sheath bulging away from the ascospore wall. This has also been demonstrated at the TEM level by McKeown *et al.* (1996) who examined collections of the fungus (made by Petersen) from Denmark. Similarities in ascospore appendage morphology, especially the thickness of the basal part and its slowness to unfurl, are found in *B. bisaccata*, *Halosarpheia trullifera* and *T. australiensis*. All possess a sheath varying in its degree of separation from the spore wall and in its degree of persistence. The appendages in these species are cap-like, rather than hamate, initially amorphous and only later unraveling to form extremely fine thread-like. There is evidence that *Halosarpheia fibrosa* may also have an exosporic sheath (Pang *et al.*, 2006). The taxonomic assignment of these taxa needs to be confirmed by a molecular study. Abdel-Wahab *et al.* (2001b) have shown that *H. fibrosa*, *H. trullifera* and *H. unicellularis* form a well supported clade within the Halosphaerales.

**Fig. 54. Thalespora appendiculata.** a-e. Stages in the development of ascospore polar appendages. Bars a-e = 20 µm.
Fig. 55. Taxonomic position of the new genera *Thalespora* and *Pseudolignincola*. 
SORDARIOMYCETIDAE

1. Diaporthales
2. Chaetosphaeriales
3. Ophiostomatales

1. Generally stromatic, ascomata perithecial, long-necked, interascal tissue absent, ascii thick-walled, J-apical ring, ascospores varied no germ slit, anamorphic coelomycete.............. Diaporthales

2. Paraphyses filiform and septate, ascomata superficial or immersed, perithecial, ostiolate or nonostiolate, asci subglobose, clavate or cylindrical, thin-walled, ascospores one-celled, hyaline or pigmented, with germ slit, anamorphs phialidic .... Chaetosphaeriales

3. Interascal tissue absent or thin-walled and inconspicuous.............................. Sordariales

3. Ascomata perithecial rarely cleistothecial, thin-walled, long necked, ostiolar setae, asci small, evanescent, formed in chains, ascospores small, unicellular, appenedged or with eccentric wall thickening, anamorphs hyphomycetes .............. Ophiostomatales

1. DIAPORTHALES

1. Ascospores with appendages.............. Diaporthe

2. Ascospores lacking appendages or sheath ............ 2

2. Ascomata in groups in a stroma, ascospores with at least one dark cell with germ pore, appenedged, generally lacking anamorphs .......... Sordariales

3. Ascomata perithecial rarely cleistothecial, thin-walled, long necked, ostiolar setae, asci small, evanescent, formed in chains, ascospores small, unicellular, appenedged or with eccentric wall thickening, anamorphs hyphomycetes .............. Ophiostomatales

Valsaceae

Cryptovalsa Ces. & De Not. ex Fuckel, Jahrb. nassauischen Vereins Naturk., 23-24: 212, 1870...................................................... (2)


Ascomata in groups in a stroma, immersed becoming erumpent, ectostroma effuse, ascocoma subglobose to broadly ellipsoidal, ostiolar, papillate, necks paraphysate, coriaceous, paraphyses septate

hyaline deliquescent, ascii clavate, truncate, long pedunculate, apical refractive non-amyloid ring, ascospores allantoid, unicellular, pale yellow to pale brown, 8-128 per ascus, no appendages or sheaths. A largely terrestrial genus, two are known from mangroves: C. halosarciicola on Halosarcia halocnemoides in Australia and C. mangrovei on Kandelia candel in Hong Kong. A third species C. sauadicola has been described from the salt marsh plant Suaeda fruticosa (Inderbitzin et al., 1999) with ascospores measuring 5-7 × ca. 1 μm.

1. Ascii 8 spored, ascospores hyaline, smooth walled, 4-7 × 1.5-2 μm .............. Cryptovalsa halosarciicola

2. Ascii 64 spored, ascospores pale yellow-pale brown, verrucose, 5.6-11 (-18) × 1.6-3.6 μm .................. Cryptovalsa mangrovei

Diaporthe Nitschke, Pyrenomycetes Germanici: 240, 1870...................................................... (1)


Ascomata in a group within a wide spreading blackened zone on the wood, individual ascomata subglobose, immersed, brown to black, coriaceous, with short necks paraphysate, penetrating the host surface, paraphyses hypha-like, filiform, tapering distally, septate and hyaline, asci cylindrical, unitunicate, thin-walled, short pedunculate, flattened apex, J-subapical ring, ascospores 1-septate, not constricted at the septum, hyaline, smooth walled, with a mucilaginous pad at each pole which swells in water and is sticky. The only Diaporthe species known from marine habitats, occurring on intertidal mangrove wood, but no anamorph has been linked to this species, although marine Phomopsis spp. are known (Vrijmoed et al., 1994). Ascospores are distinctive with a small mucilaginous pad at each end, which swells in water and attaches the spores to substrata.

Gnomonia Ces. & De Not., Soc. crittog Ital. 1: 231, 1863...................................................... (1)


This is a doubtful Gnomonia species and known only from the type collection. It is probably best referred to Halosarpheia (e.g. H. trullifera). Clearly it does not belong in
Gnomonia because of ascus and ascospore morphology and spore dimensions. Nomen rejectum.

Melanconidaceae


Ascomata solitary or gregarious; slightly stromatic; periphysate; asci clavate, thin-walled, with a refractive non-amyloid apical thickening, persistent, with a tapering stalk; paraphyses numerous, septate and broad; ascospores are hyaline, cylindrical, 0-3-septate with no appendages (Hyde and Jones, 1989b).

A monotypic genus that is infrequently reported, occurring on mangrove prop roots with the ascomata just below the surface of the bark. A molecular study is required to establish its true taxonomic position.

**DIAPORTHALES incertae sedis**

**Argentinomyces** N.I. Peña & Aramb., Mycotaxon 65: 333, 1997 ....................... (1)


Ascomata subglobose, immersed, ostiolate, papillate, periphysate, membranous, cream-coloured, solitary sometimes gregarious, paraphyses absent, asci clavate short pedunculate, unitunicate, thin-walled, thickened at the apex, without a pore, persistent, ascospores ellipsoidal, 0-3-septate, slightly constricted at the septa, hyaline, without a sheath or appendages (Peña and Arambari, 1997a) (Fig. 56). Although it has similarities with the Halosphaeriales, it clearly does not belong in that order, because of the thick-walled ascus apex, and persistent asci. It also shows similarities to the mangrove species *Rhizophila marina* and *Marinosphaera mangrovei*.

**Lasiosphaeriaceae**

**Biconiosporella** Schaumann, Veröff. Inst. Meereforsch. Bremerhaven 14: 24, 1972..... (1)


Ascomata ovoid, pyriform, flask-shaped, superficial or immersed, ostiolate, papillate, coriaceous, brown to black, solitary or gregarious, periphysate, catenophyses present, asci cylindrical, short pedunculate, thin-walled, unitunicate, persistent, with an apical plate, ascospores biconical, unequally 3-septate, thick-walled, slightly constricted at the septa, dark brown, no sheath or appendages (Schaumann, 1972). Infrequently reported and no recent taxonomic study on this species, often found on heavily decayed wood associated with sand (Jones *et al.*, 2005).

**Chaetomiaceae**

**Chaetomium** Kunze, Mykologische Hefte (Leipzig) 1: 15, 1817................................. (1)

Ascomata globose, superficial, brown to fuscous, ostiolate, epapillate, with terminal sterile hairs variously ornamented, straight curved or coiled, no paraphyses, asci clavate, thin-walled, unitunicate, hyaline, long pedunculate, no apical apparatus, deliquescing early, ascospores ovoid, pip-like, and olive brown. Isolated from sediments in the Black Sea, ascomata with spine-like appendages that are slightly bulbous at the base, longer hair-like appendages verruculose, ascospores 12.5-16 × 8-9.8 μm.

Chaetomium species are frequently noted from marine habitats but whether they are true marine species is not clear. For example, Chaetomium ramipilosum was isolated from Ammophila arenaria plant material in a sand dune system and sporulated well on seawater media (Schaumann, 1973b), while Jones (1962) reported Chaetomium erectum and Ch. globosum on submerged test blocks exposed in the sea at Langstone harbour.


Anamorph: Humicola-like.


Anamorph: Humicola-like.

Ascomata globose to subglobose, immersed but usually superficial, lacking an ostiole, coriaceous, dark brown to black, covered with septate branched hairs, solitary, paraphyses present deliquescing early, asci clavate, short pedunculate, unitunicate, with an apical ring, ascospores ellipsoidal, 1-septate, large apical olivaceous to dark brown cell and a smaller hyaline basal cell, lacking appendages or a sheath. Both Z. latipes and Z. marina have been reported with Humicola-like anamorphs and conidia produced on peg-like structures on undifferentiated hyphae, respectively (Guarro et al., 1999) and widely distributed. Zopfiella latipes has been recorded on Nypa fruticans in Thailand at salinities of 5-21 ‰ (Pilantanapak et al., 2005) and on other seagrasses (Sakayaroj, unpublished data).

1. Ascospores with subapical germ pore, basal cell broadly cylindrical, 16-22 × 10-13 μm...........Z. latipes
1. Ascospores with apical pore, basal cell elongate cylindrical, 14-20 × 10-14 μm......................Z. marina

SORDARIALES incertae sedis


Ascomata subglobose or pyriform, superficial, ostiolate, papillate, coriaceous, light brown, setose, solitary, short necks periphasyate, asci subcylindrical or fusiform, short pedunculate, unitunicate, thin-walled, no apical apparatus, persistent, ascospores subcylindrical, straight or slightly curved, 3-septate, not constricted at the septa, hyaline, appendages gelatinous cap-like, at each end of the spore. Abyssomyces was collected at depths of 631 and 641 m on hydrozoan, hydrorhiza and hydrocaulon, attached to stony corals. (Kohlmeyer and Volkmann-Kohlmeyer, 2003b). Few collections are available for study and the genus is in need of further study to determine its phylogenetic relationship.


Ascomata subglobose or ellipsoidal, immersed to superficial, ostiolate, papillate, membranous, pale brown to dark brown, necks with paraphyses, paraphyses deliquescing early, solitary or gregarious, asci elongate to cylindrical or clavate, short pedunculate,
unitunicate, thin-walled, persistent with an apical pore, ascospores 3-septate, constricted at the septa, versicoloured, apical cells hyaline, central cells brown, mucilaginous sheath around central cells, apical appendages in *S. appendiculata* (Read et al., 1993b) (Fig. 57). This genus has some similarities with members of the Halosphaeriales, in particular the nature of the paraphyses and lack or poorly developed apical pore to the ascus (Jones and Hyde, 1992). Ten species have been assigned to the genus, from freshwater or marine habitats, with *S. appendiculata* and *S. melanospora* found on driftwood associated with sand (Hyde and Jones, 1992b; Abdel-Wahab and Jones, 2000) (Fig. 57).

The genus has been referred to various higher taxa: Ascomycetes incertae sedis (Kohlmeyer, 1986b), Tripterosporaceae or Lasiosphaeriaceae in the Sordariales (Jones and Hyde, 1992), Halosphaeriales (Barr, 1990a) and Hypocreales incertae sedis (Cai et al., 2006). *Savoryella* superficially resembles *Ascotaiwania* both with versicoloured ascospores and their occurrence in aquatic habitats, but differ in the elaborate apical ascus apparatus of *Ascotaiwania*, and its *Monotosporella* and *Helicoon farinosum* anamorphs (Chang et al., 1998; Sivichai et al., 1998; Cai et al., 2006). A molecular study has failed to resolve the taxonomic position of *Ascotaiwania* (Ranghoo et al., 1999) with Cai et al. (2006) referring it to the Hypocreales incertae sedis. Their aquatic or intertidal habitat may have resulted in adaptation to these environments with consequent reduction of features of phyletic significance that may have indicated their natural affinities. Therefore, assignment of *Savoryella* species to a higher taxon on morphological criteria is difficult and warrants molecular studies to resolve its taxonomic position (Read et al., 1993b).

A recent molecular study of *Savoryella* and *Ascotaiwania* indicates they are closely related, but are not monophyletic. They do not group with any of the major taxa (Boonyuen, pers. comm.), but form an un-named clade distantly placed from the Halosphaeriales, Sordariales, Xylariales and Hypocreales incertae sedis. It is best referred to Hypocreomycetidae incertae sedis, Sordario-

Fungal Diversity

1. Asci with 2 ascospores, 36-60 × 12-16.5 µm, on mangrove wood................................. *S. paucispora*
1. Asci with 8 ascospores............................................. 2
2. Ascospores appended, 26-35 × 11-16 µm, on wood ....................................................... *S. appendiculata*
2. Ascospores not appended........................................ 3
3. Ascospores wider than 15 µm, 32-45 × 15-18 µm, on wood associated with sand.................. *S. melanospora*
3. Ascospores narrower than 15 µm, on wood............. 4
4. Ascospores 24-36 × 8-12 µm......................... *S. lignicola*
4. Ascospores 33.5-46.5 × 7.5-12 µm............. *S. longispora*

Fig. 57. *Savoryella melanospora*. Ascospore. Bar = 10 µm.

2. **CHAETOSPHAERIALES**

**Chaetosphaeriaceae**

*Chaetosphaeria* Select. fung. carpol. (Paris) 2: 252, 1863...................................................... (1)


Ascomata subglobose or pyriform, immersed or partly immersed, ostiolate, papillate, subcoriaceous, dark brown to black, solitary or gregarious, necks periphysate, paraphyses septe, ramose, asci cylindrical to clavate, long pedunculate, unitunicate, thin-walled, persistent, apical apparatus present, ascospores fusiform or elongate-fusiform, 3-septate, constricted at the septa, hyaline, with
polar and equatorial appendages formed by fragmentation of a sheath. The only marine species of a genus with 20 or more terrestrial species growing on wood, bark and leaves, and with a variety of anamorphs (Kirk et al., 2001; Rébolová and Seifert, 2008).

Chaetosphaeria chaetosa differs in a number of respects from other species in the genus, primarily in ascospores with both polar and equatorial appendages, formed by fragmentation of an exosporic sheath, while no anamorph have been reported for it (Jones et al., 1983c). Thus it differs from other Chaetosphaeria species which possess a wide range of phialidic anamorphs. Ascospores bear a resemblance to Corollospora species, but differ in lacking polar spines (Jones et al., 1983a). Although the genus has been extensively studied at the morphological and molecular level, Ch. chaetosa has not been examined (Rébolova, 1999; Huhndorf et al., 2004; Rébolová et al., 1999; Rébolová and Seifert, 2008). Its phylogenetic position needs to be confirmed by sequence data.

**OPHIOSTOMATALES**


Ascomata globose to subglobose, coriaceous, immersed to partly immersed, solitary or gregarious, neck short, cylindrical, periphysate, paraphyses and catenophyses absent, asci cylindrical to oblong-ventricose, unitunicate, thin-walled, short pedunculate, ascospores ellipsoidal, unicellular, hyaline, with longitudinal wall striations, with a crown of appendages at both ends. Appendages crown-like, radiating, delicate, subgelatinous and formed by fragmentation of an exosporium. A genus tentatively assigned by Hyde and Jones (1986b) to the Halosphaeriales, however, preliminary molecular data suggests an affinity to the Ophiostomatales (Schoch, pers. comm.).

**XYLARIOMYCETIDAE**

1. **XYLARIALES**

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**Key to xylariaceous and xylariaceous incertae sedis species:**

1. Ascospores hyaline ................................................2
2. Ascospores brown or black .......................................9
3. Ascospores apiosporous ...........................................Apioclypea nypicola
4. Ascospores not apiosporous ....................................3
5. Ascospores 0-septate .............................................4
6. Ascospores septate ................................................6
7. Ascospores with a single or bipolar caps or appendages ..........................................................5
8. Ascospores surrounded by a mucilaginous sheath ..........7
9. Ascospores filamentous, ascomata superficial under a stroma ...................................................... Linocarpon
10. Ascospores ellipsoidal, ascomata beneath host surface .......................................................... Fasciatispora nypae
11. Ascospores cymbiform, 34-44 × 7-15 µm, on Phragmites ........................................ Phragmitensis marina
12. Ascospores ellipsoid, 17-26 × 5-7 µm on *Nypa* .......................................................... Frondicola tunicricuspis
13. Ascospores 0-1-septate, filliform, on *Nypa* ...............8
14. Ascospores 1-septate elongate, 24-36 × 3-4.5 µm, on mangrove leaves .................................. Lanceispora amphibia
15. Ascospores 1-septate .............................................. 17
16. Ascospores lacking appendages or a sheath ...............13
17. Ascospores 20-33 × 8-12 µm, single polar appendage, on mangrove substrata ................................ 11
18. Ascospores 6.5-16 × 2-8 µm, single or bipolar appendages ........................................ Phomatospora
19. Ascospores 6.5-12 × 2.28 µm, immersed in mangrove wood ........................................ 15
20. Ascospores occasionally with a sheath ...................... Adonim avicennae
21. Ascospores 16-20 × 4-6 µm, prominent sheath drawn out to form polar appendages .......... Nipicola
22. Ascospores occasionally with a sheath .......................... Anthostomella
23. Ascospores with germ slits ..................................... 14
24. Ascospores lacking germ slits .................................. 13
25. Ascospores 6.5-8 × 1.2-16 µm, hyaline to pale yellow, ascomata immersed in a stroma, on mangrove wood ........................................ Eutypella naqisi
26. Ascospores 6-12 × 2.28 µm, immersed in mangrove wood ........................................ Eutypa bathurstensis
1. Cainiaceae

_Arecophila_ K.D. Hyde, Nova Hedw. 63: 82, 1996


Ascomata immersed, subglobose, ostiolate, papillate, coriaceous, brown to black, solitary to gregarious, necks periphysate, paraphyses hypha-like, septate and branched, asci cylindrical to clavate, short pedunculate, unitunicate, thin-walled, J+-amyloid ring, persistent, ascosporous ellipsoidal, 1-septate, brown, slightly constricted at the septum, with a mucilaginous sheath. This is a genus introduced by Hyde (1996) to accommodate ascomycetes collected on palms, while others are known from dead culms of bamboo (Umali et al., 1999).

Kang _et al._ (1999a) placed the genus in the Cainiaceae based on molecular evidence, formerly referred to the Amphisphaeriaceae. _Arecophila_ differs from _Amphisphaeria_ in having deeply immersed, subglobose to lenticular ascomata, with a peridium of angular cells with a small or lacking a clypeus. _Arecophila_ species develop within the host tissue beneath a clypeus (or lacking), ascomata often lenticular, paraphyses are hyphal-like, asci unitunicate, cylindrical with an apical J+-ring and brown bicellular ascosporous that are verrucose or striated. Ascosporous are surrounded by a wide mucilaginous sheath. _Arecophila nypae_ differs from other species in having ascosporous with rounded cells and occurs on the brackish water palm _Nypa fruticans_. _Arecophila_ is similar to another marine ascomycete, _Atrotorquata_ but differs in lacking an ascospore germ slit (Hyde, 1996).

**Atrotorquata** Kohlm. & Volkm.-Kohl., Syst. Ascomycetum 12: 8, 1993

Ascomata subglobose, immersed, ostiolate, papillate with a long periphysate neck (140-200 µm), coriaceous, dark brown, solitary, paraphyses, simple or branched, septate, ascus cylindrical, short pedunculate, unitunicate, thin-walled, persistent, with an apical apparatus, J+, ascosporous ellipsoidal, 1-septate, slightly constricted at the septum, brown, striate and with 5-7 germ slits at each apex, with a gelatinous sheath. A common and host-specific ascomycete on _Juncus roemerianus_ but may not be obligately marine but occurs with other marine organisms (Kohlmeyer and Volkmann-Kohlmeyer, 1993c). It was referred to the Amphisphaeriaceae, but we prefer its assignment in the Cainiaceae (Kang _et al._, 1999a, b).

2. Clypeosphaeriaceae


Ascomata subglobose, immersed underneath a weakly developed clypeus, membranous, ostiolate, brown, solitary or gregarious, paraphyses hypha-like, septate, numerous embedded in a gelatinous matrix, asci cylindrical, pedunculate, persistent, with a J+ apical apparatus, ascosporous ellipsoidal, hyaline, apiosporous, with a mucilaginous sheath. A genus erected to accommodate unitunicate ascomycetes with ascomata immersed under a clypeus, appearing as minute blackened ostiolar dots (Hyde _et al._, 1998). Ascosporous form orange ooze around ostioles. Referred to the Hyponentriaceae (Hyde, 1994b) and Clypeosphaeriaceae (Hyde _et al._, 1999a), sequence data confirms its
position in the latter family (Kang et al., 1999c,d).

**Ommatomyces** Kohlm., Volkm.-Kohlm. & O.E. Erikss., Mycologia 87: 538, 1995 ............ (1)


Ascomata broadly ovate, immersed, ostiolate, subcarbonaceous, black, short papilla, periphysate, paraphyses, septate, unbranched, thin-walled, asci cylindrical, short pedunculate, unitunicate, with an apical apparatus consisting of several rings, J+, ascospores ellipsoidal, 1-septate, slightly constricted at the septum, brown, thick-walled, with an a lacerate germ pore at each end, with subglobose gelatinous and evanescent caps and a thin sheath around the spore. Kohlmeyer et al. (1995c) assigned the genus to the Amphisphaeriaceae, but Kirk et al. (2001) place it in Xylariaceae. It differs from the previous family by its broadly ellipsoidal ascospores with elaborate lacerate germ pores, gelatinous spore caps and sheath. The species has a complex ascomycete saprobic on intertidal wood of *Rhizophora apiculata*, with large ascomata (325-520 µm high, 650-910 µm wide), immersed singly within the bark and covered by the periderm. Molecular data required to determine if this species would be better assigned to the genus *Eutypa*.

**Eutypa** Tul. & C. Tul., Select. fung. carpol. 2: 52, 1863................................................ (1)


Anamorph: coelomycetous

Ascomata deeply immersed in the wood, entostroma poorly developed, spherical to flattened, ostiole poorly developed, neck 120-200 µm periphysate, black, paraphyses numerous, persistent, asci clavate, long pedunculate, apical apparatus J-, ascospores allantoid, olive-brown, no sheath or appendages. This species differs from other species in having an ascomatal wall that is three layered, the central one thick and hyaline (Hyde and Rappaz, 1993). Anamorph produced in nature and in culture, the conidia produced holoblastically, filiform, curved, hyaline with a flattened base, 10-33 × 1.5-2 µm.


Ascomata formed beneath a raised, blackened crust-like stroma on the host surface, ascomata globose to subglobose, membranous, black, ostiolate, neck periphysate, paraphyses hypha-like, sparse, septate, hyaline, and tapering distally, asci cylindrical-clavate, long pedunculate, unituicate, thin-walled, apical apparatus J-, ascospores allantoid, unicellular, straight or curved, hyaline to pale brown, no sheath or appendages. The only known *Eutypella* species on intertidal marine mangrove wood often growing on decorticated
Avicennia species, with ascomata developing under blackened stroma, with necks collectively erumpent through pustulate discs (Hyde, 1995a).


Pseudostromatic tissue, comprising host cells and fungal hyphae, through which occur numerous darkened raised pustules with 1-4 immersed ascomata and 1-4 short necks. Ascomata large, subglobose, coriaceous, brown-black, ostiolute, papillate, necks collectively erumpent, periphysate, paraphyses filiform, simple, asci irregularly fusiform, pedunculate, unitunicate, thin-walled, apically truncate without an apical apparatus, ascospores ellipsoidal, 1-septate, not constricted at the septum, with a pronounced 3-4 lobed mucilaginous sheath. A monotypic genus occurring on the palm Nypa fruticans, and infrequently collected. Referred by Hyde (1992a) to the Clypeosphaeriaceae it is a genus that needs evaluation at the molecular level.


Phragmites australis (Wong et al., 1998). Although assigned here to the Xylariales, the asci lack an apical apparatus.

5. Xylariaceae


Ascomata globose to subglobose, immersed in the host, pale brown to dark brown to black, ostiolate, epapillate, clypeate, coriaceous, periphysate, solitary or gregarious, paraphyses numerous, simple, septate, asci cylindrical, short pediculate, unitunicate, thick-walled with a J+ apical apparatus, ascospores ellipsoid, unicellular, with germ-slits extending over the whole length of the spore, hyaline with gelatinous caps or sheaths (Kohlmeyer et al., 2002).

The two species listed here have been described from terrestrial palms, Nypa fruticans (Smith and Hyde, 2001) (Fig. 60). Astrocystis is similar to Rosellinia, but differs in ascus and ascospore morphology, asci in Astrocystis have short stipes and ascus apparatus is small, while in Rosellinia the ascus stipe is long with a massive barrel shaped ascus apparatus. A number of Astrocystis species have been described from terrestrial palms (Smith and Hyde, 2001).

The two species listed here have been described from the brackish water palm, Nypa fruticans in Kuala Selangor, Malaysia. Although there is no molecular data for the marine Astrocystis species, Astrocystis eleiodoxae (a peat swamp species) is well placed in the Xylariaceae (Pinnoi et al., unpublished data).

1. Stromata splitting stellately, ascospores 8-10 × 3-5 µm, golden brown, germ slit 4/5 of total length........

2. A. spissitecta

3. A. nypae

4. A. nypensis

5. A. torosa

Astrocystis Berk. & Broome, J. Linn. Soc. Bot. 14: 123, 1873.............................................. (2)


Ascomata erumpent, mammiform, globose to subglobose, ostiolate, minutely papillate, black, carbonaceous, solitary or gregarious, paraphyses hypha-like, septate, in a gelatinous matrix, asci cylindrical, short pedunculate, apical apparatus J+, ascospores ellipsoid, unicellular, golden brown to dark brown, germ slits run more or less the length of the spore, no sheaths or appendages to the marine species (Smith and Hyde, 2001) (Fig. 60). Astrocystis is similar to Rosellinia, but differs in ascus and ascospore morphology, asci in Astrocystis have short stipes and ascus apparatus is small, while in Rosellinia the ascus stipe is long with a massive barrel shaped ascus apparatus. A number of Astrocystis species have been described from terrestrial palms (Smith and Hyde, 2001).

Stroma dark coloured beneath the host epidermis. Ascomata immersed beneath the stroma, globose, ostiole periphysate, paraphyses persistent, septate, rarely branched, asci cylindrical, un党中央ite, thin-walled, with a J+ apical apparatus, ascospores unicellular, ellipsoidal, yellow brown to brown, with a central pallid band and pollen gelatinous appendages. *Fasciatispora* was assigned to the Amphisphaeriaceae (Hyde, 1991c, 1995b), but molecular data place *Amphisphaeriaceae* (Hyde, 1991c, 1995b), but molecular data place *F. petraki* in the Xylariaceae.

1. Ascospores with polar gelatinous appendages, **11.6-17 × 5.6-7.1** .......................................................... *F. nypae*
2. Ascospores lacking polar appendages, **8.4-14.9 × 3.9-7.5 µm** .......................................................... *F. lignicola*


*Hypoxylon oceanicum* Schatz, Mycotaxon **33**: 413, 1988.

Pseudostroma on decorticated wood, single or in clusters of up to 30 unipertichiate pseudostroma, ascomata immersed in pseudostroma, subglobose to hemispherical, soft to leathery, ostiolute, papillate, paraphyses numerous, persistent, asci cylindrical un党中央ite, J+ ascus tip, ascospores ellipsoidal, dark grey-olive to brown, wall smooth, germ slit straight, half to three quarters total length of spore, without a sheath or appendages.

*Halarosellinia oceanica* was separated from *Hypoxylon* as it did not meet the criteria for that genus: 1. *Nodulisporium* anamorph; 2. Stromata unipartite, 3. Stromatal tissue below the perithelial layer solid and homogenous and 4. Stromata not upright (Whalley *et al.*, 2000). Molecular data indicate a relationships with *Xylaria hypoxylon* (18S, 28S sequences and combined 18S and 28S data set) rather than the genus *Hypoxylon* (Smith *et al.*, 2003). However, ITS-5.8S-ITS2 sequences support a relationship with *Astrocytis eleiodoxae* with good support and a sister clade which includes *X. hypoxylon* (Pinnoi *et al.*, unpublished data) *Halarosellinia oceanica* produces a wide range of bioactive compounds, including cytochalasins, which is consistent with a taxonomic affinity to *Rosellinia* and *Xylaria* (Whalley and Edwards, 1987; Schlingham *et al.*, 1998, Li *et al.*, 2001). It is world wide in its distribution in tropical mangrove habitats. A *Nemania* species occurs frequently in mangrove habitats and this can be confused with *H. oceanica*, but differs in the smaller size of the ascospores and a pronounced decolourization of the wood around the ascomata.


 chimney *N. maritima* Y.M. Ju & J.D. Rogers, Nova Hedw. **74**: 102, 2002.

Stromata scattered, subglobose or globose enclosing 1-many ascomata that are carbonaceous, ostiolute, dark brown, asci cylindrical, short pedunculate, with a J+ apical ring, ascospores ellipsoidal, with broadly rounded end, unicellular, light brown to brown, with a straight germ slit the length of the spore (Fig. 61). A species from *Kandelia candel* mangrove wood collected in Taiwan (Ju and Rogers, 2002) and widely collected in subtropical mangroves (Jones and Abdel-Wahab, 2005). This species can be confused with *Halarosellinia oceanica* as both grow in the same habitat, but the ascospores of *N. maritima* are much smaller 9-12 × 5-6 (-6.5) µm with rounded ends and a germ slit shorter than the spore length. Unlike *H. oceanica* this species is reported to produce the teleomorph in culture but no anamorph has been encountered. Ju and Rogers (2002) believe this species could be segregated to a new genus, but did not elaborate on the grounds for this. Tang *et al.* (2007b) in ITS-RPB2 sequences show that *N. maritima* is placed in the Xylarioidae clade and *Nemania* subclade, being basal to other species. *Xylaria hypoxylon* is nested in the other subclade with *X. grammica* and a *Xylaria* sp. Pinnoi, *et al.* (unpublished data) in an ITS dataset also shows that *N. maritima* is
Fig. 58. Morphological features of *Pedumispora rhizophorae*. **a.** Exposed ascomata on wood surface. **b, d.** Filiform ascospores tapering towards both ends. **c.** Longitudinal striations on the ascospore cell wall. Bars a = 1 mm; b-d = 20 µm.

Fig. 59. Ascospores: **a.** *Anthostomella torosa*. **b.** *A. spissitecta*. Bars = 5 µm.
well placed in the Nemania clade with high bootstrap support. However, it groups with *N. confluens* with high support, in a sister clade to other *Nemania* species.

This species is also known from Hong Kong and Malaysia and is possibly widespread in its distribution. The fungus was collected at four sites in Hong Kong: Three Fathom Cove, Ting Kok, Ho Chung and Mai Po. It was recorded as the most common species at these four sites colonizing 14% of the total number of samples (Abdel-Wahab and Jones, unpublished data). The Hong Kong material had asci that measure 82-108 × 7.5-10 μm ($\bar{x} = 93.5 \times 7.7$ μm, n = 20), with a subapical ring and inverted cap in shape, ascospores 9-10 × 5 μm ($\bar{x} = 9.6 \times 5$ μm, n = 40). Figure 61, illustrates material collected in Hong Kong.


Ascomata formed under the host surface under slightly raised areas, or under a reduced blackened clypeii, globose to subglobose, ostiolate, paraphyses amphisphaeriaceous, asci broadly cylindrical, short pedunculate, subapical ring J-, ascospores lunate, unicellular, dark brown to black, with or without a germ slit, with well developed gelatinous sheaths. The two marine species occur on the intertidal palm *Nypa fruticans*, with black lunate ascospores, with a layered mucilaginous sheath and appendages at the ends. It differs from *Anthostomella* in lacking a J+, subapical ring and in its black ascospores (Hyde and Taylor, 1996).

1. Ascospores 17-20 × 4-6 μm, appendages are part of an elaborate sheath drawn out at each end, clypeus poorly developed, ascus ring J-..........*N. carbospora*

1. Ascospores 16-18 × 5-6 μm, germ slit along the entire length of the spore, elaborate mucilaginous sheath, clypeus well-developed, ascus ring J+ .......... ........................................................... *N. selangorensis*

**XYLARIALES incertae sedis**


Ascomata ampulliform to subglobose, immersed, brown, ostiolate, clypeate, paraphyses, paraphyses broad, asci cylindrical, unitunicate, thin-walled, deliquescent with a persistent apical cap, ascospore ellipsoidal, brown, unicellular, with an appendage at one end of the spore. This poorly known species was described from material collected in Australia and the Red Sea, Egypt, on *Avicennia marina*, and referred to the Phyllachorales (Schatz, 1985). It has recently been collected in New Zealand and Thailand (Lintott and Lintott, 2002; Jones et al., 2005). Collections in Thailand were on *Avicennia marina* pneumatophores.

*Lanceispora* Nakagiri, Okane, Tad. Ito & Katum., Mycoscience 38: 208, 1997 ......... (1)

*L. amphibia* Nakagiri, Okane, Tad. Ito & Katum., Mycoscience 38: 208, 1997 (*Type species*).

Ascomata globose to subglobose, immersed, olivaceous to olivaceous black, ostiolate, papillate, necks lacking paraphyses, paraphyses filiform, branched, septate, hyaline, asci cylindrical, unitunicate, long pedunculate, apical ring K+, ascospores oblanceolate, hyaline, rounded apical part, tapering towards the lower end, 1-septate, above the spore middle, lacking a sheath or appendages.

A genus referred by Nakagiri et al. (1997) to the Amphisphaeriaceae while Kirk et al. (2001) are of the opinion it is close to *Ceriospora-Urosporellopsis*. Only one species
has been reported from marine habitats while *L. phyllophila* has been described from the petiole of an unidentified dicotyledonous species in leaf litter (Sarma and Hyde, 2001). Assignment to family is unresolved: originally referred to the Amphipsphaeriaceae because of its affinities with *Leiopsphaerella* (Nakagiri et al., 1997), while Barr (1994) thought the latter genus should be assigned to the Hyponectriaceae. Wang and Hyde (1999) rejected this while Kang et al. (1999) suggested the Clypeosphaeriaceae for *Leiopsphaerella* and *Oxydothis*. Since Lanceispora has much in common with *Leiopsphaerella* then this family should be considered, but further molecular studies of this complex is required before final assessment can be made.

**Linocarpon** Syd. & P. Syd., Ann. Mycol. 15: 210, 1917...................................................... (6)


   Pseudostroma black, ascomata circular, lenticular, dome-shaped, beneath the pseudostroma, ostiolate, short papilla may be present, paraphyses filamentous, smooth, septate, hyaline, in a gelatinous matrix, asci cylindrical, pedunculate, truncate at the apex, with J- ring, ascospores filiform, hyaline, slightly curved or straight, apically gelatinous caps or pad-like appendages at both ends (Hyde, 1988; Hyde and Alias, 1999). This genus is common on *Nypa fruticans* and mangrove wood in tropical locations (Hyde and Alias, 1999; Poonyth et al., 2000a). Ascospores are filiform to needle-shaped, hyaline, and unicellular, often with polar pad-like appendages or a mucilaginous sheath. Ultrastructure studies of *L. appendiculatum* show that the asci are thin-walled (ca. 70 nm thick) with a C-shaped apical ring with subapical projections into the epiplasm, ascospores at their tips have a collar-like structure that encloses microfibrils. Appendages are hair-like, wavy, and separate fibrils are surrounded by a thin membrane, which is also present in the ascospores of *L. nipae* (Poonyth et al., 2000a). It was referred to the Hyponectriaceae by Hawksworth et al. (1995), although Wang and Hyde (1999) excluded it from this family.

1. Ascospores needle-shaped, lacking appendages, 57.5-87.5 × 3.5-6 µm ......................... *L. angustatum*
2. Ascospores filamentous with appendages ............................ 2
3. Ascospores with appendages at both ends, 90-139 × 2.3 µm........................................ *L. bipolare*
4. Ascospores with a single appendage........................ 3
5. Ascospores C-shaped or sigmoid, one end rounded, one end tapering with mucilage, 124-140 × 2.5-3 µm .................................................. *L. longisporum*
6. Ascospores not markedly curved ................................4
7. Ascospores 75-120 × 2-3.5 µm, with thistle-shaped appendage, on mangrove wood..............................
   8. Ascospores 91-124 × 3.5-4 µm, with a mucilaginous pad at one end, on mangrove wood......... *L. nipae*

   **Neolinocarpon** K.D. Hyde, Bot. J. Linn. Soc. 110: 104, 1992 ........................................... (2)

   Ascomata immersed in the host, oval to subglobose, ostiolate, coriaceous, black, neck short with periphyses, paraphyses tapering, septate, simple, longer than the asci, asci long cylindrical, pedunculate, unitunicate, thin-walled, ring-like refractive apical apparatus, ascospores filiform, straight or curved, hyaline, unicellular, with apical cap-like mucilaginous appendages. This genus marginally differs from *Linocarpon*, and molecular data are required to resolve its taxonomic affinities. A second *Neolinocarpon* species has been described from the dead aerial rachids of *Nypa fruticans* (Hyde and Alias, 1999). They differ as follows: *Neolinocarpon* has deeply immersed ascomata forming below a slightly raised or flattened clypeus and with a refractive globose body below the apical ascus ring, while *Linocarpon* has ascomata that are superficial or slightly immersed and lack a
Ultrastructure studies of selected Linocarpon and Neolinocarpon species failed to yield characters for the delineation of the genera (Yanna et al., 2003). Currently the genus cannot be assigned to any family within the Xylariales.

1. Ascomata formed under a clypeus, solitary, ascospores 70-119 × 2-3 µm ...........N. globosicarpum
1. Ascomata deep within a stroma, ascospores 92-117 × 2-4 µm....................................N. nypicola

Oxydothis Penz. & Sacc., Malpighia 11: 505, 1898.............................................................. (2)

Ascomata beneath the host epidermis, globose to subglobose, ostiolate, periphysate, brown to black gregarious, paraphyses numerous, filamentous, hyaline, asci cylindrical, pedunculate, unituncate, thin-walled, with an apical ring J+, ascospores filiform, straight or curved, hyaline, 0-1-septate, not constricted at the septum, with mucilage at the tip of the spore (Hyde and Nakagiri, 1989). Both species occur on ageing or cut fronds of the palm Nypa fruticans that have fallen into the water and are well placed in the genus. Oxydothis nypae appears to be the most common species, recorded from a variety of collections (Hyde and Alias, 2000; Pilantanapak et al., 2005). Kang et al. (1999a) referred the genus to the Clypeosphaeriaceae.
1. Ascospores 1-septate, diameter more than 6 µm, 74-92 µm long, fusiform, with apiculate ends.................
Ascomata globose to subglobose, immersed, pale brown to black, membranous, ostiolar, short papillate, solitary, necks periphysate, paraphyses hypha-like, straight, septate, tapering distally, numerous, asci cylindrical, ununiculate, thin-walled, pedunculate, with a J+ refractive ring, ascospores unicellular, ellipsoidal, hyaline, with longitudinal striae and with or without polar appendages. A genus frequently encountered on mangrove wood, Nypa fruticans, Phragmites australis and the fern Acrostichum speciosum, while other species await description (Jones, unpublished data). Cai et al. (2006) refer the genus to Soradriomycetes incertae sedis, but suggest that 18S rDNA sequences indicate a close relationship to the Magnaporthaceae. This hypothesis requires further study to determine assignment to a family and an order.
1. Ascospores lacking an appendage Ph. nypicola
2. Appendages at both ends..............................................3
3. Appendages at one pole ..............................................5
4. Ascospore appendages pad-like Ph. bellaminuta
5. Ascospore appendages bifurcate .....................................4
6. Ascospores 6.5-9.5 µm, on Nypa Ph. nypae
7. Ascospores 7.5-1.5 µm, on Phragmites Ph. phragmiticola
8. Ascospore appendages prominent, ascospores 6-7 × 2-3 µm, on a fern Ph. acrostichi
9. Ascospores 1-septate, diameter less than 6 µm, 82-113 µm long, ends rounded with mucilage Ph. kandeliae

SORDARIOMYCETES incertae sedis
1. Ascocarps perithecial, immersed in host tissue, subiculate or without subiculum, periphysate, paraphysate, ascals clavate to fusiform, unitunicate, deliquescent, ascospores septate, hyaline, thick-walled, no apical chambers or sheaths .............................................. Koralionastetales
1. Ascocarps perithecial, immersed in host tissue, often clypeate, ostioles periphysate, paraphyses wide thin-walled, ascals cylindrical, persistent with inconspicuous J-apical ring, ascospores asceptate, anamorph coelomycetes Phyllachorales
1. Ascocarps perithecial, immersed or superificial, often staining the substratum, paraphysate, paraphyses wide at the base tapering apically, ascals cylindrical, ununiculate, ascospores septate, often filiform, hyaline, yellow to brown .............................................. Magnaporthales

1. LULWORTHIALES

Key to the genera
1. Ascospores with apical chambers or appendages ...2
2. Ascospores lacking appendages Ph. kandeliae
3. Ascospores 0-septate ..............................................3
4. Ascospores septate ..............................................7
5. Ascospores filiform ..............................................6
6. Ascospores fusiform, ellipsoidal ................................4
7. Ascospores appendages tubular longer than 35µm .............................................. Kohlmeyeriella
8. Ascospores appendages apiculate or conical, less than 35 µm long ..............................................5
9. Ascomata superficial, with sterile hairs, parasitic on red algae Spathulospora
10. Ascomata immersed in a gall, lacking sterile hairs, on brown algae Haloguignardia
11. Ascomata with bell-like structure within the centrum Rostrupiella
12. Ascomata lacking the bell-like structure Lulworthia
13. Ascospores 1-septate Lulwaana
14. Ascospores many times septate Lulwoidea

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Lulworthiaceae


Ascomata subglobe, superficial, subiculate, ostiolate, papillate, subcarbonaceous, black, solitary often associated with sand, asci fusiform to clavate, unitunicate, thin-walled, deliquescing early, ascospores unicellular, fusiform to clavate, unitunicate, thin-walled, deliquescing early, lacking an apical apparatus, ascospores filiform, many times septate (up to 50), not constricted at the septa, with a globose to semiglobose gelatinous appendage on wood. Species on seagrasses with coriaceous ascomata immersed in the host, and lacking an apical swelling or appendage. Molecular data indicate that this genus is distantly related to the Halosphaeriales and Kohlmeyer et al. (2000) have assigned it to the Lulworthiales.

The genus appears to be polyphyletic with *Lindra obtusa* forming a basal group to the order, while *L. crassa* and *L. marinera* are distantly placed within the Lulworthiales (Campbell et al., 2005) (Fig. 62). *Lindra inflata*, the type species, needs to be sequenced before further taxonomic changes are undertaken. Morphologically *L. inflata* differs from *L. marinera* and *L. thalassiae* in the deeply embedded carbonaceous ascomata in wood, thick-walled peridium, ascospores 30-50-septate with a globose swelling gelatinous apical appendage (Wilson, 1956).

1. Ascospores markedly swollen at their tips, 30-51-septate, 210-415 × 4-6 μm, on wood ........... *L. inflata*
   1. Ascospores not markedly swollen at their tips........ 2

2. Ascospores more than 8 μm wide, 320-520 μm, 15-23-septate, on marine angiosperms and algae........
   2. Ascospores less than 8 μm wide, septa fewer than 30
      ......................................................................... *L. crassa*

3. Ascospores longer than 230 μm, 230-390 × 3-6 μm, on sea grasses.............................. *L. thalassiae*

4. Ascospores shorter than 230 μm, on other hosts...... 4

1. Ascospores narrow, 140-205 × 5-8 μm........... *K. crassa*

1. Ascospores wider, 137-152 × 17.5-18.5 μm..........
   ........................................................................... *K. tubulata*


- **L. obtusa** Nakagiri & Tubaki, Mycologia 75: 488, 1983.

**Fungal Diversity**

**Anamorph:** *Anguillospora marina* Nakagiri & Tubaki


Ascomata semiglobose or ellipsoidal, immersed, carbonaceous to subcarbonaceous, black, ostiolate, papillate or epapillate, solitary or gregarious, asci cylindrical to clavate, unitunicate, thick-walled, deliquescing early, lacking an apical apparatus, ascospores filiform, many times septate (up to 50), not constricted at the septa, with a globose to semiglobose gelatinous appendage on wood. Species on seagrasses with coriaceous ascomata immersed in the host, and lacking an apical swelling or appendage. Molecular data indicate that this genus is distantly related to the Halosphaeriales and Kohlmeyer et al. (2000) have assigned it to the Lulworthiales.


Anamorph: Zalerion maritima (Linder) Anastasiou

Ascomata superficial or immersed, globose to subglobose, ostiolate, coriaceous, dark brown or black, neck short, asci fusiform, curved in the ascoma, unitunicate, thin-walled, deliquescent early, ascospores filiform, hyaline, 1-septate, with conical end chambers containing mucilage which is released as a drop when mounted in water and forms an adhesive pad for attachment of the ascospores. A genus erected based on a single morphological character of a 1-septate ascospore, a Zalerion maritima anamorph and sequence data (Campbell et al., 2005) (Fig. 62).


Lulworthia hawaiiensis


Anamorph: Zalerion maritima (Linder) Anastasiou

Ascomata superficial or immersed, globose to subglobose, ostiolate, coriaceous, dark brown or black, neck short, asci fusiform, curved in the ascoma, unitunicate, thin-walled, deliquescent early, ascospores filiform, hyaline, 1-septate, with conical end chambers containing mucilage which is released as a drop when mounted in water and forms an adhesive pad for attachment of the ascospores. A genus erected based on a single morphological character of a 1-septate ascospore, a Zalerion maritima anamorph and sequence data (Campbell et al., 2005) (Fig. 62).


Ascomata superficial, generally attached to sand grains by subicula, subglobose to ellipsoidal, carbonaceous, asci clavate, pedunculate, unitunicate, thin-walled, deliquescent early, ascospores filiform, hyaline, multisepate, with polar end chambers filled with mucilage which is released through a pore at maturity when in water. Another genus erected based on sequence data and a single morphological character of ascospores with numerous septa (31-38). A species generally found on sand grains associated with buried wood (Koch and Jones, 1984).


Anamorph: Zalerion maritima (Linder) Anastasiou

Ascomata superficial or immersed, globose to subglobose, ostiolate, coriaceous, dark brown or black, neck short, asci fusiform, curved in the ascoma, unitunicate, thin-walled, deliquescent early, ascospores filiform, hyaline, 1-septate, with conical end chambers containing mucilage which is released as a drop when mounted in water and forms an adhesive pad for attachment of the ascospores. A genus erected based on a single morphological character of a 1-septate ascospore, a Zalerion maritima anamorph and sequence data (Campbell et al., 2005) (Fig. 62).
described by Barghoorn and Linder (1944) as *Halophiobolus*, but subsequently transferred to the earlier taxon *Lulworthia* (Sutherland, 1916b) by Cribb and Cribb (1955). Because of the deliquescing asci and ascospores with an end chamber containing mucilage it was assigned to the Halosphaeriales (Kohlmeyer, 1972a). Kohlmeyer et al. (2000) have shown that at the molecular level these species have no affinities with the Halosphaeriales and erected a new order to accommodate them.

Since no type material of *Lulworthia fucicola* could be traced, Campbell (2005) designated a neotype with a *Lulworthia* collection from Chile. However this is a lignicolous strain while *L. fucicola* was described from a brown alga. We do not accept the argument that the significant morphological differences between the algicolous and lignicolous strains are substrate-induced.
Furthermore we reject the synonymy of *Lulworthia cylindrica* with *L. fucicola* (Cribb and Cribb, 1955). Greater efforts must be made to collect *Lulworthia* species from marine algae.

Nakagiri (1984) reviewed the available morphological characters for the separation of the genera *Lindra* and *Lulworthia*: peridial wall structure, ascospore septation, possession of end chambers filled with mucilaginous material and their anamorph conidial development. For their selected examples, only the latter two characters were considered significant at the generic level. Peridial wall structure depends on the habitat of the species: arenicolous species (*L. crassa*, *L. lignoarenaria*) have a single outer-layer of thick-walled, large cells, but these were not observed in the lignicolous species (*L. unisepata*). Similar trabeculate carbonaceous outer cells have been observed in *Corollospora besarispora*, another arenicolous fungus (Sundari et al., 1996). This demonstrates that the environment can markedly influence the phenology of an ascomycete, as has also been demonstrated for the variability in the length of the necks in *Lulworthia* and *Halosphaeria appendiculata* (Jones, 1962).

The genus has been shown to be polyphyletic based on 18S and 28S sequences analysis and two new genera erected to accommodate species that do not group within the genus *Lulworthia sensu stricto* (Campbell et al., 2005). However, further species need to be studied at the molecular level to fully resolve the taxonomic position of the various species. We include three species not recognized by Kohlmeyer and Volkmann-Kohlmeyer (1991a) and Hyde et al. (2000): *L. floridana* with ascospores measuring 230-266 × 3.6-5.7 μm and with dark brown ascomata; *L. purpurea* with a thin ascomatal wall comprising only two layers of cells, purplish brown ascomata turning green in lactophenol and median ascospores 185-265 × 3-4 μm and *Rostrupiella danica*, a new species with distinctive inhibition hyphae in the wood and a pad of parenchymatous tissue separating the centrum from the ostiole in the neck (Koch et al., 2007). *Lulworthia purpurea* differs from many *Lulworthia* species in the thin nature of the ascomata, which is only two-layered.

Anamorphs of members of the Lulworthiales include: *Anguillospora marina* (*Lindra obtusa*), *Cirrenalia pygmea*, *Cirrenalia tropicalis*, *Cumulospora varia* and *Orbimyces spectabilis* (all with different *Lulworthia* spp.) and *Zaleron maritima* (*Lulwoana unisepata*) (Jones et al., 2008) (Figs. 62, 63).

As the result of sequence analysis of 18S and 28S a number of transfers have been proposed: *Lulworthia crassa* to Kohlmeyeriella, *Lulworthia linoarenaria* to Lulwoidea and *Lulworthia unisepata* to Lulwoana (Campbell et al., 2005), but a key to the new genera was not provided. Although there is good molecular support for the separation of Lulwoidea and Lulwoana from *Lulworthia*, morphological differences are few.

1. Ascospores 9-12-septate, 170-240 × 4 μm.................... *L. lindroidea*

1. Ascospores with no septa............................................ 2

2. Lignicolous species...................................................... 3

2. On other substrata................................................. 6

3. Ascospores over 500 μm long (500-756 × 3-5 μm) tropical.................................................. *L. grandispora*

3. Ascospores shorter than 500 μm................................... 4

4. Ascomata deeply embedded in the wood......................... 5

4. Ascomata more superficial, dark brown, 230-266-320 × 3.6-4.2-5.7 μm.......................... *L. floridana*

5. Ascospores 155-299 × 3.3-4 μm........... *L. longirostris*

5. Ascomata purple in colour, elongate, ascospores 200-350 μm elongate........................................ *L. purpurea*

6. Ascomata on coral or coralline algae............................ 7

6. Ascomata on marine grasses or on *Fucus*.................... 9

7. Ascospores over 200 μm (200-270 × 2.5-6 μm)............ *L. kniepii*

7. Ascospores shorter than 200 μm................................. 8

8. Ascospores 80-150 × 5.5-8.5 μm, on coral rock.............. *L. calicola*

8. Ascospores 120-180 × 4-5 μm, coralline red algae, conch shells, coral reef................................................... *L. curalli*

9. On the brown alga *Fucus*, ascospores 70-100 (-126) × 4-6 μm.................................................. *L. fucicola*

9. On marine grasses.......................................................... 10

10. On *Zostera* rhizomes and leaves, ascospores 230-308 × 2-4 μm.................................................. *L. halima*

10. On culms of *Spartina* species, ascospores 350-526 μm.................................................. *L. medusa*

Ascomata ellipsoidal-cylindrical, ostiolate, gregarious, deeply embedded, subhyaline, cylindrical neck brown, periphysate, lacking paraphyses or catenophyses, asci cylindrical, short pedunculate, uni- or bitunicate, thin-walled, no apical pore, deliquescing early, no apical apparatus, ascospores ellipsoidal to fusiform, unicellular, hyaline, with a conical acute chamber at each pole. An unusual genus forming galls on the larger brown algae (Cystoseira, Halidrys, Sargassum) with unicellular, hyaline ascospores with polar cap-like appendages that are divided into a series of chambers containing mucous. Kohlmeyer and Volkmann-Kohlmeyer (2003b) illustrate H. irritans with mucous released from the ascospore end chambers through an apical pore. Although they classify the genus in the Phyllachoraceae, Phyllachorales, Inderbitzin et al. (2004) have shown that Haloguignardia irritans clusters within the Lulworthia complex, as a separate branch from the L. uniseptata and L. cf purpurea clade (Fig. 62.) Clearly further investigations at the ultrastructural and molecular level are required to finally resolve the taxonomic position of the genus.

1. In the brown algae Cystoseira or Halidrys ............ 2
1. In Sargassum species ................................................ 3

2. Ascospores longer than 60 μm............. H. cystoseirae
2. Ascospores shorter than 60 μm............ H. irritans

3. Ascospores with persistent appendages .................. .......................................................... H. tumefaciens
3. Ascospore appendages deciduous............... 4

4. Ascospores shorter than 35 μm............ H. decidua
4. Ascospores longer than 35 μm............. H. oceanica

Spathulosporaceae

S. phycophila A.R. Caval. & T.W. Johnson, Mycologia 57: 927, 1965 (Type species).
Thallus crustose on algal host, though not always evident, ascomata subglobose, ovoid, pyriform, subulate, ostiolate, papillate or epapillate, coriaceous or leathery, dark brown, sterile hairs enclosing ascoma, lacking paraphyses, asci clavate, thin-walled, unitunicate, deliquescent early, ascospores fusiform, cylindrical, ellipsoidal, 0-3-septate, hyaline, with an appendage at each pole. Antheridia, spermatia and trichogynes reported (Kohlmeyer and Kohlmeyer, 1979). All species are parasites of the marine red algal genus Ballia (B. callitrichia, B. hirsuta, B. scoparia) often colonizing a single cell of the filamentous thallus. Primarily known from Australia, New Zealand, Antarctic and sub-Antarctic waters, and more recently from Argentina, Chile and Kerguelen and Falkland Islands waters (Kohlmeyer and Kohlmeyer, 1975a). Initially Spathulospora was thought to be a primitive ascomycete evolved from a red seaweed ancestor, with its hyaline, unicellular ascospores, conical appendages filled with "mucous", hairs bearing antheridia, simple trichogynes and asci that deliquesce early in development. Sequence data of the genera Spathulospora and Haloguignardia phylogenetically place them in the Lulworthiales although no formal taxonomic transfer has been undertaken (Inderbitzin et al., 2004; Campbell et al., 2005) (Figs 62, 63).

1. Ascomata without hairs, ascospores 40-50 × 4-9 μm...
   1. Ascomata without hairs, ascospores 20-30 × 2-3 μm... S. antarctica
   2. Ascospores longer than 65 μm.......................... 3
   3. Ascospores shorter than 65 μm.......................... 4

2. KORALIONASTETEAL

Koralionastetaceae

This is a new order erected to accommodate the genera Koralionastes and Pontogeneia, previously not assigned with confidence in any order (Campbell et al., 2008). These two genera form a monophyletic clade basal to the Lulworthiales clade. Morphologically they differ in the mature hamathecium, presence of periphyses, (absent in the Lulworthiales) but present in Koralionastetales; and the absence of apical mucous-filled polar appendages in Koralionastes and Pontogeneia.

Key to the genera

1. On coral rock, associated with crustose sponges......
   1. On algae............................................... Pontogeneia


A unique group of fungi occurring on coralline-coated rocks and sponges, known from the Atlantic Ocean, Belize, Central America (Kohlmeyer and Volkmann-Kohlmeyer, 1987b) and Pacific Ocean, Queensland, Australia (Kohlmeyer and Volkmann-Kohlmeyer, 1990b). Characterised by large ascoma (500-1220 μm diam.), simple septate paraphyses, clavate asci, short pedunculate, deliquescent at maturity, no apical apparatus, ascospores hyaline, thick-walled and septate near the apices, no appendages, with spermatia.

1. Ascospores ovoid, peridium 3-4 strata.................. 2
   2. Ascospores 4-septate (1-6), 94-131 × 50-77 μm, peridium 4 strata, 30-60 μm............. K. ovalis
   3. Ascospores 2-septate (2-6), 123-170 × 61-89 μm, peridium 3 strata, 125-190 μm............. K. giganteus

2. Koralionastes


A unique group of fungi occurring on coralline-coated rocks and sponges, known from the Atlantic Ocean, Belize, Central America (Kohlmeyer and Volkmann-Kohlmeyer, 1987b) and Pacific Ocean, Queensland, Australia (Kohlmeyer and Volkmann-Kohlmeyer, 1990b). Characterised by large ascoma (500-1220 μm diam.), simple septate paraphyses, clavate asci, short pedunculate, deliquescent at maturity, no apical apparatus, ascospores hyaline, thick-walled and septate near the apices, no appendages, with spermatia.

1. Ascospores ovoid, peridium 3-4 strata.................. 2
   2. Ascospores ellipsoidal, peridium 2 strata........... 4
4. Ascospores 6-septate (1-8), 81-127 × 27-45 μm, peridium 40-70 μm..........................K. ellipticus
4. Ascospores 8-septate (6-10), 81-122 × 18-28 μm, peridium 60-90 μm..........................K. angustus


Phycomelaina laminariae

Castagnea chordariiformis

Polystigma apophlaeae

Spartina......................................

3. MAGNAPORTHALES see p. 137, 144

4. PHYLLACHORALES

Key to Phyllachorales and Phyllachorales incertae sedis

1. Ascospores unicellular ............................................. 2
   1. Ascospores septate ............................................. 3
   2. Ascospores ellipsoidal, 15-18 × 5-6 μm parasitic on the alga Apoplaea hyalii ... Polystigma apoplaeae
   3. Ascospores subglobose to ellipsoidal, 13.5-18.5 × 9-12 μm, saprobic on Spartina................................. Phyllachora paludicola
   3. Ascospores 1-septate, 18-28 × 6-8 μm, parasitic on brown algae......... Phycomelaina laminariae
   3. Ascospores 3-septate ........................................... 4
   4. Ascospores 26-31 × 6-8.5 μm, not constricted at the septa, many oil globules per cell, no sheath ......................... Marinophyris mangrovei
   5. Ascospores 25-39 × 12-14 μm, with a sheath .......................................................... Mangrovispora pemphis

Phyllachoracea

Phyllachora Nitschke ex Fuckel, Jahrb. des Nassauischen Vereins Naturk. 23-24: 216, 1870.............................................................. 1

Described from dead leaves of Spartina alterniflora and collected widely in the USA. Well developed, prominent stromata 1.3-4 cm long, about 0.5 cm wide, with 5-20 ascomata, ostiolate, coriaceous, light brown, arranged in two to four parallel rows, no necks, periphysate; septate paraphyses, apically free; asci cylindrical, short pedunculate, thick-walled, unitunicate, without an apical apparatus, J-; ascospores subglobose to ellipsoidal, unicellular, hyaline, orange-yellowish in mass, and lacking a sheath or appendage (Fig. 65) (Kohlmeyer and Volkmann-Kohlmeyer, 2003a). Well placed in the Phyllachoraceae, Phyllachorales.

Polystigma DC., Fl. Fr. 6: 164, 1815 ........... (1)

Parasitic on the alga Apophlaea lyallii causing discolouration of the thallus, and known from a limited number of collections (Kohlmeyer and Demoulin, 1981). Ascospores 15-18 × 5-6 µm, hyaline, unicellular and lacking a sheath or appendage. Further collections are required to determine its phylogenetic relationship within the ascomycetes. Some 70 names are listed for Polystigma but many are referred to other genera, therefore the position of P. apophlaeae remains to be resolved (Index Fungorum). Polystigma sonneratiae has been described as a parasite causing leaf spots of the mangrove tree Sonneratia caseolaris and known from

Fig. 63. One of the MPTs inferred from LSU rDNA sequences of selected lulworthialean taxa, to show the phylogenetic relationship of the genus Rostruipilla. Bootstrap values higher than 50% are given above branches.
Fig. 64. *Rostrupiella danica*. a. Bell-like structure (arrowed) and base of the neck (arrowed N). b. Higher magnification of the neck region (arrowed N) with bell layer. c. Neck within the woody substratum filled with pseudoparenchymatous hyaline cells (arrowed). d. Base of the neck at the tip of the centrum. e. Bell-like structure pseudoparenchymatous cells (arrowed o) and bladder-like cells (arrowed B). Bars = 10 μm. Reproduced with permission from Botanica Marina.
collections in Australia and Philippines (Hyde and Cannon, 1992). This species is of terrestrial origin and may not be correctly assigned to this genus (Hyde and Cannon, 1992).

Fig. 65. Phyllachora patudicola. Ascospore. Bar = 10 µm.

**PHYLLACHORALES incertae sedis**


Described from intertidal decayed roots of *Pemphis acidula* with ascomata that are immersed beneath a thin stroma, globose to subglobose, hyaline, membranous, ostiolate, papillate, solitary or gregarious, periphysate, paraphyses numerous, branched, septate in a gel, asci cylindrical, fissitunicate, pedunculate, unitunicate, thin-walled, faint apical tube and apical thickening, ascospores ellipsoidal to fusiform, hyaline, 3-septate, slightly constricted at the septa, thin-walled and with a sheath like structure (Hyde, 1991a). Hawksworth *et al.* (1995) referred the genus to the Hyponectriaceae while Wang and Hyde (1999) excluded it from this family. Further studies are required before this little collected species can be assigned with confidence to any family.

*Mariosphaera* K.D. Hyde, Can J. Bot. 67: 3080, 1989.................................................... (1)

☼ *M. mangrovei* K.D. Hyde, Can J. Bot. 67: 3080, 1989 (*Type species*).

Ascomata ellipsoidal, globose, subglobose, elongate, immersed, ostiolate, papillate, membranous, light to dark brown, solitary to gregarious, periphysate, paraphyses wide, simple, septate, asci clavate, short pedunculate, persistent, unitunicate, thin-walled, J- subapical plate and pore, ascospores broad ellipsoidal to fusiform, initially 0-septate but becoming distinctly 3-septate, hyaline, smooth-walled and lacking a sheath or appendages (Fig. 66). The species is easily identified by its wide, regularly septate paraphyses.

Hyde (1989b) initially placed the genus, with reservations, in the Phyllachoraceae, but this has received little support (Kirk *et al*., 2001). The ascus tip is thickened, with a small flattened ocular chamber but no spore discharge has been observed (Read *et al*., 1995). Molecular results, based on SSU and LSU rDNA analyses, revealed that *Marinosphaera* does not have any affinities with the Phyllachorales. Phylogenetically, *M. mangrovei* is located between the Halosphaeriales and the Microascales, but without any closely related taxa (Fig. 67). Therefore its taxonomic position is not fully resolved at this time, suggesting a further group of fungi remains to be discovered. This is a common species, often found as an early colonizer of mangrove wood (Alias, 1996).


*P. laminariae* (Rostr.) Kohlm., Phytopathol. Z. 63: 350, 1968 (*Type species*).


Pseudostroma black ellipsoidal spots on cortex of algae, ascomata subglobose or ampulliform, immersed in the pseudostroma, ostiolate, epapillate, leathery, hyaline to brown, clypeus dark brown, gregarious, papillae with periphysoids. Originally described by Rostrup (1894) it has been transferred variously to other genera until Kohlmeyer (1968b) assigned it to this genus. It occurs on the brown marine algae: *Laminaria* species and possibly *Alaria esculenta*. Still not assigned with authority to an order and requiring further investigation.

**Unitunicate ascomycetes family incertae sedis**

Key to unitunicate ascomycetes *incertae sedis*

1. In seaweeds .......................................................... 2
2. In wood and other cellulosic materials ...................... 5
2. On green algae ......................................................... 3
2. On red seaweeds ...................................................... 4
3. Ascospores elongate ellipsoidal, 8.5-17.5 × 3-5 µm, on Prasiola................................. Mastodia tessellata
3. Ascospores broad ellipsoidal, 8.5-14 × 3.5-7 µm, on Blidingia.................................. Turgidoscum ulvae
4. Ascospores with polar appendages, 10-18 × 3-6 µm .............................................. Retrostium amphiroae
4. Ascospores lacking appendages, 35-68 × 12-20 µm ............................................. Hispidicarpomyces galaxauricola
5. Ascospores unicellular ............................................. 6
5. Ascospores septate ................................................... 7
6. Ascospores hyaline ................................................. 7
6. Ascospores yellow to pale brown ........................................ 8
7. Ascospores smooth walled, filiform 110-180 × 3-4 µm ........................................ Gaeumannomyces medullaris
7. Ascospores verrucose, broadly ellipsoidal, 14-18 × 7.5-9.5 µm .................................. Papulosa amerospora
8. Ascospores 5-7-septate, 34-44 × 8-10 µm .................................................... Pseudohalonectria halophila
8. Ascospores 3-septate, 37-66 × 9.5-14 µm ................................................................. Buergenerula spartinae

**Hispidicarpomycetaceae**

*Hispidicarpomyces* Nakagiri, Mycologia **85**: 639, 1993...(1)

*H. galaxauricola* Nakagiri, Mycologia **85**: 639, 1993 (Type species).

An unusual ascomycete with large ascomata on the red alga *Galaxaura falcata*, 700-1600 µm high, 800-2100 µm diam. Breaking through from the medullary layer of the host, solitary, ostiolate, epapillate, black arising from collapsed spermochia. Peridium composed of three-layers, the outer layer with thick-walled short hyphal projections. Paraphyses 1-3-septate, branched. Asci are obclavate to obpyriform, thin-walled, unitunicate, deliquescing early and lacking an apical apparatus. Ascospores are ellipsoid to elliptic-fusiform, unicellular, hyaline and without appendages or sheath. A feature of the species is the production of verticilliate spermatophores, with closely packed ampulliform phialides terminating in a column and producing hyaline, thin-walled spermatia, inflated at the apex and cupulate at the base. Trichogynes are 2-4-septate, simple, cylindrical, brown and thick-walled at the base. Not only is the genus different from *Spathulospora*, but is sufficiently so to warrant erection of a new family, the Hispidicarpomycetaceae (Nakagiri, 1993a).

Diagnostic features are the hyphoid thalli, spermochia multiverticilliate and the hispoid ascoma, which develops by radial growth of hyphae of the ascoma initial (Nakagiri, 1993). The affinity of *Spathulospora* with the Lulworthiales raises the question as to the phylogenetic position of Hispidicarpomyces.

**Spathulosporaceae**

*Retrostium* Nakagiri & Tad. Ito, Mycologia **89**: 485, 1997...................................................... (1)

*R. amphiroae* Nakagiri & Tad. Ito, Mycologia **89**: 485, 1997 (Type species).

Ascomata are conical to hemispherical, superficial, solitary or united, carbonaceous, ostiolate, epapillate, and black. Peridium 45-85 µm thick, but thinner at the base, and two-layered. Ostiolar canal forming a tube-like projection into the centrum but lacking periphyses. Asci subglobose to obpyriform, thin-walled, unitunicate early deliquescing and without an apical apparatus. Ascospores oblong to ellipsoidal, unicellular, hyaline, with polar mucilaginous, subglobose appendages.

Pincilliate spermatophores and trichogynes are also present. Nakagiri and Ito (1997) are of the opinion that *Retrostium* represents a phylogenetic link between spathulosporalean fungi and other algal-inhabiting marine fungi in *Spathulospora*, the genera *Chadefaudia* and *Haloguignardia*. This observation was prophetical in view of the recent referral of *Haloguignardia* to the order Lulworthiales (Inderbitzin et al., 2004; Campbell et al., 2005).

**MAGNAPORTHALES**

*Magnaporthaceae*

Since this monograph was accepted for publication, Thongkantha et al. (2008) erected the order Magnaporthales. The genera *Buergenerula*, *Gaeumannomyces* and *Pseudohalonectria* are now included in this order. See page 144 for further discussion.
Buergenerula Syd., Ann. Mycol. 34: 392, 1936.............................................................. (1)


Ascomata subglobose to obpyriform, immersed, ostiolate, papillate, coriaceous, light to dark brown, solitary or gregarious, necks periphysate, paraphyses filamentous, simple, or branched, septate, asci cylindrical to subfusiform, short pedunculate, unitunicate, thick-walled, with an apical apparatus, ascospores clavate, thick at the apex, 3-septate, hyaline, lacking a sheath or appendages.

A species widely reported from Spartina species, usually growing on senescing or dead culms. It has been confused with Sphaerulina pedicellata, initially described from wood panels (Johnson, 1956) because of the thick-walled asci when young and thought to be bitunicate. Buergenerula spartinae is paraphysate, with unitunicate thick-walled asci and producing hyphopodia on the host. Although a Pyricularia anamorph has been reported for the genus, no anamorph has been

![Fig. 66. Marinosphaera mangrovei. a. Immersed ascomata with long necks on the wood surface. b. Cylindrical asci with subapical structures. c. Wide-septate, chain-like paraphyses. d. Ornamented ascospores full of oil globules. Bars a = 200 µm; b = 20 µm; c, d = 10 µm.](image)
Fig. 67. One of two MPTs inferred from combined SSU and LSU rDNA of Marinosphaera mangrovei, generated with maximum parsimony analysis. Bootstrap values higher than 50% given above branches. Scale bar indicates 10 character state changes.
reported for *B. spartinae*, except for spermatial like structures (Kohlmeyer and Gessner, 1976).


Anamorph: *Trichocladium medullare* Kohlm. & Volkm.-Kohlm.

Ascomata ellipsoidal, immersed, ostiolate, coriaceous, dark brown, solitary, necks cylindrical and periphysate, paraphyses numerous, unbranched, septate, tapering, asci fusoid to cylindrical, short pedunculate, thin-walled, unitunicate, with an apical ring, persistent, ascospores filiform, slightly tapering towards the base, without a sheath or apical appendages. The only marine species in the genus and found on the inundated parts of the culms of *Juncus roemerianus*. This species differs from other *Gaeumannomyces* species in having a *Trichocladium* anamorph (Kohlmeyer et al., 1995c). Cannon (1994) and Cannon and Kirk (2007) referred the genus to the Magnaporthaceae while Thongkantha et al. (2009) have erected a new order for the family.


Ascomata obpyriform, immersed, ostiolate, coriaceous, light to dark brown, long neck (130-410 µm) protruding beyond the substratum, paraphyses thin-walled, septate, unbranched, asci fusiform, short pedunculate, unitunicate, persistent, with a refractive tip below the ring, J-, ascospores ellipsoidal to ovoid, unicellular, hyaline, lacking a sheath or appendages. A frequent inhabitant of fragmented old leaves and culms of *Juncus roemerianus*, and the first *Pseudohalonectria* species from marine waters (Kohlmeyer et al., 2005). It most closely resembles *P. adversaria* and *P. fuxianii*, but differs in that it is obligately marine and does not grow on wood. It also had distinctly broader ascospores than *P. adversaria*, and more septa than *P. fuxianii* (Kohlmeyer et al., 2005).

**Mastodiaceae**


**Fig. 68. Pseudohalonectria halophila.** Ascospore. Bar = 5 µm.

Ascomata subglobose, immersed in the algal thallus between the upper and lower algal cell layers, dark brown, papillate, ostiolate closed by a gelatinous plug, periphysate, no paraphyses, asci clavate developing all around the inside of the ascomata, pedunculate, unitunicate, thick-walled but deliquescent, ascospores ellipsoidal to ovoid, unicellular, hyaline, lacking a sheath or appendages. A parastic ascomycete on *Blidingia minima* var. *vexata*, and with a restricted known distribution (Schatz, 1980; Kohlmeyer and Volkmann-Kohlmeyer, 2003b).

Ascomata subglobose, immersed in the algal thallus, ostiolate, epapillate, coriaceous, dark brown, solitary or gregarious, necks periphysate, paraphyses not observed in mature specimens, centrum filled with a gelatinous matrix, asci clavate to subcylindrical, short pedunculate, unitunicate, lacking an apical apparatus, deliquescing, ascospores elongate-ellipsoidal to cylindrical, rounded ends, unicellular, hyaline, lacking a sheath or appendages. Kohlmeyer and Kohlmeyer (1979) give a detailed history of the placement of this taxon. A much confused taxon in need of re-evaluation, especially at the molecular level.

Papulosaceae  

Ascomata subglobose to ellipsoidal, immersed, ostiolate, papillate, coriaceous, dark brown, solitary, necks periphysate, lateral paraphyses tapering toward the tip, simple or branched, asci cylindrical, short pedunculate, persistent, with an aical ring, J+, ascospores broadly ellipsoidal, unicellular, hyaline, verruculose, with a thin gelatinous sheath. Saprophyte of senescent culms of Juncus roemerianus (Kohlmeyer and Volkmann-Kohlmeyer, 1993b). Winka and Eriksson (2000) refer P. amerospora to a new family, Papulosaceae in the sub-class Sordariomycetidae, and most closely related to the orders Ophiostomatales, Diaporthales, Sordariales and Phyllachorales. Insufficient ununiticate marine taxa have been sequenced to enable this family to be assigned to any order.

Untuncate ascomycetes genera incertae sedis

1. Ascomata perithecid............................................... 2  
2. Ascomata cleistothecial........................................ 7  
2. Ascosporas 0-septate............................................... 3  
3. Ascosporas 3-septate............................................... 5  
4. Ascosporas with more than 3 septa......Saccardella  
5. Ascosporas 3-septate............................................... 5  
6. Ascosporas with more than 3 septa......Saccardella  
7. Ascosporas 0-septate, with bipolar crown of delicate appendages................................................. Eiona  
8. Ascosporas with thread-like spirally unfolding appendages................................................. 9  
9. On wood, often associated with sand.....Dryosphaera  
10. Ascosporas with polar and lateral appendages........... ................................................... Marisolaris  
10. Ascosporas with a mucilaginous sheath..........Biflua  


Ascomata subglobose, immersed, ostiolate, coriaceous, sea-green to blue, neck long (165-345 µm) within the host, periphysate, paraphyses septate, unbranched in a gelatinous matrix, asci cylindrical, short pedunculate, thin-walled, ununiticate with an apical ring J-, ascospores fusiform, 3-septate, not constricted at the septa, hyaline lacking a sheath or appendages (Kohlmeyer et al., 1995d). Sporulating on the base of culms of Juncus roemerianus and regarded as an obligately marine ascomycete (Kohlmeyer et al., 1995d), characterized by sea-green to blue ascomata that are deeply embedded in the substratum. Kohlmeyer et al. (1995d) were unable to suggest a suitable family for its assignment and
further evaluation is dependent on fresh material for a molecular study.

**Aropsicus** Kohlm. & Volkm.-Kohlm., Syst. Ascomycetum **13**: 24, 1994 ................. (1)


Ascomata embedded in the outer small-celled tissue of *Juncus roemerianus*, cream-coloured, necks breaking through the cuticle, periphysate, periphysoids present, ascospores hyaline, 3-septate with a striated spore wall (Kohlmeier and Volkmann-Kohlmeier, 1994). The genus cannot be assigned to any order or family of the Ascomycota.


Cleistothecia globose or slightly flattened, coriaceous, white-light buff colour, gregarious, paraphyses absent, attached to wood by thick-walled hyphae with broad ascomatal appendages, asci clavariform to cylindrical, pedunculate, persistent, lacking an apical pore, ascospores ellipsoidal, 1-septate, constricted at the septum, hyaline and appendaged. Appendages appear as a ball of spirally arranged threads frequently terminating in ball-like structures (Koch and Jones, 1989).

Kirk *et al.* (2001) relegate this genus to *genera incertae sedis*. One of three marine cleistothecial ascomycetes, with sterile appendages on the peridium and growing on wood in association with sand (Koch and Jones, 1989). Their taxonomic relationship is unknown, and all require study at the molecular level, but are infrequently collected, possibly they are overlooked because of the small size of the ascomata. These cleistothecial ascomycetes are generally confined to cold waters and develop on cold incubation of wood samples, and remain in good condition for 2-3 weeks (Koch, pers. comm.).

**Crinigera** I. Schmidt, Nat. Naturschutz Mecklenburg 7: 11, 1969 .................... (1)

**C. maritima** I. Schmidt, Nat. Naturschutz Mecklenburg 7: 11, 1969 (*Type species*).

A genus of doubtful validity collected on the seaweed *Fucus*. Koch and Jones (1989) have shown the species is based on two taxa, and erected the genus *Dryosphaera* for the material on wood.


Cleistothecia globose, slightly flattened, superficial, white-light buff coloured, coriaceous, gregarious, attached to wood by thick-walled hyphae branched at their tips, ascomata covered with short appendages, each with a stalk and a terminal crown of repeatedly divided branches, asci numerous, developed on lobed hymenium, thick-walled when young, possibly bitunicate, broadly clavate, short pedunculate, persistent, paraphyses absent, ascospores 1-septate, constricted at the septum, hyaline and appendaged. Appendages appear as a ball of spirally arranged threads frequently terminating in ball-like structures (Koch and Jones, 1989).

Papers published by Russian mycologists on marine fungi are rarely cited in the general literature (Kopytina and Andrienko, 1998) and consequently new taxa remain unknown.

1. On *Zostera*, ascospores 8.6-13.3 × 2.2-3.9 μm, appendages 9.4-17.6 × 0.3-1.1 μm.............. *D. tenuis*
2. On wood associated with sand......................... *D. tropicalis*
3. On wood associated with sand................................. *D. navigans*


Ascomata cleistothecial, subglobose, superficial, no ostiole, coriaceous, brown to
Fig. 69. Dryosphaera tenuis. Ascospore. Bar = 5 μm.

green, gregarious, lacking paraphyses, asci broadly clavate or ellipsoidal, uniloculate, thin-walled, scattered throughout the ascoma cavity, early deliquescing and lacking an apical apparatus, ascospores ellipsoidal, unicellular, hyaline, with a crown of appendages at both ends of the spore (Kohlmeyer and Kohlmeyer, 1979). Ascospore appendages formed by fragmentation of a sheath (Jones and Moss, 1978). This species is in need of a molecular study to determine its ordinal rank as it may not belong in the Eurotiaceae. Collected in abundance on wood associated with sand (Koch and Jones, 1983; Farrant et al., 1985).


An unusual ascomycete with large ellipsoidal ascomata (>750 μm), deeply embedded in mangrove roots of Rhizophora mangle, necks almost as thick as the ascoma, and the ostiolar canal filled with a network of thin hyphae, embedded in a matrix. Peridium 3-layered and a paraphysate hamathecium, the upper third of the locule filled with thin anastomosing hyphae in a gelatinous matrix. Asci thick-walled, not fissitunicate with an ocular chamber with a net-like apical apparatus, J-, and ascospores ellipsoidal to ovoid, 59-77 × 33-44 μm, unicellular and hyaline (Kohlmeyer and Volkmann-Kohlmeyer, 1991b). No known anamorph and monotypic. It superficially resembles Lignincola tropica or Saagaromyces abonnis, but differs in ascoma ontogeny, asci with a net-like substructure to the ascus tip and ascospores that are unicellular.


Ascomata globose, coriaceous, white-light buff coloured, gregarious, superficial on wood, and attached to the surface by thick-walled hyphae, ascomata covered by numerous simple horn-like appendages, tapering, paraphyses absent, asci broadly clavate, pedunculate, persistent, bitunicate with an exotunicate and endotunica visible when mounted in water, ascospores 1-septate, not constricted at the septum, hyaline with single polar and four equatorial appendages, each appendage comprising an inner part which is looped like a bridge and an outer part a sheath that envelopes the spore. Another genus, which at the present time, cannot be assigned to any taxonomical group and is only known from a few collections on wood associated with sand (Koch and Jones, 1989).

Orcadia G.K. Sutherl., Trans Br. Mycol. Soc. 5: 151, 1915.......................... (1)

O. ascothylli G.K. Sutherl., Trans Br. Mycol. Soc. 5: 151, 1915 (Type species).

Ascomata subglobose or pyriform, immersed, ostiolate, papillate, coriaceous, subhyaline, gregarious, necks a papilla or long (80-180 μm), periphysate, paraphyses? septate, simple or anasotmosing, deliquescing early, asci clavate, subcylindrical or subfusiform, short pedunculate, thin-walled, uniloculate, with an apical thickening but no apical apparatus, operculum present, ascospores cylindrical, slightly curved, 3-septate, constricted at the septa, hyaline, no sheath or appendages. Initially referred by Sutherland (1915) to the Hyponectriaceae, Xylariaceae. Rossman et al. (1999) excluded the genus from the Hypocreales because of the reported operculate asci, broad opening of the ascomata, and numerous interthecial elements (Kohlmeyer and Kohlmeyer, 1979). A poorly researched species, parasitic/saprophytic on the larger brown algae (Ascophyllum, Fucus, Pelvetia). Rossman et al. (1999) suggested an affinity with the Pezizales because of the operculate asci.
**Rhizophila** K.D. Hyde & E.B.G. Jones, Mycotaxon 34: 527, 1989 ............................ (1)  
**R. marina** K.D. Hyde & E.B.G. Jones, Mycotaxon 34: 528, 1989 (Type species).  
Ascomata large (500-965 µm wide, 425-730 µm long), globose to subglobose, immersed, ostiolate, papillate, periphysate, coriaceous, dark brown to black, solitary or gregarious, paraphyses irregular shaped cells, septate, asci clavate, pediculate, unitunicate, thin-walled, with a slight apical thickening, no apical apparatus, ascospores ellipsoidal to fusiform, unicellular, hyaline but becoming yellowish brown, lacking a sheath or appendages. Often found deeply embedded in mangrove wood and the droppers of *Rhizophora* species (Hyde and Jones, 1989a, Jones, unpublished data).  
Similarities with the Phyllachoraceae and *Glomerella* were reported by Hyde and Jones (1989a), but molecular sequences suggest that it may be better placed in the Microascales or Hypocreales (Spatafora and Blackwell, 1994; Winka and Eriksson, 2000).

**Saccardoella** Speg., Michelia 1: 461, 1879…(3)  
Ascomata globose to subglobose, immersed or erumpent, ostiolate, papillate, coriaceous, carbonaceous, solitary or gregarious, dark brown to black, clypeate, no periphyses, paraphyses numerous, filamentous, hypha-like, branching and anastomosing in gelatinous matrix, asci long-cylindrical, short pediculate, thin-walled, unitunicate, apically flattened or flattened with a subapical ring, ascospores fusiform, 3-9-septate, not constricted at the septa, with acute ends, variable septation, hyaline, with a thin to well developed gelatinous sheath. A genus referred to the Clypeosphaeriaceae and Barr (1994) later revised and extend the limits of the genus. There is confusion about the ascus structure in *Saccardoella* as in slide preparations the ascus may appear thickened and behave like a bitunicate ascus. Mathiassen (1989) was of the opinion that the asci are bitunicate in *Saccardoella transylvanica*, but Barr (1990b) does not concur with that view. Geographically the genus is well distributed with terrestrial, marine and freshwater species (Hyde, 1992; Tsui *et al*., 1998).

1. Ascospores with 7-9 septa, 26-33 × 6-8 µm .......................... ...............................  
   .............................................................................................................. *S. mangrovei*  
1. Ascospores with fewer than 7 septa ................................. 2  
2. Ascospores with (4-) 5-(-6) septa, 19-26 × 6-8 µm ..  
   .............................................................................................................. *S. rhizophorae*  
2. Ascospores with 3 septa, 25-31 × 7.5-10 µm............  
   .............................................................................................................. *S. marinospora*  

**MAGNAPORTHALES MAGNAPORThACEAE**

Canon and Kirk (2007) accepted the Magnaporthaceae in the Sordariomycetes, a small family of unitunicate perithecial ascomycetes, comprising 13 genera and 93 species (Kirk *et al*., 2008). *Gaeumannomyces* (2 species) and *Magnaporthe* (5 species) are the key members of the family as many species are economically important plant pathogens. *Magnaporthe grisea* (anamorph *Pyricularia oryzae*) is the cause of rice blast and a wide variety of plants (Yaegashi and Herbert, 1976). Because few of the Magnaporthaceae have been sequenced, placement at the ordinal level has remained unresolved (Hibbett *et al*., 2007, while Lumbsch and Hundorf (2007) and Zhang *et al*. (2006) merely refer the family to the Sordariomycetidae along with two other poorly studied families, Annulatascaceae (Wong *et al*., 1998) and Papulosaceae (Winka and Eriksson, 2000).

Thongkantha *et al*. (2008) investigated the molecular phylogeny of selected genera in the Magnaporthaceae (*Buergenerula spartinae*, *Gaeumannomyces* spp., *Magnaporthe* spp., *Mycoleptodiscus coloratus*, *Ophioceras* spp. and *Pseudohalonectria* spp.), using 18S and 28S rDNA phylogeny. These genera formed a monophyletic clade, closely related to the Diaporthales and Ophiostomatales. However, the Magnaporthaceae could not be accommodated in any known fungal order and consequently they erected a new order, the Magnaporthales (Thongkantha *et al*., 2008).

Marine representatives of the Magnaporthaceae, Magnaportheales are *Buergenerula*
Spartinae, Gaeumannomyces medullaris and Pseudohalonectria halophila. Only G. medullaris has a known anamorph in Trichocladium (T. medullare). The anamorphs of Gaeumannomyces are generally Phialophora species.

Ascomycetes, and their anamorphs comprise the largest marine fungal group (424 + 94 species, respectively) and the most intensively studied. The orders Halosphaeriales and Lulworthiales have been extensively studied at the molecular level, both forming distinct clades in the Sordariomycetidae incertae sedis (Hibbett et al., 2007). These results have shown that the Halosphaeriales are a sister group to the Microascales and are secondary invaders of the marine environment (Spatafora et al., 1998). It has been confirmed that the Lulworthiales are morphologically and phylogenetically distinct from the Halosphaeriales (Kohlmeyer et al., 2000). Another significant taxonomic result has been the erection of a new order the Koralionastetales to accommodate the little known genera Koralionastes and Pontogeneia, previously not assigned with authority to any group (Campbell et al., 2008). Molecular studies have also enabled a better understanding of the generic relationships of many marine ascomycetes: Corollospora (Campbell et al. (2002), Halosarpheia, Lignincola and Nais (Pang et al., 2003a, b), Antennospora (Pang et al., 2008) and anamorphic Lulworthiales (Jones et al., 2008).

In comparison the bitunicate marine ascomycetes have been less well served at the molecular level. Some 40 marine bitunicate ascomycetes have been sequenced, but assignment to families remain unresolved. This reflects the genera lack of resolution within the bitunicate ascomycetes. Sequences of Manglicola guatemalensis places it in the Jahnulales.

**TOTAL ASCOMYCETES.......................... (424)**
Section C:
ANAMORPHIC FUNGI
(COELOMYCETES and HYPOMYCETES)

1. Spores produced on hyphae ............... Hyphomycetes
2. Spores produced in sporocarps.........Coelomycetes

HYPOMYCETES
1. Conidia hyaline .............................................. 2
1. Conidia coloured............................................. 11
2. Conidia 1-celled............................................. 3
2. Conidia septate.............................................. 7
3. Conidia produced in a sporodochium......... 4
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   each end, conidia in short chains, on algae, drift 
   plant material ........................................ Cladosporium algarum
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   chains, slightly constricted at the septa, with short 
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   14.5-20.5 µm ..................................Bactrodesmium linderi
Mycelium septate, branched, phialides erect, simple, solitary or in groups, conidia elliptical, obovoid, broadly-ellipsoidal, short, truncate basal hilum, hyaline, forming a ball of conidia in a mucilaginous matrix (Tubaki, 1973b; Zuccaro et al., 2004). Acremonium fuci was isolated from the brown algae Fucus serratus (Germany) and F. distichus (Canada) with conidia measuring 5-8 (-15) × 3.2-5 (-6.0) µm (Fig. 70). This species groups within a marine clade of Emericellopsis and Stanjemonium species primarily isolated from marine habitats, and Zuccaro et al. (2004) suggest that further new species remain to be described from this environment.

Acremonium polyaleurum was recovered from coastal muds and characterized by its small conidia, the formation of aleuriospores and its better growth on seawater media when compared with growth on freshwater media. No teleomorphs have been reported for the two marine species listed above. Zuccaro et al. (2004) list a number of Acremonium species isolated from the sea: Acremonium potronii (skin lesion of a dolphin); A. tubakii (Fucus serratus); Emericellopsis minima (mangrove soil, Fucus serratus) and E. stolkiae (mud saline lake). Acremonium species are frequently encountered on incubated mangrove wood in the topics and warrant further investigation. See section on Emericellopsis, page 72.

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**Acremonium** Link, Magazin Ges. naturf. Freunde, Berlin, 3: 15, 1809. (2)


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**Fig. 70.** Conidiophores and conidia of *Acremonium fuci*. Bar = 5 µm.
**Allescheriella** Henn., Hedw. 36: 244, 1897. (1)


Sporodochial superficial, conidiophores monoblastic, terminal, determinate, cylindrical, straight, hyaline to pale brown conidia acrogenous, solitary, ellipsoidal to fusiform, unicellular, thick-walled, smooth, and pale brown (after Kohlmeyer, 1977). Only known from a collection made on wood from the Tongue of the Ocean, off the Bahamas Islands (Kohlmeyer, 1977).

**Alternaria** Nees, Syst. Pilze (Würzburg): 72, 1816..............................# Alternaria spp.

It is uncertain if these are truly marine fungi, but numerous collections have been listed in the literature. These include *Alternaria maritima* on a wide range of substrata (Sutherland, 1916; Johnson and Sparrow, 1961), *A. radicina* (Anastasiou, 1963b) and *A. tenuis* (Siepmann and Johnson, 1960; Anastasiou, 1963b). Kohlmeyer and Volkman-Kohlmeyer (1991a) do not regard any *Alternaria* species as obligately marine.

**Amorosia** Mantle & D. Hawksw., Mycol. Res. 110: 1373, 2006 ........................................... (1)


Teleomorph: may be found in the Sporormiaceae, Pleosporales (Mantle et al., 2006).

A dematiaceous hyphomycete isolated from the littoral zone in the Bahamas and producing the novel axa-anthraquinone scorpinone and caffeine. Conidiophores micromenatus or semi-macronematous, arising singly sympodially, monoblastic, determinate, subhyaline to pale brown and smooth walled. Conidia arising singly, 3-4-septate, pale brown to brown, smooth-walled lacking appendages or a sheath, 24-27.5 (-29) × 5.5-6.5 (-8) µm (Fig. 71). It most closely resembles *Trichocladium* species: *T. asperum*, *T. lignicola*, *T. opacum* and *T. pyriforme* but are not phylogenetically related (Mantle et al., 2006).

**Anguillospora** Ingold, Trans. Br. Mycol. Soc. 25: 401, 1942 .................................................. (1)

**A. marina** Nakagiri & Tubaki, Mycologia 75: 488, 1983.

Teleomorph: *Lindra obtusa* Nakagiri & Tubaki.

Mycelium septate, hyaline, conidiophore simple or branched, hyaline, conidiogenous cells hyaline, monoblastic, terminal, precurrent, without a separating cell, conidia solitary, filiform, straight or curved, 9-13 (-19)-septate, swollen at both ends, hyaline, no sheath or appendages.

**Arthrobotrys** Corda, Pracht-Fl. Eur. Schimmelbild.: 43, 1839............................. (12)


**A. cladodes** var. **macroides** Drechsler, Mycologia 36: 144, 1944.

*Trichothecium cladodes* var *macroides* (Drechsler) Soprunov, Predacious fungi - Hyphomycetes and their...


**A. dactyloides** Drechsler, Mycologia **29**: 486, 1937.

**Arthrobotrys anochia** Drechsler, Mycologia **46**: 762, 1954.


**A. musiformis** Deschler, Mycologia **29**: 481, 1937.


**A. oligospora** Fresen., Beitr. Mykol. **1**: 18, 1850.

**Arthrobotrys superba** var. oligospora (Fresen.) Coem.

**Didymozooaphaga oligospora** (Fresen.) Soprunov & Galiulina, Microbiol., Reading **20**: 493, 1951.

**A. polycephala** (Drechsler) Rifai, Reinwardtia **7**: 371, 1968.

**Dactylaria polycephala** Drechsler, Mycologia **29**: 530, 1937.


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**Didymozooaphaga superba** (Corda) Soprunov & Galiulina, Microbiol., Reading **20**: 493, 1951.


Teleomorph: in the Orbiliaceae.

Colonies white to cream to yellow, fast growing. Mycelium hyaline, septate and branched. Conidiophores erect 100-900 µm long 1.5-5 µm wide, septate, rarely producing side branches, proliferating and bearing numerous conidia. Conidia are hyaline, 1-5-septate, variously shaped, elongate, ellipsoidal, pyriform, rarely constricted at the septa, up to 60 µm long (Fig. 72). These fungi from adhesive network devices for trapping nematodes. Johnson and Autery (1961) were the first to document a predacious fungus from brackish water habitats when they tentatively identified Arthrobotrys dactyloides growing on pine panels (Pinus taeda) submerged for 37 days in the saline zone of the Neuse River estuary, North Carolina. Meyers et al. (1963) have documented the relationship between marine filamentous fungi and nematodes. Generic delineation of predacious fungi varies between different authors, but generally based on the morphology of the nematode trapping structures.

1. Conidia predominantly 1-septate ......................... 2
2. Conidia with 2 or more-septate ......................... 6
3. Conidiophores up to 850 µm, conidia elongate, obovoidal, ellipsoidal. 13-26 × 7-10 µm. 8-20 conidia per conidiophore ........................................ A. cladodes
4. Conidiophores 100-280 µm, conidia broad-ellipsoidal 16-22 × 7-9 µm, 5-14 conidia per conidiophore ................. A. arthrobotryoides
5. Conidiophores 220-400 µm, conidia obovoid to clavate, 20-37.5 × 7.5-10 µm ...................... A. javanica
6. Conidiophores up to 900 µm ......................... 5
7. Conidiophore up to 700 µm, conidia elongate-clavate 24-36 × 6-8 µm .................................... A. dactyloides
This is a species widely reported as causing widespread mortalities of sea fans (Gorgonia ventailina, G. flabellum) in the Bahamas, Caribbean, Costa Rica, Cuba, Mexico, USA and Venezuela (Nieves-Rivera, 2002). Its identification as the causal pathogen was determined by a combination of morphology, virulence assays, histopathology and molecular analysis of the 18S of rDNA (Geiser et al., 1998).

Other Aspergillus species have been frequently reported from sediments, but treatment of these must await further studies.

4. Conidiophores up to 440 µm, conidia ovoid to pyriform, 17.5-28.8 × 10-16 µm, 10-15 conidia per conidiophore .......................... A. oligospora

5. Conidiophores up to 830 µm, conidia elongate, obovoidal, ellipsoidal, slightly curved, 25-40 × 8.8-12.5 µm............................. A. musiformis


7. Conidiophores 90-270 µm, conidia ellipsoidal 12.5-5 × 3.5-4.5 µm, three dimensional networks ..........

8. Conidiophores 78-580 µm, conidia cylindrical or elongate-ellipsoidal 20-45 × 5-12.5 µm, trapping with constricting rings.............. A. brochopaga

7. Conidiophores 150-500 µm, conidia 38-52 × 10-11 µm............................................ A. pyriformis

**Fig. 72.** Arthrobotrys mangrovispora. Conidiophores and conidium. Bar = 10 µm. (after Sue et al., 2008).

**Arthrinium** Kunze, Mykologische Hefte (Leipzig) 1: 9, 1817................................................ (1)

**A. algicola** (N.J. Artemczuk) N.J. Artemczuk  

Described as a *Papularia* species it is referred here to *Arthrinium*, and isolated from the brown alga Cystoseira barbata. Colonies terminal, hyaline, becoming dark, reverse colony pale brown, conidiophores hyaline, conidia lentiform, brown 10.5-15.3 × 5.8-7.9 µm and similar to *Papularia sphaerosperma*.

**Aspergillus** Link, Observ. Mycol. (Lipstae) 1: 16, 1809.............................................. (1)

**A. sydowii** (Bainier & Sartory) Thom & Church, The Aspergilli 147, 1926.

**Sterigmatocystis sydowii** Bainier & Sartory, Annls. Mycol. 11: 25, 1913.

**Fig. 73.** Sea fan (*Annella* sp.) showing tissue loss due to fungal infections (arrowed) (Photo by Sakanan Plathong).

**Fig. 74.** White encrustation spreading over the axial skeleton of sea fan (*Annella* sp.) (Photo by Sakanan Plathong).
As a result of the 2004 tsunami, many gorgonian sea fans of the genus *Annella* at Mu Ko Similan National Park, Andaman Sea, Thailand were destroyed or became infected by unknown microbes. These infections were characterized by white encrustations spreading rapidly over the axial skeleton causing tissue loss and finally death of the colony (Figs. 73, 74). Phongpaichit et al. (2006) in a preliminary report noted an *Aspergillus* sp. and other fungal strains had infected the sea fan based on morphological and molecular data.


Colony on agar, greenish-brown, becoming pale brown, mycelium septate, branched, hyaline to brown, conidiogenous cells cylindrical, subglobose to subclavate, hyaline, from which arise up to 12-14 conidia, conidia ovoid to obpyriform, thin-walled, brown, develop singly, first terminal, others laterally, with a short stalk or denticles, conidial mass released in a cluster. A common species isolated from sand with unicellular conidia forming cruciate arrangement of cells. When grown on different media and under different light regimes the conidia can become septate (Jones and Ward, 1973).

*Bactrodesmium* Cooke, Grevillea 12: 35, 1883.  
*B. linderi* (J.L. Crane & Shearer) M.E. Palm & E.L. Stewart, Mycotaxon 15: 319, 1982 ...... (1)  

Colonies sporodochial, hyaline becoming black, conidiophores micronematous, smooth, thin-walled, hyaline or thick-walled brown, conidiogenous cells holoblastic, integrated, terminal or intercalary, smooth, cylindrical, determinate, conidia solitary, subglobose to obpyriform, 1-2-septate, not constricted at the septa, dark brown to black 20-33.6 × 14.5-20.5 µm. Moved to *Bactrodesmium* because of its compact sporodochia, not a feature of *Trichocladium* which has mononematous and scattered conidiophores. Extremely common on mangrove wood and often confused with *Trichocladium* species, especially *T. nypae* which has smaller conidia 15-20 × 10-15 µm, 2-septate, both occurring in marine habitats (Goh and Hyde, 1999). No teleomorph reported for *B. linderi*, but other species show affinities with *Stuartella* (Dothideales, incertae sedis).

*Blodgetia* Harv., Smithson. Contrib. bot. 10: 42, 46, 1858.................................................. (1)  

B. bornetii E.P. Wright, Trans. R. Ir. Acad. 28: 25, 1881.

A confusing taxon, symbiotic (mycophycobioses) with the green algae *Cladophora caespitosa* and *C. fuliginosa* and collected from various localities (Kohlmeyer and Kohlmeyer, 1979). Mycelium growing within the inner and outer wall layer of the host, septate, branched, occurring as chlamydospores 35-150 × 8-33 µm, 1-7-septate terminal or intercalary chains, constricted at the septa, hyaline, yellow to yellow-brown (after Kohlmeyer and Kohlmeyer, 1979).

*Botryophialophora* Linder, Farlowia 1: 403, 1944.................................................. (1)  
*B. marina* Linder, Farlowia 1: 404, 1944 (*Type species*).

Hyphae septate, branched, hyaline to pale brown, conidiophores subglobose, lateral or apical, conidiogenous cells phialidic, flask-shaped, hyaline, conidia globose, unicellular, hyaline, no sheath or appendage. Reported from a wide range of substrata, wood, test panels, sand, sediments, but Kohlmeyer and Kohlmeyer (1979) question its marine status.

*Brachysporium* Sacc., Syll. fung. (Abellini) 4: 423, 1886 (emend Mason & Hughes)........... (1)  

Mycelium superficial on substratum, septate, pale brown, conidiophores simple, erect, septate, pale brown, conidia broadly pyriform, 21-27 × 10-17.5 µm, 2-3-septate, pale brown, and attached to the conidiophores by long spirally coiled pedicels. No sheath or appendages. This is the only species known from marine habitats and is most similar to the genera *Trichocladium* and *Cirrenalia*.  

Fungal Diversity
Collected by Schaumann (1973a) on drift bark in the sea at Heligoland, Germany, however Kohlmeyer and Kohlmeyer (1979) do not list it as a marine species.


Teleomorph: in the Halosphaeriales.


Teleomorph: in the Lulworthiales.


Teleomorph: in the Lulworthiales.

Conidiophores present or lacking, cylindrical, septate or lacking septa, hyaline to pale brown, conidiogenous cells monoblastic, integrated, terminal, determinate, conidia solitary, helicoid, 2-12-septate, generally constricted at the septa, brown, the apical cell generally the largest. The morphology and dimensions of the apical cell determine the species. A number of terrestrial species have been described but in our opinion these are not well placed in the genus (Raghukumar et al., 1988). The genus is not monophyletic (See Fig. 62) with teleomorphs in different ascomycete genera while new anamorphic genera need to be described (Jones, personal observation). Reported from a wide range of substrata in the sea.

1. Conidia 6-septate or more .......................... 2
2. Conidia 5-septate or less .......................... 3

2. Apical cell 6-12 µm, 4-9-celled, hyaline to pale brown, on *Juncus* ........................................... *C. adarca*

2. Apical cell 10-20 µm, 6-12-septate, reddish-brown, on wood............................................. *C. tropicalis*

3. Apical cells shorter than 16 µm ........................... 6
4. Apical cells over 16 µm long .................................. 4

3. Apical cell not hooked ........................................ 5
4. Apical cell hooked appearance, black to fuscous ........ *C. pygmea*

4. Apical cell large, 16-23 µm, conidia 3-4-septate, ............................................. *C. fusca*

5. Apical cell 11-22 µm, 2-4-septate, brown to dark brown ............................................. *C. pygmea*

5. Apical cell 16-20 µm, 3-6-septate, fuscous to grey-brown ............................................. *C. pseudomacrocephala*

6. Apical cell 9-16 µm, 3-5-septate, pale brown .................. .......... *C. basiminuta*
6. Apical cell 6-14 (17) µm, 2-6-septate, reddish-brown ............................................. *C. macrocephala*

**Cladosporium** Link Mag. Ges. naturf. Feunde, Berlin 7: 37, 1816 .......................... (1)

*C. algarum* Cooke & Massee, Grevillea 16: 80, 1888.

Hyphae septate, branched, pale brown, conidiophores macronematous, cylindrical, septate, simple, straight, smooth, brown, conidiogenous cells polyblastic, integrated, terminal with prominent scars, conidia ellipsoidal, with a basal scar, 0-3-septate, not constricted at the septa, smooth, thick-walled, olive-brown, no sheath or appendages. Reported from drift brown seaweeds and sea grasses. *Cladosporium* species are widely reported from drift material but no investigation has been carried out on the marine taxa.


**C. bulbosa** (Anastasiou) Nakagiri & Tubaki, Bot. Mar. 28: 489, 1985 (*Type species*).


Teleomorph: *Corollospora pulchella* Kohlm., I. Schmidt & N.B. Nair.

Conidia dark brown, composed of a basal bulbous cell and 1-3 radiating arms, 3-6-septate, hyaline to pale brown, cells constricted at the septa, in culture the bulbous basal cell may be absent and conidia develop as a single row of brown cells. Kohlmeyer and Kohlmeyer (1979) refer to these as chlamydospores. A common species on various substrata, particularly wood, when incubated with a layer of water over the surface.

152
**Cumulospora** I. Schmidt, Mycotaxon 24: 420, 1985.............................................................. (2)

**C. marina** I. Schmidt, Mycotaxon 24: 421, 1985 (Type species).


Teleomorph: in the Lulworthiales.

Mycelium septate, branched, superficial or immersed, pale brown, conidiophores absent, conidiogenous cells holoblastic, integrated, terminal, determinate, conidia initially spiral, cell division in several planes leads to a tangled knot of cells, numbering up to 40 or more, dark brown to black and constricted at the septa (Fig. 75). *Cumulospora varia* is well placed in the Lulworthiales (100% bootstrap value and 1.00 posterior probability). The two isolates of *Cumulospora varia*, isolated from Mu Ko Chang Island, Thailand, from different collections, are monophyletic, and form a sister group to *Lulwoana uniseptata* and its anamorph *Zalerion maritima* (Jones et al., 2008).

1. Conidia 52-91 × 40-71 μm, up to 20 cells, cells up to 30 μm .................................................... C. marina
2. Conidia 24-87 × 21-51 μm, up to 40 cells, cells up to 20 μm ................................................. C. varia

**Dactylellina** M. Morelet, Bull. Soc. Sci. naturelles Archeologie, Toulonet et du Var 178: 6, 1968.......................................................... (2)


**D. huisuniana** is well placed in the Lulworthiales (100% bootstrap value and 1.00 posterior probability). The two isolates of *Cumulospora varia*, isolated from Mu Ko Chang Island, Thailand, from different collections, are monophyletic, and form a sister group to *Lulwoana uniseptata* and its anamorph *Zalerion maritima* (Jones et al., 2008).

**Dendryphiella** Bubák & Ranoj., Ann. Mycol. 12: 417, 1914 ............................................... (2)


Teleomorph: in the Pleosporales, Pleosporaceae.

Hyphae septate, branched, pale brown, conidiophores macronematous, cylindrical, 1-3-septate, simple, apically swollen, pale brown to olive-brown, scars visible when conidia shed, conidia ellipsoidal, cylindrical, 1-11-septate, constricted at the septa, pale brown to olivaceous, solitary, with short stalks but not denticulate. Molecular sequence places these species in the Pleosporales (Jones et al., 2008). However the taxonomic position of the species needs needs resolution. Ellis (1976) referred the species to *Scolecobasidium*, however in the marine *Dendryphiella* species conidiogenous cells are enteroblastic and denticles are absent.

**Fig. 75.** *Cumulospora varia*. Conidium. Bar =10 μm.
Ellis (1976) described pegs on the conidiogenous cells but these may be confused with extensions from the conidia as seen in SEM micrographs (Fig. 76). A new genus may be warranted for the marine species.

1. Conidia 1-3-septate, 9-20 × 4-6 µm........... D. arenaria
1. Conidia 2-9-septate, 14-75 × 6-10 µm........... D. salina

**Dictyosporium** Corda, Beitr. Gesammten Natur-Heilwiss. 1: 87, 1836....................... (2)


Speira pelagica Linder, Farlowia 1: 407, 1944.

**Halenospora** E.B.G. Jones gen. nov............ (1)


**Fusarium** sp.

A number of *Fusarium* species have also been isolated from sediments and sand dunes including *Fusarium oxysporum* (Nicot, 1958) and *F. solani* growing on recovered submerged twigs of *Tamarix aphylla* (Anastasiou, 1963b), but none of these have been considered to be marine.

**Halenospora** E.B.G. Jones gen. nov............ (1)

Mycobank 513077

Holotypus: Halenospora varia (Anastasiou)

E.B.G. Jones [= Zalerion varium Anastasiou]

*Etymology:* From halen = welsh for salt in reference to its marine habitat and spora = spore.

Fungus leotiacearum mitosporarum. Mycelio hyalino, septato, ramoso; conidiophoris hyalinis, simplicibus, interdum nullis; conidiis fuscis vel nigris, conidiarum cellulis catenatis tandem tortuosis denique dictyosporiformibus terminalibus. Pneumocandin nullis.

Anamorphic Ascomycota (Leotiaceae).

Conidiophores simple or absent, conidia dark brown to black, cells formed in a chain, becoming tortous and appearing as terminal dictyospores. Pneumocandin negative. Phylogenetically groups with Glarea lozoyensis in the Leotiaceae.

Halenospora E.B.G. Jones comb. nov. Fig. 77, Mycobank 513086.

Zalerion varia (Anastasiou) E.B.G. Jones, comb. nov. Fig. 77, Mycobank 513086.

*Teleomorph:* In the Leotiaceae, Leotiales.

Zalerion varia (as Z. varium) E.B.G. Jones, comb. nov. Fig. 77, Mycobank 513086.

Zalerion varia (Anastasiou) E.B.G. Jones, comb. nov. Fig. 77, Mycobank 513086.

Worldwide in its distribution occurring on intertidal wood, submerge leaves, seedling of *Rhizophora mangle*. No teleomorph in the Leotiaceae has been identified for the species.

Although the conidia of both Halenospora and Zalerion initially are simple coil, they differ in that in *H. varia* they “produce a lateral rather than a terminal spiral as in *Z. maritima*” (Anastasiou, 1963a). The
individual cells in *H. varia* are narrower than those of *Z. maritima*, and form knot-like structures (Fig. 77) but they are not phylogenetically related. A number of fungi with similar morphology have been observed in tropical locations and await further identification and description (Jones, pers. comm.).

**Fig. 77. Halenospora varia.** Highly convoluted, knot-like conidia. Bars = 10 µm.


Teleomorph: *Corollospora luteola* Nakagiri & Tubaki.


Teleomorph: In *Corollospora* close to *C. luteola*.


Teleomorph: In *Corollospora*.

Mycelial hyphae branched, septate, hyaline. Conidiophore hyaline pleurogenous on the mycelium initially short and simple then becoming longer and septate. Conidiogenous cells holoblastic, terminal, sympodial or irregularly sympodial and denticulate with schizolytic secession. Conidia aleuriospores, C to U-shaped, rarely sigmoid, solitary, septate, hyaline, terminal and basal cells of mature conidia devoid of contents when mature (Fig. 78).

*Halosigmaidea* differs from *Sigmoidea* in the following respects: (1) Conidia markedly coiled, rarely sigmoid. (2) Conidial cells slightly swollen. (3) Conidial ends cells lacking contents. (4) Phylogenetically placed in the Halosphaeriales and (5) Marine species found predominantly on decaying seaweeds, especially members of the Fucales (Haythorn *et al*., 1980; Zuccaro and Mitchell, 2005). Mature conidia are generally not constricted at the septa, but before germination each conidial cell becomes rounded and separate into individual cells or several cell clusters, from which hyphae germinate.

1. Conidia less than 100 µm, 4-5 µm wide near the middle, with indentation at some septa.... *H. parvula*
2. Conidia 110-180 × 4.5-10 µm near the middle, colony pale.............................................. *H. marina*
2. Conidia 108-222 × 4.5-7.5 µm near the middle, colony bright yellow .................................... *H. luteola*


Colonies on wood black and glistening, conidiophores macronematous, unbranched, pale brown, smooth, 1-4-septate, conidiogenous cells indeterminate, terminal, polydenticulate,
conidia ellipsoidal or globose, irregularly helicoid, very tightly coiled, constricted at the septa, 15-20 × 12-15 μm, holoblastic produced on denticles by schizolysis, multisepitate, smooth and brown, occurring on Nypa fruticans (Hyde et al., 1999b). May be confused with Zalerion varia, but differs in the production of denticles on the conidiophores which are 1-4-septate, and long (30-70 × 2.5-4 μm).


Clavatospora stellatacula P.W. Kirk, Mycologia 61: 178, 1969

Hyphae septate, branched, hyaline, conidiophores phialidic, lageniform, simple, hyaline, conidia hyaline, 7-9 × 6-7 μm, enteroblastic-phialidic, stellate, unicellular, comprising a main axis and 3-4 subconical processes. Occurring on wood (pine test-blocks) and rarely collected since described by Kirk (1969).

**Monacrosporium** Oudem., Ned. kruidk. Archf, 2 sér. 4: 250, 1885 ............................................... (2)


Dactylaria eudermata (Drechsler) rifai, Mycologia 42: 40, 1950.


Geniculifera eudermata (Drechsler) Rifai, Mycota1x 2: 216, 1975.


Candelabrella thaumasium (Drechsler) Rifai, Reinwardtia 7: 369, 1968.

Dactylaria thaumasium (Drechsler) Rifai, Mycologia 29: 522, 1937.


Teleomorph: in the Orbiliaceae, Orbiliales.

1. Conidia 30-60 × 13-24 μm, broad at the apex, chlamydospores present.-------------------------- **M. thaumasium**

1. Conidia wider, end cells pointed, no chlamydospores .......................................................... **M. eudermatum**

**Monodictys** S. Hughes, Can. J. Bot. 36: 785, 1958.......................................................... (1)


A cosmopolitan species occurring on a wide range of substrata, largely with a temperate distribution. Conidiogenous cells monoblastic, integrated, terminal, determinate, cylindrical, doliiform or subspherical; conidia solitary, dry, acrogenous, simple, oblong rounded ends, pyriform, clavate, ellipsoidal, subspherical or irregular, muriform, brown to black, smooth or verrucose, basal cell sometimes inflated, paler and thinner walled than the other cells. Free sporulating in culture, conidial measurements vary between different collections. Teleomorph connection established by culture techniques (Mouzouras and Jones, 1985).

**Mycoenterolobium** Goos, Mycologia, 62: 171, 1970.......................................................... (1)


Conidiophores micronematous, mononematous, short, hyaline, conidiogenous cells integrated, determinate, conidia solitary, holoblastic, dictyosporus, flattened in one plane, variable shape, fan shaped, and dark brown (Nakagiri, 1993b). Numerous collections from submerged *Rhizophora stylosa* wood collected in the Shiira River, Japan.

**Orbimyces** Linder, Farlowia 1: 404, 1944 ... (1)

**O. spectabilis** Linder, Farlowia 1: 404, 1944 (Type species).

Teleomorph: In the Lulworthiales.

Conidiophores short arising from the mycelium, hyaline to pale brown, conidia with
a large black basal cell, subglobose to ovoid, thick-walled, glistening, with 1-2 branches giving rise to a crown of radiating appendages, generally one apical and 4 latter arms, each one 2-4 septa, slightly constricted at the septa, and pale brown. Sporulates in culture with a putative teleomorph in the Lulwothiales (Jones et al., 2008). 

**Orbimyces spectabilis**, an infrequently collected anamorphic fungus isolated from intertidal wood in Denmark, was basal to the **Lulwoidea** clade, but with weak support (Fig. 62). Reported from driftwood, test panels, and geographically widely distributed, but uncommon.

**Penicillium** Link, Magazin Ges. Naturf. Freunde, Berlin 3: 16, 1809 ................. (3) 


Teleomorph: *Eupenicillium limosum* S. Udea.

*Penicillium limosum* and *P. dimorphosporum* were described from marine sediments and *P. dravuni* collected on a submerged alga *Dictyosphaeria versluysii* by scuba diving off the coast of Fiji (Janso et al., 2005). *Penicillium dimorphosporum* was isolated from a mangrove swamp in Australia and has yellowish-green colonies, eventually turning deep reddish brown, conidiophores short, smooth, unbranched, phialides variable, conidia oval, smooth, later with prominent tubercles with no known teleomorph (Swart, 1970). *Penicillium dravuni* is monoverticillate, conidia spherical to subglobose, smooth-walled to finely roughened, colonies yellow-grey and belongs in the *P. thomii* series, subseries *P. turbatum* and most closely resembles *P. turbatum* (Fig. 79). Demonstrated to produce the secondary metabolites dictyosphaeric acids A and B and carviolin (Janso et al., 2005). No known teleomorphs for *P. dravuni* and *P. dimorphosporum*.

1. Colonies light brown to white, reverse amber to yellow at the margins, monoverticillate, conidia spherical, 2.5-3 µm long, 2 µm wide .......... *P. dravuni*

1. Colonies yellowish-green, becoming deep red, conidia oval, 2.4-2 \times 1.8-2 µm. *P. dimorphosporum*

1. Colonies pale, with no pigment production, irregular biverticillate, conidia globose to subglobose, 2.8-3.3 \times 2.5-3 µm ............................................ *P. limosum*
Conidiophores macronematous, monomematous, arising from hyphae on the wood, conidiogenous cells integrated, percurrent, conidia solitary, holoblastic, spathulate, 3-septate, apical cell hyaline, middle cells brown, basal cell hyaline, no sheath or appendage. Collected on intertidal wood of *Rhizophora stylosa* in the Shiira River, Shi-Ya-O, Japan (Nakagiri, 1993b). This species may be more common than reported in the literature (Hyde, 1988).

**Plectosporium** M.E. Palm, W. Gams & Nirenberg, Mycologia, 87: 398, 1995........ (1)  
Conidiophores superficial, solitary, unbranched to sparingly branched, smooth walled; conidiogenous cells phialidic, hyaline, cylindrical or subulate; conidia unicellular, hyaline, pale yellowish brown in mass, ellipsoidal, cylindrical to obovoid, sometimes curved, 3-10 × 2-4 µm, smooth-walled, guttulate, in slimy heads at the tips of the phialides (Fig. 80). The fungus is known from diseased mantis shrimp (*Oratosquilla oratoria*) collected in Yamaguchi Pref., Japan (Duc et al., in press).

**Stachybotrys** Corda, Icon. fung. (Abellini) 1: 21, 1837........................ (2)  
**S. atra** Corda, Icon. Fung. (Prague) 1: 21, 1837.  
Conidiophores, macronematous, branched, septate, hyaline to pale brown, verrucose, conidiogenous cells phialidic, in groups of 6-8 at the tip of the conidiophore, clavate, pale brown, conidia, ovoid to ellipsoid, verrucose, brown. **Stachybotrys atra** was reported from submerged twigs of *Tamarix aphylla* in the Salton Sea (Anastasious, 1963b) while **S. mangiferae** was reported on submerged wood of *Rhizophora stylosa* from the Shiira River, Japan by Nakagiri (1993b). **Stachybotrys** has been reported by others from marine habitats (e.g. Meyers and Reynolds, 1959) and is included here so that its occurrence in the sea can be documented and its ecological role determined.

**Sporidesmium** Link, Mag. Ges. naturf. Freunde, Berlin 3: 41, 1809 ......................... (1)  
Mycelium septate, branched, hyaline, annellophores borne on hyphae, hyaline, 3-18 µm, base cylindrical or slightly constricted, conidia thallic, subglobose to ovate, truncate base, rounded apex, conidial mass white, catenulate in a short chain (Tubaki, 1973a). Isolated from the seaweed *Undaria pinnatifida* (salted) and requires seawater for growth.

**Scopulariopsis** Bainier, Bull. Soc. mycol. Fr. 23: 98, 1907 ................................................. (1)  


Conidiophores macronematous, mononematous, septate, smooth or verrucose, pale brown to brown or olivaceous, solitary or in groups, conidiogenous cells monoblastic, integrated, terminal, percurrent, clavate to subglobose, thin-walled, conidia oblong, ellipsoidal, obclavate or subglobose, muriform, constricted at the septa or not, smooth, verrucose or echinulate, scar at the base, pale brown, brown or olivaceous, solitary acrogenous, no sheath or appendages. Marine species collected on various substrata: algae, salt marsh plants and on submerged wood panels in the sea (Johnson, 1957). It is doubtful if any of these belong in *Stemphylium*.

1. Conidia trigonous, conidia 40-82 × 18-46 µm, up to 12 trans-septate, 1-4-longi-septate, on the salt marsh plant *Triglochin*.............................. **S. triglochinicola**

1. Conidia ellipsoidal, on other substrata ............................... 2

2. Conidia 19-32 × 17-29 µm, 3-4-trans-septa, 2-4-longi-septa, on submerged wood panels .......................................................... **S. maritimum**

**Trichocladium** Harz., Bull. Soc. Imp. nat. Moscou 44: 125, 1871................................. (7)


Mycelium septate, branching, pale brown to brown, conidiophores poorly differentiated, short pedicels, 0-3-septate, simple, straight, smooth, conidia produced at the apex, hyaline or pale brown, conidiogenous cells monoblastic or polyblastic, integrated, terminal, solitary, clavate, obovoid, pyriform or cylindrical, 1-4-septate, thick-walled, smooth or verrucose, pale to dark brown to black (Jones et al., 2001) (Fig. 81). A number of marine species have been assigned to this genus, but they are not monophyletic, as the teleomorph connections referred to above indicates.

Goh and Hyde (1999) referred *Trichocladium linderi* to *Bactrodesmium linderi*. *Trichocladium nypae* differs only slightly from *T. linderi*. de Bertoldi et al. (1972) and Lepidi et al. (1977) pointed out that *Humicola alopallonella* was incorrectly referred to *Humicola* because it lacked one-celled conidia, thus Kohlmeyer and Volkmann-Kohlmeyer (1995) transferred it to *Trichocladium*.

1. Conidia 1-2 (3)-septate ........................................ 2

1. Conidia with more than 3-septate .............................. 3

2. Conidia 10-22 (-38) × 8-18 µm, apical cell 8.5-15.5 × 7-12 µm fuscous .......................... **T. achrasporum**

2. Conidia 6.5-13 × 3-9 µm, dark brown .................. **T. melhæ**

3. Conidia with 2-3-septa, 17-26 × 7-10 µm, distal cell fuscous, elongate ellipsoidal, on *Juncus* .................. **T. medullare**

3. Conidia with 2-3-septa, 15-20 × 10-13 (-15), curved, dark-brown on *Nypa* .............. **T. nypae**

3. Conidia with more than 3-septate ..................... 4

4. Conidia with 2-5 (-6)-septate, 25-32 × 12-17 µm, light brown, slightly constricted .......... **T. medullare**

4. Conidia with 2-4-septate .......................... 5

5. Conidia 25-47 × 8-20 µm, reddish-brown, subglobose, markedly constricted at the septa, 2-4-septate .......................... **T. constrictum**

5. Conidia 15-20 (45) × (8-) 10-24 µm, often sporodochial, dark brown, compressed, less constricted at the septa, 2-4-septate .......................... **T. achrassporum**
Tubercularia Tode, Fung. mecklenb. sel. (Lüneburg): 1: 18, 1790 ............................... (1)


Sporodochia cushion-shaped, sessile or short stalk, erumpent, conidiophores, filiform, simple, conidia produced at the apex, hyaline, conidia unicellular, ellipsoidal, hyaline to pink in a mass, smooth-walled (after Kohlmeyer and Kohlmeyer, 1979). Saprophytic on various Salicornia species and poorly known.


Teleomorph: In the genus Corollospora

Teleomorph: In the genus Corollospora.

V. anglusa Abdel-Wahab & Nagah., Mycoscience (in press).

Teleomorph: Corollospora anglusa Abdel-Wahab & Nagah.

Mycelium septate, branched, hyaline to pale brown, conidiophores cylindrical, septate, simple, conidiogenous cells monoblastic, integrated, generally terminal, conidia acrogenous, solitary, branched, septate, hyaline, main axis from which arise 2-3 side branches, typically tetra-radiate, and sporulating profusely on wood in a layer of seawater (Fig. 82).

Xylomyces Goos, R.D. Brooks & Lamore, Mycologia 69: 282, 1977 ............................. (1)


Xylomyces produces only chlamydospores of variable form, with 5 species described from freshwater and one on mangrove wood (Goos et al., 1977; Goh et al., 1997; Kohlmeyer and Volkmann-Kohlme yer, 1998d). Chlamydospores in Xylomyces rhizophorae mostly apical, single or in chains, rarely branching, filamentous, straight or curved, mostly widest at the tips, tapering towards the base, dark brown, 11-34-septate and constricted at the septa (Kohlmeyer and Volkmann-Kohlme yer, 1998d). They also reported and illustrated Xylomyces chlamydosporus from a saline location in Bay Minette, Alabama. We also include this species in the key as it may be encountered in marine habitats.

1. Chlamydospores with 11-34 (-64)-septa, 95-370 (-500) × 8-16 µm ........................................... X. rhizophorae

   1 Chlamydospores with 5-19-septate, 95-420 × 26-42 µm ........................................... X. chlamydosporus


Helicoma maritimum Linder, Farlowia 1: 405, 1944.

Helicoma salinum Linder, Farlowia 1: 406, 1944.


Teleomorph: Lulwoana uniseptata.

Conidia pluricellular, monacrogenous, single or branched, on simple conidiophores, filaments variable in length and septation, coiled irregularly, producing a balled appearance, and subhyaline to fuscous. Three Zalerion species were accepted (Kirk et al., 2001), two marine and one of terrestrial origin (Buczacki, 1973), while four species described by Moore and Meyers (1962), based largely on their different enzyme activity, have been reduced to synonymy with Z. maritima. Isolates of Z. arboricola (a terrestrial species) are not congeneric with Z. maritima and isolate ATCC 20868 was transferred to a new genus Glarea lozoyensis, based on DNA fingerprinting (Bills et al., 1999). Zalerion varia likewise is not congeneric with Z. maritima, but groups with G. lozoyensis in the Leotiaceae, Leotiales, and is therefore assigned to the new genus Halenospora (see page 154). Zalerion varia isolates differ greatly in their morphology and collections made may not be monophyletic. A strain of Z. xylestrix clusters with Z. maritima and is considered by Campbell et al. (2005) to be conspecific with it, supporting the findings of Anastasiou (1963a)

COELOMYCETES

1. Conidia in an acervulus................................. 2
2. Conidioma eustromatic.............................. 3
3. Conidioma pycnidial................................ 4

4. Conidia with no polar spines, hyperparasite of Haloguignardia species, conidia 2-5 × 2.5-4 μm ................................................... Gloeosporidina cecidii
5. On Rhizophora wood, roots and seedlings, conidia 3-6 × 1-1.5 μm.............................. Cytospora rhizophorae
6. On Phragmites, conidia 17-5-75 × 2.5-5 μm ............................................. Cytoplacosphaeria phragmiticola
7. On Nypa fruticans, conidia 3-4.5 × 1.2-1.6 μm ...................................... Plectophomella nypae

8. Conidia hyaline .............................................. 5
9. Conidia coloured ....................................... 13

10. On wood, conidia 2.5-4.5 × 2.5-2.5 μm................................. Phleumaroloma litoralis
11. On Rhizophora, conidia 11-18 × 3-4 μm................................. Phomopsis mangrovei
12. On various substrata, pycnidia flask-shaped superficial or submerged ..................................... Phoma and Macrophoma species
13. Conidia 1-2-septate, with three polar appendages, on various substrata........................................ 12
14. Conidia unicellular, cylindrical, 39-49 × 6.5-8.5 μm, with 3-4 apical appendages formed by fragmentation of a sheath, on Juncus roemerianus ............................................. Tiarosporella balmyra
15. Conidiogenesis phialidic, conidia 16-23 × 2.5-4 μm, on Phragmites communis ............................................. Pseudorobillarda phragmitis
16. Conidiogenesis holoblastic, conidia 10-14 × 3-4.5 μm, on Rhizophora mangle, and other Rhizophora species ............................................. Robillarda rhizophorae
17. Conidia one-celled........................................ 14
18. Conidia one transverse septum.......................... 15
19. Conidia muriform......................................... 17
20. Conidia with funnel-shaped polar appendages, fusiform or naviculate ..................................... Koorchaloma
21. Conidia ellipsoidal, dark brown, thick-walled, with 5-9 tentacle-like appendages ..................................... Octopodotus stupendus
22. Conidia with no appendages, 4.8 × 4.6 μm ............................................. Coniothyrium obiones

23. Saprobic on salt marsh plants............................................. 16
24. Saprobic on driftwood, conidia yellowish-brown, 6-8 × 3.5-4.5 μm ............................................. Diplodia orae-maris

Fungal Diversity
16. On Halimione, conidia yellow-brown, 9-12 × 4-5 μm.................................Ascochyta obiones
16. On Salicornia, conidia olive to light brown, 4-8 × 4-6 μm.................................Ascochyta salicorniae

17. Conidia with no sheath, 3-transverse septate, 1-longi-septate, 10-20 × 7-13 μm.................................Camarosporium roumeguerii
17. Conidia with a polar cap-like appendage at each end, 22-42 × 10-17 μm, on Ammophila....................Amarenographium metableticum
17. Conidia with a pronounced mucilaginous sheath, 5-transverse septate, 1-longiseptate, 20-34 × 9-20 μm.................................Camarosporium palliatum

Amarenographium O.E. Erikss., Mycotaxon 15: 199, 1982 .......................................................... (1)

Camarosporium metableticum Trail, Scottish Naturalist 8: 267, 1886.
Diplodina ammophilae Trail, Scott. Natural. 10: 76, 1889.
Leptosphaeria ammophila (Lasch) Rehm, Asc.: 225, 1949.
Teleomorphic: Amarenomyces ammophilae (Lasch) O.E. Erikss.

Pycnidia subglobose, immersed, ostiolate, papillate, clypeate?, coriaceous, black, solitary, conidiogenous cells cylindrical, conidia ellipsoidal to trapezoidal, muriform, 3-9 transverse septate, 1-2 longitudinal septate, slightly constricted at the septa, fuscous, apical cells lighter, bearing cap-like, gelatinous, striate appendages at either end of the conidium. Reported from bark, maritime grasses and salt marsh plants.

Ascochyta Lib., Pl. Crypt. Arduenna 1 (Praef.): 8, 1830.......................................................... (2)

Ascochytila obiones (Jaap) Died., Annls mycol. 10: 141, 1912.


Ascochyta salicorniae var. salicorniae-patulae Trotter, Annls. Mycol. 3: 30, 1905.
Ascochyta salicorniae Trotter, Annls. Mycol. 2: 536, 1904, nom. illegit
Pycnidia immersed, erumpent, ovate, subglobose, ellipsoidal or pyriform, ostiolate, epipellate to papillate, coriaceous, olive brown, brown to black, solitary or gregarious, conidiogenous cells phialidic, flask-shaped to pyriform, hyaline, conidia blastic, ellipsoidal, obovate or cylindrical, 1-septate, slightly constricted at the septum, smooth-walled, hyaline to yellowish to pale brown. Parasitic or saprophytic on the salt marsh plants Halimione portulacoides, Salicornia europaea, S. herbacea and S. patula.

1. Ascospore with a sheath, hyaline to yellowish or light brown, 10-12 × 4-7 μm,......................A. salicorniae
1. Ascospores without a sheath, 9-12 × 4-5 μm, pale yellowish to brown.........................A. obiones


Pycnidia immersed or erumpent, subglobose or ellipsoidal, ostiolate, epipellate or papillate, dark brown, solitary or gregarious, paraphyses present, simple, hyaline, filiform, nonseptate, conidiogenous cells phialidic, flask-shaped, simple, hyaline, conidia subglobose, ellipsoidal or oblong, enteroblastic, monophialidic, muriform, 1-6 transverse septa, 1-4 longitudinal septa, slightly constricted at the septa, smooth, gold, yellowish-brown, olive-brown to brown, with a gelatinous sheath, lacking appendages. Both species occur on the salt marsh plants Halimione portulacoides, and various Salicornia species.

1. Conidia 5-septate, 20-34 × 9-20 μm, with a pronounced gelatinous sheath, on Salicornia species.................................C. palliatum
1. Conidia 3-septate, 10-20 × 7-13 μm, lacking a sheath, on stems and leaves of salt marsh plants.................................C. roumeguerii
Coniothyrium Corda, Icon. Fung. (Abellini) 4: 38, 1840 ...................................................... (1)


Pycnidia subglobose, immersed to erumpent, ostiolate, short papillate, coriaceous, brown, gregarious, conidiogenous cells phialidic, flask-shaped, unicellular, hyaline, conidia 4-8 × 3.5-6 µm, ellipsoidal, ovoid, subglobose, unicellular, smooth-walled, olivaceous to pale brown, lacking a sheath or appendages. Occurs on the salt marsh plant Halimione portulacoides.

Cytoplacosphaeria Petr., Annls mycol. 17: 79, 1920 .......................................................... (1)  


Pycnidia large (circa 800 µm), loosely aggregated into a stroma with 1-5 locules, immersed in the substratum (Phragmites communis), ostiole indistinct, brown, ellipsoidal to lenticular, conidiogenous cells enteroblastic, phialidic, pronounced collarette, conidia 17.5- 75 × 2.5-5 µm, straight or slightly curved, thin-walled, 0-5 septate, not constricted at the septa, hyaline (Poon and Hyde, 1998).

Cytospora Ehrenb., Sylv. mycol. berol. (Berlin): 28, 1818 ........................................................ (1)  


Pycnidia immersed, composed of several locules, irregular morphology, ostiolate, epapillate, coriaceous, brown, solitary or gregarious, conidiophores cylindrical, filiform, simple, septate producing conidia apically, hyaline, conidia 3-6 × 1.1-1.5 µm, allantoid or ellipsoidal-cylindrical, unicellular, hyaline, lacking a sheath or appendages, conidia released in a mass. Frequently collected on mangrove trees, particularly roots and seedlings of Rhizophora species (Kohlmeier and Kohlmeier, 1971).


Acervuli cupulate, superficial, greyish-black, sessile, setae needle-shaped, brown scattered over the surface, conidiophores simple, septate, elongate-cylindrical, hyaline, conidiogenous cells cylindrical, smooth, hyaline, producing conidia at their tips, conidia 11-15 × 2.5-3.5 µm, fusoid-allantoid, unicellular, smooth, hyaline, with a single hair-like appendage at each end. Reported from driftwood and rarely collected since its original description.


\textbf{D. orae-maris} Linder, Farlowia 1: 403. 1944.  


Pycnidia immersed to erumpent, subglobose, ostiolate, papillate, pale to dark brown, glabrous, membranous or coriaceous, solitary or gregarious, conidiophores short cylindrical, hyaline, conidia 1-3-septate, slightly to markedly constricted at the septa, ovoid, ellipsoidal, cylindrical, yellow to brown, yellow in mass. Collections of \textit{D. orae-maris} on driftwood while \textit{D. thalassia} was isolated from marine sediments (Fig. 83, Artemczuk, 1980).

1. Conidia 6-8.5 × 3.5-7.5 µm, on wood. \textbf{D. orae-maris}  
1. Conidia larger 8.5-12 × 5.5- 6 µm, in sediments ........ .......................................................... \textbf{D. thalassia}  

Fig. 83. Diplodia thalassia. Bar = 5 µm.

Gloeosporidina Petr., Annls. mycol. 19: 214, 1921 .......................................................... (1)  


Acervuli discoid, olive coloured, later black, conidiogenous cells phialidic, cylindrical or slightly attenuated, simple with funnel-shaped mouths, conidia unicellular, hyaline, smooth-walled, ellipsoidal, 3-4.5 × 1.8-2.5 µm,
truncate at the base, with a cylindrical basal appendage. Growing on the galls of *Haloguignardia* species on *Sargassum natans*.

**Koorchaloma** Subram., J. Indian bot. Soc. 32: 124, 1953.......................................................... (2)


Conidiomata stromatic, sporodochial, punctiform, scattered, superficial, salmon to orange, with dark brown setae that are 3-4-septate, conidiophores erect, branched, thin-walled, smooth, hyaline, conidiogenous cells monoblastic, terminal, subcylindrical with collarettes, smooth, hyaline, conidia blastophialidic, solitary, fusiform or naviculate, with gelatinous appendages at both ends, smooth, hyaline, appendages formed by fragmentation of a sheath?, becoming inverted, funnel-shaped, then splitting into thin, radiating filaments, conidial secession schizolytic and released in a slimy mass (Figs. 84a, b) (Sarma et al., 2001). *Koorchaloma galateae* was described from *Juncus roemerianus* (Kohlmeyer and Volkmann-Kohlmeyer, 2001b) occurring between 5-25 cm above the rhizome while *K. spartinicola* occurs throughout the intertidal range of its host *Spartina alterniflora*, with a salinity range of 14 to 29 ‰ (Sarma et al., 2001).

1. Conidiomata setae 40-65 × 6.5-10 µm, conidia 15.5-21.5 × 4.5-6.5 µm, on *Juncus roemerianus*..................K. galateae

1. Conidiomata setae 45-80 × 3-5 µm, conidia 14.5-20.5 × 4.5-6.8 µm, on *Spartina alterniflora*..........................K. spartinicola

**Phialophorophoma** Linder, Farlowia 1: 403, 1944.............................................................. (1)


A wide range of *Macrophoma* strains have been isolated from intertidal wood, mangrove roots, marsh plants, seawater and sediments. However few have been fully identified.

**Nypaella** K.D. Hyde & B. Sutton, Mycol. Res. 96: 210, 1992 .......................................................... (1)


Conidiomata pycnidial, immersed in the mesophyll between vascular bundles of leaves of *Spartina alterniflora*, light brown, ostiolate with a short papilla, peridium 6-12 µm thick; conidiophores reduced to conidiogenous cells that are discrete, conoid or irregular polygonal all around the peridial wall; macroconidia aseptate, ellipsoid, dark brown, thick-walled, verruculose, surrounded by a gelatinous sheath and with 5-9 tentacle-like appendages. Hyaline macroconidia also produced on the peridium near the ostiolar canal (Kohlmeyer and Volkmann-Kohlmeyer, 2003a).

**Phialophorophoma** Linder, Farlowia 1: 403, 1944.......................................................... (1)

**P. litoralis** Linder, Farlowia 1: 402, 1944.

Pycnidia immersed, subglobose or ellipsoid, ostiolate, papillate or epapillate, subcarbonaceous, brown to black, glaborous,
solitary, conidiophores cylindrical, branched, septate, with terminal phialides, conidiogenous cells monophaelidic, enteroblastic, conidia ellipsoidal, obovoid or clavate, unicellular, smooth-walled, hyaline, no sheath or appendages (Kohlmeyer and Kohlmeyer, 1979). Occurring on a variety of substrata, drift and intertidal wood, bark and dead roots of *Avicennia marina*.

**Phoma** Sacc., *Michelia* 2: 4, 1880 ............... (8)


*Aposphaeria fibricola* (Berk.) Sacc., *Syll. fung.* 14, 1933.

**P. alternariaceum** F.T. Brooks & Searle, *Phomopsis* 1, 1922 ................................................. (1)


Teleomorph: In the Diaporthales?

Pyenidia immersed, ellipsoid or subglobose, ostiolate, solitary or gregarious, black, conidiophores branched, stout to filiform, septate, hyaline, conidiogenous cells phialidic, determinate, integrated, hyaline, cylindrical with a terminal collarette, conidia holoblastic, fusiform or ellipsoid, 11-18 × 3-4 μm, straight, unicellular, hyaline, rounded apically, truncate at the base, no sheath or appendages (Hyde, 1991d). Intertidal on prop roots of *Rhizophora* species, no teleomorph reported.

**Plectophomella** Moesz, Magyar Bot. Lapok. 21: 13, 1922 .................................................... (1)


Conidiomata pycnidial, pale, immersed, ostiolate; conidiophores hyaline, 1-septate; conidiogenous cells phialidic, conidia holoblastic, hyaline, unicellular, smooth, flask-shaped, conidia ellipsoidal to subglobose, unicellular, hyaline, smooth walled, with no sheath or appendages. Species marked * have all been isolated from marine soils (Pawar et al., 1967), and thus may not be regarded as obligately marine.

*Phoma* species are ubiquitous, geographically widespread, occurring in a variety of environments and habitat niches, as saprophytes, endophytes, as biodeteriogens and parasitic on plants and animals. Because of difficulties in their identification, most are simply referred to as *Phoma* species. Some 3,000 *Phoma* epithets have been recorded in MycoBank (Crous et al., 2004), but Borerema et al. (2004) only accept *circa* 223 species. Aveskamp et al. (2008) questioned the validity of some of these and proposed avenues for future research, including DNA-barcoding (Herbert et al., 2002).

We have not attempted a key to *Phoma* species recovered from marine habitats as the only way to resolve their taxonomy is to examine cultures and undertake molecular sequencing of their DNA.

**Phomopsis** (Sacc.) Bubák, Öst. bot. Z. 55: 78, 1905 .................................................. (1)

*Plectophomella* Moesz, Magyar Bot. Lapok. 21: 13, 1922 .................................................... (1)


Conidiomata pycnidial, pale, immersed, ostiolate; conidiophores hyaline, 1-septate; conidiogenous cells phialidic, conidia holoblastic, hyaline, unicellular, smooth,
cylindrical 3-4.5 × 1.2-1.6 µm. Collected on Nypa fruticans.

**Pleurophomopsis** Petr., Annls. mycol. 22: 156, 1924.............................................................. (1)


Conidiomata pycnidial, superficial, reddish brown, central orange ostiole; conidiophores at the base and sides of conidiomata; conidiogenous cells phialidic; conidia holoblastic, hyaline, aseptate ellipsoid to fusiform, smooth 3.5-5 × 2-2.5 µm and saprotrophic on Nypa fruticans. Hyde and Sutton (1992) indicate that the assignment of this species to “Pleurophomopsis” is debatable, but there appears to be no better choice at present. Cultures of these three coelomycetes (Nypaella, Plectophomella, Pleurophomopsis) are required to enable determination of their phylogenetic relationship.


Teleomorph: in the Dothideomycetes, (Rungjindamai et al., unpublished data). Pycnidia immersed, scattered, globose, dark brown, paraphyses present, conidiogenous cells subcylindrical, lageniform, colourless, smooth, conidia 1-septate, fusiform, both ends rounded, hyaline, smooth, eguttulate, 16-23 × 2.5 µm, with 2-4 appendages, growing on grasses (Plaingam et al., 2005). Appendages in *Pseudorobillarda sojiae* are non-cellular and arise from the outer wall layer of the conidium as an outgrowth (Plaingam, 2002). *Pseudorobillarda phragmitis* (Fig. 85) was collected on pine and yellow poplar panels from estuarine waters (salinity 3-16‰) by Johnson and Hughes (1960) but originally known from *Phragmites communis* (Cunnell, 1958).

Although *Pseudorobillarda* and *Robillarda* morphologically share some common features (pycnidial, septate hyaline conidia with 3-4 polar appendages), phylogenetically they are distantly related (Rungjindamai et al., unpublished data).

**Rhabdospora** (Durieu & Mont.) Mont., Syll. Gen. Spec.: 277, 1856................................. (1)


Pycnidia immersed, subglobose, unilocular, ostiolate, papillate or epapillate, coriaceous, dark brown to black, solitary or gregarious, conidiophores cylindrical or attenuate, simple, conidia produced at their apex, hyaline, conidia filiform, 9-12.5 × 1.5-2 µm, unicellular, straight mostly curved, hyaline, lacking appendages or a sheath (Kohlmeier and Kohlmeier, 1979). Occurring on bark and pneumatophores of *Avicennia* and proproots and trunks of *Rhizophora* trees, releasing conidia in a cirrus.

**Robillarda** Sacc., Michelia 2: 8, 1880........... (1)


Teleomorph: in the Amphisphaeriaceae, Xylariales (Rungjindamai et al., unpublished data). Pycnidia immersed or erumpent, ellipsoidal, unilocular, epapillate, subcoriaceous, black, glabrous, solitary or gregarious, conidiogenous cells conical or cylindrical, hyaline, conidia ellipsoidal, 1-septate, slightly constricted at the septum, smooth-walled, hyaline, with 3-4 apical radiating appendages. All collections of *R. rhizophorae* appear to be from *Rhizophora* wood.

**Stagonospora** (Sacc.) Sacc., Syll. fung. (Abellini) 3: 445, 1884................................. (1)


**Stagonospora** spp.

Pycnidia immersed to superficial, subglobose, ostiolate, epapillate, coriaceous, dark brown, solitary or gregarious, conidiogenous cells conoidal, simple, hyaline, conidia formed at the apex, conidia holoblastic, 20-27.5 × 3.5-4.5 µm, fusiform with rounded ends, 3-septate, slightly constricted at the septa, hyaline, smooth-walled, with an mucilaginous cap on the upper cell. Occurring on the brown seaweed *Pelvetia canaliculata* (Kohlmeier, 1973a) and known only from the type collection. Many *Stagonospora* species have been reported from salt marsh plants,
especially *Spartina*, *Phragmites*, *Juncus* and *Carex* and warrant further study (Jones, 1963; Jones and Oliver, 1964; Hughes, 1969; Henningson, 1974; Gessner and Kohlmeyer, 1976).


Pycnidia ellipsoidal, obpyriform, immersed, ostiolate, papillate, dark brown, solitary, conidiogenous cells cylindrical to elongate conical, conidia cylindrical, unicellular, hyaline, smooth, with 3-4 apical appendages that are tentaculiform, undulate, gelatinous, tapering to a thin tip, formed by fragmentation and eversion of a sheath (Kohlmeyer and Volkmann-Kohlmeyer, 1996). Found on senescent culms of *Juncus roemerianus*, 7 to 63 cm above the rhizome and considered to be facultative species.

**TOTAL ANAMORPHIC ASCOMYCETES ..... (103)**

**Concluding remarks**

The past 50 years has seen a remarkable advance in our knowledge of marine fungi, a group that some might regard as a minor assemblage of fungi of little general interest. However, marine fungi play a vital role in the recycling of organic matter in coastal and oceanic waters. They are particularly important in the ecology of mangrove ecosystems, recycling leaf and ligno-cellulose, creating particulate material and dissolved organic matter for other organisms in the food web. Yet much needs to done to quantify this activity, especially for filamentous fungi.

Marine ascomycetes account for the greatest diversity of filamentous fungi, also occurring on diverse substrata (Kis-Popa, 2005). However despite intense studies at the molecular level, many genera cannot be assigned to families, and some do not fit into any orders that have been described to date. Often new orders have to be erected to accommodate them: Jahnulales (Pang et al., 2002), Lulworthiales (Kohlmeyer et al., 2000) and Koralionastetales (Campbell et al., 2008).

Despite an earlier view that some marine ascomycetes had originated in the marine environment, we now have documented evidence that they are secondary invaders of the marine milieu. There is no information as to when this event(s) occurred, but the fact that they are worldwide in their distribution suggests an early migration, even before the separation of land masses.

Currently we can distinguish several marine lineages; for example

**Basidiomycota:**

1. Physalaciaceae clade in the eugarics
2. *Nia* clade, eugarics
3. Peniophoraceae clade
4. Ustilaginomycetes clade
5. Tremellomycetes, Cystofilobasidiales clade
6. Agaricostilbomycetes, Agaricostilbales group
7. Microbotryomycetes, Sporidiobolales group
8. Leucosporidiales group

**Ascomycota:**

9. Saccharomycetales group
10. Halosphaeriales clade
11. Lulworthiales clade
12. Hypocreales clade
13. Koralionastetales clade
14. *Torpedospora/Swampomyces* clade
15. Jahnulales clade
16. Verrucariales clade
17. Cleistothecial bitunicate ascomycetes.
Thus there has been multi-transitions from terrestrial to marine habitats often resulting in a reduced fruiting body, probably and adaptation to the aquatic habitat (Binder et al., 2006). Undoubtedly this transition was from terrestrial to freshwater and possibly mangrove ecosystems to completely oceanic conditions. There is an overlap in the genera found in terrestrial/freshwater/mangrove ecosystems, e.g. Leptosphaeria, Phaeosphaeria and Massarina species, occur in all these ecosystems and are also found in fully saline waters. However, few occur under fully submerged conditions. An interesting group has been members of the Jahnulales, initially described from freshwater and terrestrial habitats, but also in a peat swamp and with Manglicola a marine genus (Pinruan et al., 2002; Suetrong et al., 2009).

So what of the future of marine mycology? While some geographical areas have been widely surveyed (temperate coastal lignicolous fungi, tropical mangrove fungi) vast areas have not been studied (South America, Africa) and cold water areas. Similarly, while some substrata have been intensively studied (cellulosic and lignocellulose, sand dwelling species, fungi on seagrasses), there is much to be done to sample seaweeds, root inhabiting species, parasites of marine animals, endophytes of marine plants and animals (Kis-Papo, 2005; Raghukumar, 2008).

Taxonomic studies of marine fungi have made considerable progress in the last 20 years, especially with advent of molecular techniques. Our understanding of the physiology and biochemistry of marine fungi still remains patchy, with most studies confined to the effect of salinity on growth, movement of ions into mycelium, their ability to degrade cellulose and lignin (Mouzouras et al., 1988; Pointing et al., 1998). Another area that has attracted research interest is the source of new chemical structures and bioactive compounds from marine fungi. However, this has been confined to meet the needs of the pharmaceutical industry (Höller et al., 2000; Pan et al., 2008; Jones, 2008; Jones et al., 2008), rather to explore their role in the ecology of marine fungi. Few have undertaken broad enzymatic studies or pathological studies of those infecting commercial fish (Duc et al., 2009).

Most studies have been directed at the filamentous fungi, in particular the lignicolous ascomycetes, while anamorphic fungi present in mangrove mud’s, ocean sediments are neglected and not considered part of the marine fungal community. There needs to be a new direction set for many taxa remain to be discovered in these habitats. Too rigid delineation of what is marine must be overcome, the important fact is they are repeatedly isolated from marine habitats, what is their role in nature? Sam Meyers in the early 1960’s proposed the term thalassiomycetes for those fungi recovered from marine habitats. Perhaps we would have made greater advancement in the study of fungi in the sea, had such a term been adopted.

New species included in this volume, and published since Hyde et al. (2000).

**Basidiomycota**

*Haloaleurodiscus mangrovei* N. Maek., Suhara & K. Kinjo

**Ascomycota**

*Bitunicate*

*Caryospora australiensis* Abdel-Wahab & E.B.G. Jones

*Decaisnella formosa* Abdel-Wahab & E.B.G. Jones

*Leptosphaerulina mangrovei* Inderb. & E.B.G. Jones

*Mauritiana rhizophorae* Poonyth, K.D. Hyde, Aptroot & Peerally

*Platystomum scabridisporum* Abdel-Wahab & E.B.G. Jones

*Trematosphaeria malaysiana* Alias, McKeown, S.T. Moss & E.B.G. Jones

**Unitunicate**

*Alisea longicola* J. Dupont & E.B.G. Jones

*Anthostomella spissiteta* Kohlm. & Volkm.-Kohl.

*A. torosa* Kohlm. & Volkm.-Kohl.

*Astrocytis nypae* G.J.D. Smith & K.D. Hyde

*A. selangorensis* G.J.D. Smith & K.D. Hyde

*Corollospora anghusa* Abdel-Wahab & Nágah.

*C. baravispora* Steinke & E.B.G. Jones sp. nov.
C. indica Pasannarai, K. Ananda & K.R. Sridhar
C.portsaidica Abdel-Wahab & Nagah.
Dryosphaera tennuis Andrienko
Halosarpeia unicellularis Abdel-Wahab & E.B.G. Jones
Havispora longyearbyensis K.L. Pang & Vrijmoed
Nemania maritima Y.M. Ju & J.D. Rogers
Phyllachora paludicola Kohlm. & Volkm.-Kohlm.
Pontogeneia microdictyi Kohlm. & Volkm.-Kohlm.
Pseudohalonectria halophila Kohlm. & Volkm.-Kohlm.
Pseudolignincola siamensis Chatmala & E.B.G. Jones
Remispora minuta E.B.G. Jones, K.L. Pang & Vrijmoed
Remispora spitsbergenensis K.L. Pang & Vrijmoed
Sablecola chinensis E.B.G. Jones, K.L. Pang & Vrijmoed
Savoryella melanospora Abdel-Wahab & E.B.G. Jones
Swampomyces aegyptiacus Abdel-Wahab, El-Shar. & E.B.G. Jones
Swampomyces clavatispora Abdel-Wahab, El-Shar. & E.B.G. Jones
Thalespora appendiculata Chatmala & E.B.G. Jones
Tirispora mandoviana V.V. Sarma & K.D. Hyde

Hyphomycetes
Acremonium fuci Summerb.,Zucarco & W. Gams
Amorosia littoralis Mantle & D. Hawksw.
Arthrobotrys mangrovispora Swe, Jeewon, Pointing & K.D. Hyde
Cumulospora varià Chatmala & Somrith.
Halenospora varia (Anastasiou) E.B.G. Jones.
Halosigmoidea parvula Zucarco, J.I. Mitch. & Nakagiri
Penicillium dravuni J.E. Janso
Plectosporium oratosquillae Duc, Yaguchi & Udagawa

Trichocladium melhae E.B.G. Jones, Abdel-Wahab & Vrijmoed

Coelomycetes
Koorchaloma spartinicola V.V. Sarma, S.Y. Newell & K.D. Hyde

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