

Review

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Updates on the classification and numbers of marine fungi

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Abstract: This article revises the documented diversity of known marine fungi from nine phyla, 33 classes, 107 orders, 273 families, 767 genera and 1898 species reported worldwide. A member of the Aphelidiomycota, *Pseudaphelidium drebesii*, is reported for the first time from the marine environment, on a diatom. Likewise, the phylum Mortierellomycota is listed

following taxonomic changes, as are six subclasses: Chaetothyriomycetidae, Savoryellomycetidae, Sclerococcomycetidae, Agaricostilbomycetidae, Auriculariomycetidae and Aphelidiomycotina. Thirty-three orders and 105 family names with marine species are added to the checklist, along with 641 species in 228 genera, bringing the total to 1898. New additions of species added to the list of marine fungi are highlighted. Four new combinations are proposed: *Stigmatodiscus mangrovei*, *Diaporthe krabiensis* and *Diaporthe xylocarpi*, while the hyphomycete *Humicola alopallonella* is referred to the genus *Halosphaeriopsis*, as *Halosphaeriopsis alopallonella*.

Keywords: aquatic fungi; fungal systematics; fungal taxonomy; marine biodiversity; microbial ecology

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1 Introduction

The classification of marine fungi has been continuously updated with the incorporation of molecular data in taxonomic studies. This resulted in an increase in the estimated numbers of fungi from marine environments and has been shown in series of papers on the classification of higher orders of marine fungi: 530 (Jones et al. 2009), 624 (Abdel-Wahab and Bahkali 2012), 1112 (Jones et al. 2015), 1257 (Jones et al. 2019). Since Jones et al. (2019) listed the marine fungi documented at that time, a further 641 species, 231 genera, 58 families, 14 orders, two classes and two phyla have been added. Some of these are due to nomenclature changes while the Microsporidia were not included in the earlier publications. In this manuscript we highlight the major changes that have occurred in the past four years.

Table 1 is a snapshot of marine fungi assigned to higher order taxa of the fungi, which illustrates the dominance of the Ascomycota in marine habitats. This dominance is reflected in every ecological habitat surveyed: mangroves (Devadatha et al. 2021), salt marshes (Calabon et al. 2021), and planktonic marine fungi (Hassett et al. 2020). However, parasites of marine animals are dominated by microsporidia (Bojko and Stentiford 2022; Pang et al. 2021).

Table 1: Taxonomic classification of marine fungi.

Phylum	Species	Genus	Family	Order	Class
Ascomycota	1561	590	176	63	10
Basidiomycota	158	86	49	27	10
Microsporidia	128	56	26	7	3
Chytridiomycota	29	18	12	5	5
Mucoromycota	17	12	6	1	1
Olpidiomycota	2	2	1	1	1
Aphelidiomycota	1	1	1	1	1
Blastocladiomycota	1	1	1	1	1
Mortierellomycota	1	1	1	1	1
Total	1898	767	273	107	33

2 Selected notes on marine fungi

2.1 Phyla and subclasses

Since the last checklist of marine fungi in 2019, numerous novel species, genera, families, orders, and subclasses have been discovered. This can be accounted for by the sampling of a wider range of substrata (e.g., algae, sea grasses, seawater), sampling of deep-sea locations, and innovation in sampling, such as Sanger dideoxy chain-termination sequencing, high throughput sequencing (HTS) platforms 454-Pyrosequencing and Illumina (Abdel-Wahab et al. 2021; Calabon et al. 2021; Poli et al. 2020a; Vargas-Gastélum and Riquelme 2020; Varrella et al. 2021; Walker and Robicheau 2021; Wang et al. 2014, 2019). Significant changes have been made to the higher classification of the fungi as the result of a number of phylogenetic studies based on a wider range of loci sequenced and divergence time estimates (Hongsanan et al. 2020a,b; Hyde 2022; Hyde et al. 2020b; Phukhamsakda et al. 2022; Senanayake et al. 2022). Higher order classifications have been proposed by various authors from Hibbett et al. (2007) and Hyde et al. (2017) to Tedersoo et al. (2018).

Since 2019, the phylum Aphelidiomycota has been added to our survey of marine fungi while the Mortierallales has been raised in rank to Mortierellomycota (Tedersoo et al. 2018). We add six subclasses which include marine fungi: Chaetothyriomycetidae (Doweld 2001), Savoryellomycetidae (Hongsanan et al. 2017), Sclerococcomycetidae (Réblová et al. 2017), Agaricostilbomycetidae (Swann et al. 2001), Auriculariomycetidae (Jülich 1982), and Aphelidiomycotina (Tedersoo et al. 2018).

Currently, marine microsporidia total 128 species in 56 genera, parasitic primarily on crustacea, fish, less frequently on annelid worms (such as the genera *Capitella*, *Echiurida*), rarely striped dolphin (*Stenella coeruleoalba*), and the California sea-lion (*Zalophus californianus*). Microsporidia are a particular problem as the cause of diseases in

aquaculture. A survey of 150 pre-stocked ponds in Thailand found the prevalence of the microsporidian *Enterocytozoon hepatopenaei* to be 49 %, with the resultant economic loss \$32,000 per hectare (Shinn 2016). They are worldwide in distribution with Sapir et al. (2014) reporting on a new microsporidian *Nematocenator marisprofundi* from the deep sea, that infects benthic nematodes in methane seeps on the Pacific Ocean floor.

2.2 Orders

2.2.1 Eremithallales (Dothideomycetes, Ascomycota)

Eremithallales was introduced for a single species *Eremithallus costaricensis* (Lücking et al. 2008), with a divergence time estimated as 238 MYA (stem age, Hongsanan et al. 2020b). The order comprised one family Eremithallaceae which has now been synonymized under Melaspileaceae, and *Eremithallus costaricensis* is included in the genus *Melaspilea* (Ertz and Diederich 2015). One marine ascomycete has been referred to *Melaspilea*, namely *M. mangrovei* (Vrijmoed et al. 1996), but this has not been confirmed by molecular data.

2.2.2 Golubeviales (Exobasidiomycetes, Basidiomycota)

The order was introduced for the genus *Golubeva* with *G. pallescens* as the type species (Wang et al. 2015). In a multigene phylogeny and taxonomic revision of yeasts in the Ustilaginomycotina, two species in the genus *Tilletiopsis* (*T. albescens*, *T. pallescens*) grouped separately from the *Tilletiopsis* clade and these were referred to new genera, *Robbauera* and *Golubeva*, respectively. These genera served as new families and orders in the Ustilaginomycotina. *Golubeva* is the type genus for the Golubeviaceae, Golubeviales (Wang et al. 2015), a new name for the checklist.

2.2.3 Lobulomycetales (Lobulomycetes, Chytridiomycota)

Lobulomycetales was introduced by Simmons et al. (2009) based on genetic analyses, morphology, and ultrastructural data, with *Lobulomyces* (Lobulomycetaceae) and *L. angularis* as the type genus and species, respectively. Features of the order are a polycentric or monocentric thallus, multiple rhizoidal axes, spherical motile zoospores with or without a flagellar plug, ultrastructural details of the kinestosome, growing on chitin in soil and freshwater/seawater. Two families are assigned to the order Lobulomycetaceae and (Alogomycetaceae). *Alogomyces tanneri* (Alogomycetaceae)

is known from marine habitats; based on environmental DNA samples from the deep ocean (Le Calvez et al. 2009; Yan et al. 2020).

2.2.4 Monoblastiales (Dothideomycetes, Ascomycota)

The genus *Heleiosa* was introduced by Kohlmeyer et al. (1996), for the type species *H. barbatula*, growing on leaves of *Juncus roemerianus* in salt marshes, and referred to the Dothideomycetes *incertae sedis*. Subsequently it was attributed to Monoblastiaceae (Monoblastiales) which includes both lichenized and non-lichenized ascomycetes (Wijayawardene et al. 2022). Monoblastiales was introduced by Hyde et al. (2013), and *H. barbatula* was referred to this order by Hongsanan et al. (2020b).

2.2.5 Muyocoproneales (Dothideomycetes, Ascomycota)

Muyocoproneae was invalidly introduced by Luttrell (1951) and later reintroduced by Hyde et al. (2013) while the order Muyocoproneales was introduced by Mapook et al. (2016). *Ellisiodothis inquinans* (Muyocoproneae) was reported from *Spartina alterniflora* in Buenos Aires, Argentina by Gessner and Kohlmeyer (1976), but there is no further documentation.

2.2.6 Myrmecridiales (Sordariomycetes, Ascomycota)

The order Myrmecridiales (Sordariomycetes) includes one salt marsh fungus *Myrmecridium schulzeri*, an asexual morph with subhyaline, obovoid or fusiform, 1-celled, conidia that can be distinguished from *Ramichloridium* by having hyaline mycelium, pale brown to hyaline conidiogenous cells with pimple-like denticles (Arzanlou et al. 2007). *Myrmecridium schulzeri* is recorded for the first time as saprobic on *Distichlis spicata* (saltgrass) in Buenos Aires, Argentina (Calabon et al. 2021; Eliades et al. 2007).

2.2.7 Neophaeothecales (Dothideomycetes, Ascomycota)

Phaeotheca salicorniae was introduced by Crous et al. (2016) and transferred to the new genus *Neophaeothea* by Abdollahzadeh et al. (2020) and the type for the new family and order Neophaeothecaceae, and Neophaeothecales, respectively. *Neophaeothea salicorniae* and *Neophaeothea triangularis* are black yeasts reported from hypersaline

waters in salterns (Chung et al. 2019; Gunde-Cimerman et al. 2000).

2.2.8 Pleurotheciales (Sordariomycetes, Ascomycota)

Two *Phaeoisaria* species are found in marine habitats: *Ph. sedimenticola* isolated from surface marine sediment in the inter-tidal zone, Shandong, China (Cheng et al. 2014) and *Ph. clematidis* in mangrove litter (Devadatha et al. 2021; Maria and Sridhar 2003). Pleurotheciaceae was introduced by Réblová et al. (2016) in Pleurotheciales (Sordariomycetes) and is included for the first time in the checklist of marine fungi.

2.2.9 Sakaguchiales (Cystobasidiomycetes, Basidiomycota)

In our 2019 checklist of marine fungi (Jones et al. 2019), we listed the Basidiomycota genus *Sakaguchia* in the Sakaguchiaceae and order Erythrobasidiales. Zhao et al. (2017) introduced the order Sakaguchiales and this is accepted in this revision.

2.2.10 Sclerococcales (Eurotiomycetes, Ascomycota)

Within the Eurotiomycetes, the discovery of an older name for the genus *Dactylospora* (*Sclerococcum*) has led to the introduction of a new subclass Sclerococcomycetidae for the order and family Sclerococcales, and Sclerococcaceae, respectively (Réblová et al. 2017). Four apothecial marine fungi are included in this change: *Sclerococcum haliotrepum*, *S. mangrovei*, *S. vrijmoediae* from mangrove wood (Jones et al. 1999; Kohlmeyer and Kohlmeyer 1965; Pang et al. 2014) and *S. canariense* from driftwood (Kohlmeyer and Volkmann-Kohlmeyer 1998).

2.2.11 Sporidesmiales (Sordariomycetes, Ascomycota)

Sporidesmiales was introduced by Crous et al. (2018b) with a single family (Sporidesmiaceae) and genus (*Sporidesmium*) saprobic on woody debris in terrestrial and aquatic habitats or mycoparasites of fungi. The divergence time for Sporidesmiales is estimated as 81 MYA (Hyde et al. 2020b), which is evidence of a family status but ranking it as an order may need revision following further study. One marine species (*Sporidesmium salinum*) has been reported on submerged wood at Millport, Isle of Man, UK as an asexual morph (Jones 1963). No further reports of the species are known and

further collections are required to obtain sequence data and determine its taxonomic affiliation.

2.2.12 Stigmatodiscales (Dothideomycetes, Ascomycota)

Asterodiscus tamaricis was introduced by Voglmayr et al. (2016) from material collected on dead twigs of *Tamarix tetrandra* (Austria) but later transferred to *Stigmatodiscus*, *S. tamaricis*, by Voglmayr and Amengual (2018). A second species, *Asterodiscus mangrovei* was described by Dayarathne et al. (2020a) from decaying submerged wood at a mangrove strand in Thailand. Voglmayr et al. (2016) referred *Stigmatodiscus* to the new family and order (Stigmatodiscaceae, Stigmatodiscales) and recorded for the first time for the marine fungi checklist. In the present study, we transfer *Asterodiscus mangrovei* to *Stigmatodiscus* as *S. mangrovei*.

Stigmatodiscus mangrovei (Dayar., E.B.G. Jones et K.D. Hyde) M.S. Calabon, E.B.G. Jones et K.L. Pang, comb. nov.

Mycobank number: MB848521.

≡ *Asterodiscus mangrovei* Dayar., E.B.G. Jones et K.D. Hyde, *Mycosphere* 11(1): 86 (2020).

Sexual morph: Descriptions and illustrations refer to Dayarathne et al. (2020a). Asexual morph: Not observed.

Distribution: THAILAND, Krabi Province, on decaying wood at a mangrove strand (Dayarathne et al. 2020a).

Notes: Holotype MFLU 16–1216. LSU (MN017861), SSU (MN017926), ITS (MN047095) sequence data are available.

2.2.13 Xenosporidiales (Sordariomycetes, Ascomycota)

Xenosporidiales, is a monotypic order in the class Sordariomycetes and based on the family Xenosporidaceae introduced by Hernández-Restrepo et al. (2017). It comprises eight genera of which *Lentomitella* has been reported from the marine environment, although generally known from wood in terrestrial and freshwater habitats (Ding et al. 2011). Members of Xenosporidiales were reported from various marine substrata (Ding et al. 2011).

2.3 Families

Many of the new family names listed in this study are due to additional species reported from the marine environment.

2.3.1 Amorosiaceae

Amorosiaceae (Pleosporales) was introduced by Thambugala and Hyde (in Thambugala et al. 2015) for the

monotypic hyphomycete genus *Amorosia* (type species *A. littoralis*) isolated from intertidal sediment, associated with *Rhizophora*, in the Bahamas (Mantle et al. 2006). Conidia are solitary, dry, lateral, elongate-clavate, pale brown to brown, 1–3-septate, 3–4-septate when mature, constricted at the septa, smooth-walled, and are lacking any mucilaginous sheath or appendages. Previously assigned to Sporangiaceae, Thambugala et al. (2015), in a multi-gene phylogenetic analysis, showed it grouped with *Angustimassarina* in a well-supported clade, in between a clade comprising *Decaisnella formosa*, *Thyridaria macrostomoides* and a new genus, *Lignosphaeria* and Sporangiaceae. They therefore introduced a new family for the two genera *Amorosia* and *Angustimassarina*. It is the source of three new chlorinated compounds: two propenylphenol derivatives, chlorophenol A and B (1 and 2), and one benzofuran derivative, chlorophenol C (3) and other compounds (Ren et al. 2022).

2.3.2 Cordieritidaceae

Fryar et al. (2019) introduced the genus *Annabella* with *A. australiensis* as the type species collected on decaying decorticated branches of *Avicennia marina* in South Australia and referred it to the Cordieritidaceae (Helotiales) in the subclass Leotiomycetidae (Leotiomycetes). This is the first marine species record of this subclass introduced by Kirk et al. (2008) and the family Cordieritidaceae. *Annabella australiensis* differs from other taxa within Cordieritidaceae in having hyaline to yellowish perithecioid apothecia, contrasting with the usually dark-coloured apothecia of other members of the family (Fryar et al. 2019). Due to this absence of perithecioid pigment, *Annabella australiensis* differs from other taxa in the family. Ascospores are hyaline, vary in shape from ellipsoid to fusoid to oblong, are aseptate, and lack appendages or sheaths.

2.3.3 Cyphellophoraceae

Cyphellophoraceae, typified by *Cyphellophora laciniata*, was introduced by Réblová et al. (2013). Presently, only one species, *Cyphellophora europaea*, has been reported from deep-sea hydrothermal vents, deep-sea, and deep subsurface sediments using culture-based approaches (Xu et al. 2017).

2.3.4 Cyliindrosympodiaceae

Shen et al. (2020) introduced the family Cyliindrosympodiaceae in the Venturiales (Dothideomycetes) to accommodate the type species *Cyliindrosympodium variabile*. A number of genera are

assigned to the family: *Cylindrosymposium*, *Pseudoanungitea*, *Sympodiella*, *Tothia* and *Septonema*, with *Septonema strictum* (= *Taeniolella stricta*) reported from marine habitats (Sridhar and Maria 2003, 2006). *Septonema* was previously assigned to the Mytiliniaceae and is polyphyletic with many species awaiting sequencing (Crous et al. 2007b).

2.3.5 Lachnaceae

In the 2019 checklist, *Lachnum spartinae* was classified under Hyaloscyphaceae, but here we correct this and refer it to the new family Lachnaceae introduced by Raitviir (2004).

2.3.6 Linocarpaceae

Konta et al. (2017) introduced Linocarpaceae, typified by *Linocarpon pandani*, to accommodate *Linocarpon* and *Neolinocarpon*. In marine habitats, two species have been recorded, *Linocarpon livistonae* and *L. pandani* (Hawksworth 2000; Hyde 1988a,b, 1989; Hyde and Alias 2000). This is a new family introduction to the marine fungi checklist.

2.3.7 Lophiotremataceae

Lophiotrema rubi is recorded from collections made from algae and seagrass (Gnavi et al. 2017; Panno et al. 2013) and is referred in the present work to family Lophiotremataceae introduced by Hirayama and Tanaka (2011), based on morphological characters and molecular phylogenetic data using LSU and SSU sequence data. This is a new family introduction to the marine fungi checklist.

2.3.8 Myrotheciomycetaceae

Jones et al. (2019) referred marine *Emericellopsis* species to the Hypocreales *incertae sedis*, but Crous et al. (2018b) introduced the family Myrotheciomycetaceae (Hypocreales, Sordariomycetes) for this genus, and this is followed here. Seven novel *Emericellopsis* species have been introduced in the last decade from a variety of substrata: *E. atlantica* on *Stelletta normani* in Ireland, *E. cladophorae* on the green alga *Cladophora*, *E. phycophila* both from Portugal (Gonçalves et al. 2020; Hagestad et al. 2021). This brings the number of marine *Emericellopsis* to twelve. Hagestad et al. (2021) sequenced the genome of an *Emericellopsis* sp. TS7 from a marine origin.

2.3.9 Nigrogranaceae

Nigrogranaceae was introduced by Jaklitsch and Voglmayr (2016) for the genus *Nigrograna* and two novel species *Ni. hydei* and *Ni. obtusispora*, based on phylogenetic analyses of a combined ITS-TEF1a sequence dataset. The genus includes two marine species: *Ni. samueliana* on decaying wood of *Avicennia marina*, and *Ni. rhizophorae*, on submerged propagule of *Rhizophora* sp. They are recorded for the first time from mangrove habitats (Hyde et al. 2020b)

2.3.10 Phaeoseptaceae

Phaeoseptaceae (Pleosporales) was introduced by Hyde et al. (2018) for *Phaeoseptum* which was previously placed in Halothiaceae (Zhang et al. 2013). *Phaeoseptum* is a monotypic genus and includes two marine species: *P. carolshearerianum* on decaying wood of *Avicennia marina*, and *P. manglicola* on decaying wood of *Avicennia marina* and *Suaeda monoica* (Dayarathne et al. 2020a). This is the first record of the family in the marine fungi checklist.

2.3.11 Pleomassariaceae

Pleomassariaceae (Pleosporales) was introduced with *Pleomassaria* as the type by Barr (1979) and to include fungi characterized by distoseptate, dark brown ascospores and ascomatal walls which are thickened at sides and thin at the base. The family includes *Splanchnonema* with the taxon *S. britzelmayrianum* reported for the first time from the marine environment. A new family record for the marine fungi checklist.

2.3.12 Pseudoastrophaeriellaceae

Phookamsak et al. (2015) introduced the family Pseudoastrophaeriellaceae to accommodate a single genus *Pseudoastrophaeriella* for taxa originally described in the genus *Astrophaeriella* (Hawksworth and Boise 1985). Hyde et al. (2017) accommodated the two marine species of *Carinispora* in Pseudoastrophaeriellaceae based on morphology and phylogenetic analyses. Later, Phookamsak et al. (2019) introduced a third genus, *Pseudoastrophaeriellopsis* with one new species from mangroves in India. Currently the family includes three genera and 10 species, of which three taxa were described from marine habitats.

2.3.13 Saccotrochiaceae

Jones et al. (2019) referred *Aureobasidium pullulans* (collected in the marine environment) to the family Dothioraceae, while Thambugala et al. (2014) included it in the new family Aureobasidiaceae, a family already introduced by Ciferri (1958). However, an earlier name for Aureobasidiaceae is Saccotrochiaceae, established by Bonorden (1864) to accommodate *Saccotrochium*, and is considered as a distinct family in Dothidiales. Saccotrochiaceae can be distinguished from Dothideaceae by immersed to erumpent, uniloculate ascostromata and aseptate to multi-septate, hyaline ascospores (Hongsanan et al. 2020a). Currently seven genera are accepted in Saccotrochiaceae with three marine species: *Aureobasidium leucospermi*, *A. pullulans*, and *A. melanogenum*.

2.3.14 Stigmatodiscaceae

Voglmayr et al. (2016) established the family Stigmatodiscaceae to accommodate two genera: *Asterodiscus* and *Stigmatodiscus*. However, Voglmayr and Amengual (2018) synonymized the two genera based on indistinguishable morphology and molecular characteristics. Currently, Stigmatodiscaceae contains *Stigmatodiscus* with seven new species. *Stigmatodiscus touroultii* was described from *Salvadora angustifolia*, a saline tree (Poncet et al. 2022). Dayarathne et al. (2020a) described *Asterodiscus mangrovei* from mangroves in Thailand. In the present study, *Asterodiscus mangrovei* is transferred to *Stigmatodiscus* as *S. mangrovei* (see notes in Stigmatodiscales).

2.3.15 Striatiguttulaceae

Zhang et al. (2019b) introduced two new genera *Longicorpus* and *Striatiguttula* in the new pleosporalean family Striatiguttulaceae, collected on mangrove plants. A multi-gene dataset (LSU, SSU, TEF-1 α , RPB2) showed that the two genera formed a monophyletic clade (Striatiguttulaceae) and a new lineage in the Pleosporales, and close to Ligninsphaeriaceae, Pseudoastrospiraellaceae, Testudinaceae, and Tetraplospiraellaceae. Two new species of *Striatiguttula nypae* and *S. phoenicis* were collected on *Nypa fruticans* and *Phoenix paludosa*, respectively, and characterized by black, immersed ascostromata with a short papilla, and ascospores that are hyaline to brown, fusiform or ellipsoidal, 1–3-septate, striate, with paler end cells and surrounded by a mucilaginous sheath. *Longicorpus* is based on *Trematosphaeria striataspora* introduced by Hyde (1988a) and later transferred to *Astrospiraellia striataspora* (Hyde 1992) but formed a distinct well supported clade in Striatiguttulaceae, and characterized

by black ascostromata that are immersed to erumpent, clypeate, with a long neck, and ascospores hyaline to brown, fusiform, upper middle cell slightly swollen towards the central septum, and the end cells paler and smaller, striate, surrounded by a mucilaginous sheath. *Longicorpus striataspora* was found on two mangrove palm species, *Nypa fruticans* and *Phoenix paludosa*. A divergence time estimate analysis indicated the crown age to be 39 (20–63) MYA and stem age 60 (35–91) MYA for Striatiguttulaceae (Zhang et al. 2019b).

2.3.16 Teratosphaeriaceae

Crous et al. (2007a) introduced Teratosphaeriaceae to accommodate *Teratosphaeria* (with a *Readeriella*-like asexual morph) and 11 asexual genera. The family comprises around 60 genera and represents one of the largest families in Dothideomycetes (Crous et al. 2011c; Wijayawardene et al. 2022). The members of the family are saprobes, plant and human pathogens, rock-inhabiting, and endophytes (Crous et al. 2009a,b, 2011a,b; Egidi et al. 2014; Quaedvlieg et al. 2014). *Hortaea werneckii* (Teratosphaeriaceae) is a very common taxon in marine habitats (Abdel-Wahab et al. 2014).

2.3.17 Thyridariaceae

Thyridariaceae was introduced by Hyde et al. (2013) with *Thyridaria incrustans* as the type genus and species, in the Pleosporales, Dothideomycetes. *Thyridaria* previously had been referred to some six different families. Three genera in Thyridariaceae have marine species: *Thyridariella*, *Parathyridaria* and *Pseudothyridariella*. Devadatha et al. (2018) introduced the new genus *Thyridariella* with two new marine species (*T. mangrovei*, *T. mahakoshae*) on decaying wood of *Avicennia marina* from India. Based on phylogeny of 18S, 28S, ITS rRNA, RPB2, and TEF-1 α genes, *Thyridariella* formed a sister relationship with a clade comprising *Thyridaria* and *Parathyridaria* in the Thyridariaceae. *Thyridariella* has ascostromata with ostiolar necks thickened laterally, hyaline, and centrally constricted muriform ascospores with a single longitudinal septum in each segment and surrounded by a mucilaginous sheath (Devadatha et al. 2018). *Parathyridaria* differs in having pale to grayish brown, rarely muriform ascospores and one half of the spores is slightly larger than the other half (Jaklitsch and Voglmayr 2016). *Thyridaria* differs from *Thyridariella* mainly in ascospore morphology, i.e., phragmosporus in *Thyridaria* without a sheath, while muriform in *Thyridariella* with a sheath (Devadatha et al. 2018; Jaklitsch and Voglmayr 2016). *Thyridariella mahakoshae* was subsequently transferred to the new genus *Pseudothyridariella* by Mapook et al. (2020) as *Ps. mahakoshae*. Three further

marine species were referred to Thyridariaceae with the introduction of the genus *Parathyridariella* with *Pa. dematiacea* as the type species, found on the green alga *Flabellia petiolata* and the seagrass *Posidonia oceanica*. *Parathyridaria tyrrhenica* was described from the brown alga *Padina pavonica* and *Flabellia petiolata*; and *Pa. flabelliae* from *F. petiolata* (Poli et al. 2020b). Unfortunately, all were described from mycelial cultures without sexual and asexual morphology.

2.3.18 Trichomeriaceae

Chomnunti et al. (2012) in a phylogenetic study, showed that the *Trichomerium* species (type species *T. coffeicola*), form a monophyletic clade within Chaetothyriales and established the new family Trichomeriaceae. Members of *Trichomerium* are generally foliar epiphytes (sooty moulds), mostly occurring on the surface of living leaves as ascostromata with setae with dark brown mycelia (Chomnunti et al. 2012). Genera assigned to the family include: *Bradomyces*, *Lithohypha*, *Neostrelitziana*, and *Knufa*. *Knufia* is a dematiaceous hyphomycetous genus introduced by Hutchison et al. (1995) with *K. cryptophialidica* as the type species. Two marine *Knufa* species are known: *Knufia petricola* isolated from the green marine alga *Flabellia petiolata* (Gnavi et al. 2017); *K. epidermidis* isolated from deep sea sediments (Wei et al. 2018).

2.3.19 Trimorphomycetaceae

Trimorphomycetaceae is a family in the order Tremellales (Basidiomycota) and currently contains four genera: *Carlosrosaea*, *Saitozyma*, *Sugitazyma* and *Trimorphomyces*, the type genus, and most are only known from their yeast states (Liu et al. 2015). *Torula flava* was introduced by Saito (1922) and proposed as a new genus *Saitozyma* in Liu et al. (2015) with five species. *Saitozyma podzolica* (syn. *Cryptococcus podzolicus*) is a yeast reported from the marine environment. Hoondee et al. (2019) and Kunthiphun et al. (2019) have isolated *S. podzolica* from sediment in mangroves of Thailand. The species is of interest as it is an oleaginous yeast yielding single cell oil and gluconic acid.

2.3.20 Zygosporiaceae

Li et al. (2017) introduced the Zygosporiaceae as a new family in the Xylariales (Sordariomycetes) based on phylogenetic analyses of a combined LSU and ITS sequence data generated under maximum likelihood and Bayesian criteria that showed *Zygosporium* species forming a strongly supported

monophyletic lineage basal to the Conioeciaceae. Zygosporiaceae had been previously introduced by Locquin (1984) but was invalidly published (Nom. inval., Art. 39.1, Melbourne). The type species of *Zygosporium* is *Z. oscheoides* (Montagne 1842) with 23 currently accepted species. *Zygosporium gibbum* has been reported from the marine environment on cellulosic substrata in salt marshes (Fell and Hunter 1979) and mangroves (Sarma and Vittal 2000; Vittal and Sarma 2006). *Zygosporium gibbum* is characterised by stalked vesicular conidiophores produced directly from the superficial mycelium, and spherical, hyaline, smooth to finely verruculose conidia (Whitton et al. 2003).

2.4 Notes on marine fungal genera

2.4.1 Diaporthe

Dayarathne et al. (2020a) described three marine *Diaporthe* species: *D. krabiensis*, *D. marina*, *D. salinicola*, from mangrove wood. The scientific name *Diaporthe salinicola* is preoccupied by an earlier fungus (Spegazzini 1912), and so the new '*Diaporthe salinicola*' was invalidly described (Nom. illegit., Art. 53.1). *Diaporthe krabiensis*, a species isolated from submerged wood of *Bruguiera* sp., was published without nomenclatural repository identifier (Nom. inval., Art. F.5.1 [Shenzhen]). In the present work, we validly publish *Diaporthe salinicola* and *Diaporthe krabiensis*.

Diaporthe xylocarpi (Dayar.) M.S. Calabon et E.B.G. Jones, comb. nov.

Mycobank number: MB848445.

Basionym: *Diaporthe salinicola* Dayar., Mycosphere 11(1): 91 (2020).

Eymology: Name referring to the host genus *Xylocarpus*.

Sexual morph: Descriptions and illustrations refer to Dayarathne et al. (2020a). Asexual morph: Not observed.

Distribution: THAILAND, Ranong Province, on decaying wood of *Xylocarpus* sp. (Dayarathne et al. 2020a).

Notes: Holotype MFLU 18-0553. ITS (MN047098, MN047099) and TEF-1 α (MN077073, MN077074) sequence data are available.

Diaporthe krabiensis (Dayar.) M.S. Calabon et E.B.G. Jones, comb. nov.

Mycobank number: MB848522.

Basionym: *Diaporthe krabiensis* Dayar., Mycosphere 11(1): 92 (2020).

Sexual morph: Not observed; Asexual morph: Descriptions and illustrations refer to Dayarathne et al. (2020a).

Distribution: THAILAND, Krabi Province, on decaying submerged wood of *Bruguiera* sp. (Dayarathne et al. 2020a).

Notes: Holotype MFLU 17–2618. ITS (MN047100, MN047101), TEF-1 α (MN433215), β -tubulin tub2 (MN431495), and from Krabi, Thailand.

2.4.2 *Parasarocladium*

Summerbell et al. (2018) introduced the genus *Parasarocladium* to accommodate three *Acremonium* species: *P. breve*, *P. gamsii* and *P. radiatum* that formed a distinct clade based on 18S, ITS, 28S rDNA and actin genes. Currently, *Parasarocladium* comprises nine species listed in the Index Fungorum (April 2023) and MycoBank databases. The nine species were isolated from soil (five species), one species from decaying leaves and three as endophytes from marine algae. Crous et al. (2018a) erected the family Sarcocladiaceae based on multigene phylogenies to accommodate the genera: *Parasarocladium* and *Sarcocladium* and described *Parasarocladium debruynii* from a soil sample in the Netherlands. Gonçalves et al. (2019) described three new marine *Parasarocladium* species *P. aestuarinum*, *P. alavariense* and *P. fusiforme* as endophytes of macroalgae (*Enteromorpha*, *Fucus*, *Ulva* and unidentified Rhodophyta), sea water and sponges that were collected from Ria de Aveiro estuary, Portugal based on ITS and β -tubulin (tub2) and actin (act1) genes. Crous et al. (2020) recorded for the first time the sexual stage of the new species *Parasarocladium tasmanniae* that was recorded from leaves of *Tasmannia insipida* collected from Limpinwood Nature Reserve, New South Wales, Australia. The new species was described based on morphology and ITS, LSU, actA, TEF-1 α and tub2 genes. Crous et al. (2021) described *Parasarocladium wereldwijnianum* from a soil sample collected from Utrecht Province, the Netherlands. *Parasarocladium wereldwijnianum* differs from the phylogenetically related species *P. aestuarinum* and *P. alavariense* by having olivaceous buff colonies, irregularly branched conidiophores, and hyaline, smooth-walled, ellipsoidal to obovoid, with truncate base.

The three species were described as endophytes of the marine algae (*Fucus*, *Ulva*), sea water and sponges. *Parasarocladium aestuarinum* is phylogenetically closely related to *P. alavariense*, however, both species differ in conidial morphology and dimensions with 0.013 p-distance of nucleotide sites among the ITS and β -tubulin genes. *Parasarocladium fusiforme* formed a basal clade to the other eight species of *Parasarocladium* (Crous et al. 2021; Gonçalves et al. 2020).

2.4.3 *Sclerococcum*

Traditionally *Sclerococcum* comprised lichenized species that produce sporodochial asexual morphs (Diederich et al. 2013; Hawksworth 1975, 1979), while *Dactylospora* species are sexual fungi that produce black apothecial ascomata with asci covered with an external, amyloid apical gelatinous cap (Hafellner 1979). Molecular phylogenetics of the type species of *Dactylospora*, *D. parasitica*, placed it in a monophyletic clade with the type species of *Sclerococcum*, *Sclerococcum sphaerale*, and the two genera were merged into the older genus name *Sclerococcum* under the family Dactylosporaceae and the recently described Sclerococcales (Diederich et al. 2018; Pino-Bodas et al. 2017; Réblová et al. 2017). Diederich et al. (2018) listed sixty-four *Sclerococcum* species and Joshi (2021) described two new species of *Sclerococcum* from India, so that 66 species of the genus are known worldwide. Of these, four species were recorded from marine habitats: *S. canariense*, *S. haliotrephum*, *S. mangrovei*, *S. vrijmoediae*. Marine species are saprobic and recorded from driftwood and decaying, submerged parts of the mangroves (Jones et al. 1999; Kohlmeyer 1967; Kohlmeyer and Kohlmeyer 1965; Pang et al. 2014).

Nine discomycete species have been previously described from the marine environment, of which four belong to the genus *Sclerococcum*. Apothecia of the four *Sclerococcum* species are similar, however, they differ in the ascospore shape, ornamentation, and the presence/absence of appendages (Jones et al. 1999; Kohlmeyer and Kohlmeyer 1965; Kohlmeyer and Volkmann-Kohlmeyer 1998; Pang et al. 2014). Ascospores of *Sclerococcum haliotrephum* are ellipsoidal with uneven cells; while they are ellipsoidal to subglobose in *S. vrijmoediae* and elongate-ellipsoidal in both *Sclerococcum mangrovei* and *Sclerococcum canariense*. Ascospores of *Sclerococcum canariense* and *Sclerococcum vrijmoediae* are appendaged, while they are ornamented in *S. haliotrephum* and *S. mangrovei*.

Kohlmeyer (1967) recorded *Sclerococcum canariense* from driftwood collected from Tenerife, Canary Islands and misidentified it as *Banhegyia uralensis*. Kohlmeyer and Volkmann-Kohlmeyer (1998) described the taxon in *Dactylospora* as *D. canariensis* as the second marine member of the genus. Olariaga et al. (2019) placed all non-lichenized *Dactylospora* species with clavate to cylindrical asci covered with an amyloid gelatinous apical cap in *Sclerococcum* including *D. canariensis*. The molecular data of *S. canariense* are unknown and the sequences of relevant genes are needed in order to confirm its taxonomic placement.

2.4.4 *Microascus*

Six *Microascus* species have been reported from marine habitats, isolated from seawater, sponges, corals and the deep sea (see <https://marinefungi.org>). We illustrate

two species *Microascus cinereus* and *M. trigonosporus* (Figures 1 and 2) isolated from intertidal wood collected from the coasts of the Yellow Sea and Bohai Sea, China, that are new records for marine fungi in China (Jin et al. 2004, 2005).

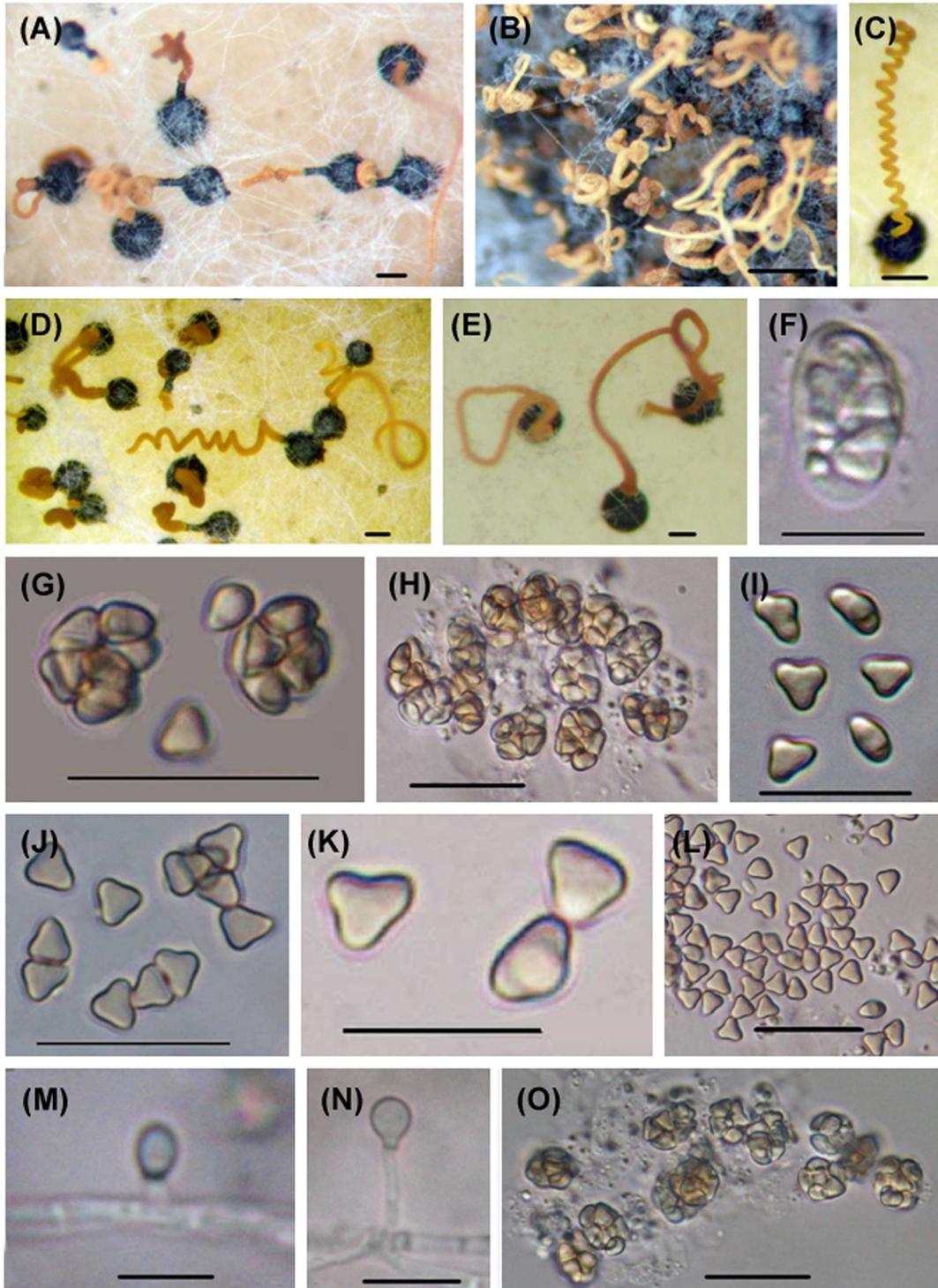


Figure 1: *Microascus trigonosporus*. (A–E) Perithecia with spore cirrus. (F) Young ascus. (G, H, O) Mature asci. (I–L) Ascospores. (M, N) Anamorphic *Scopulariopsis trigonosporus* of *Microascus trigonosporus*. Scale bars: (A–E) = 100 μm , (G, H, O) = 20 μm , (F, I–N) = 10 μm .

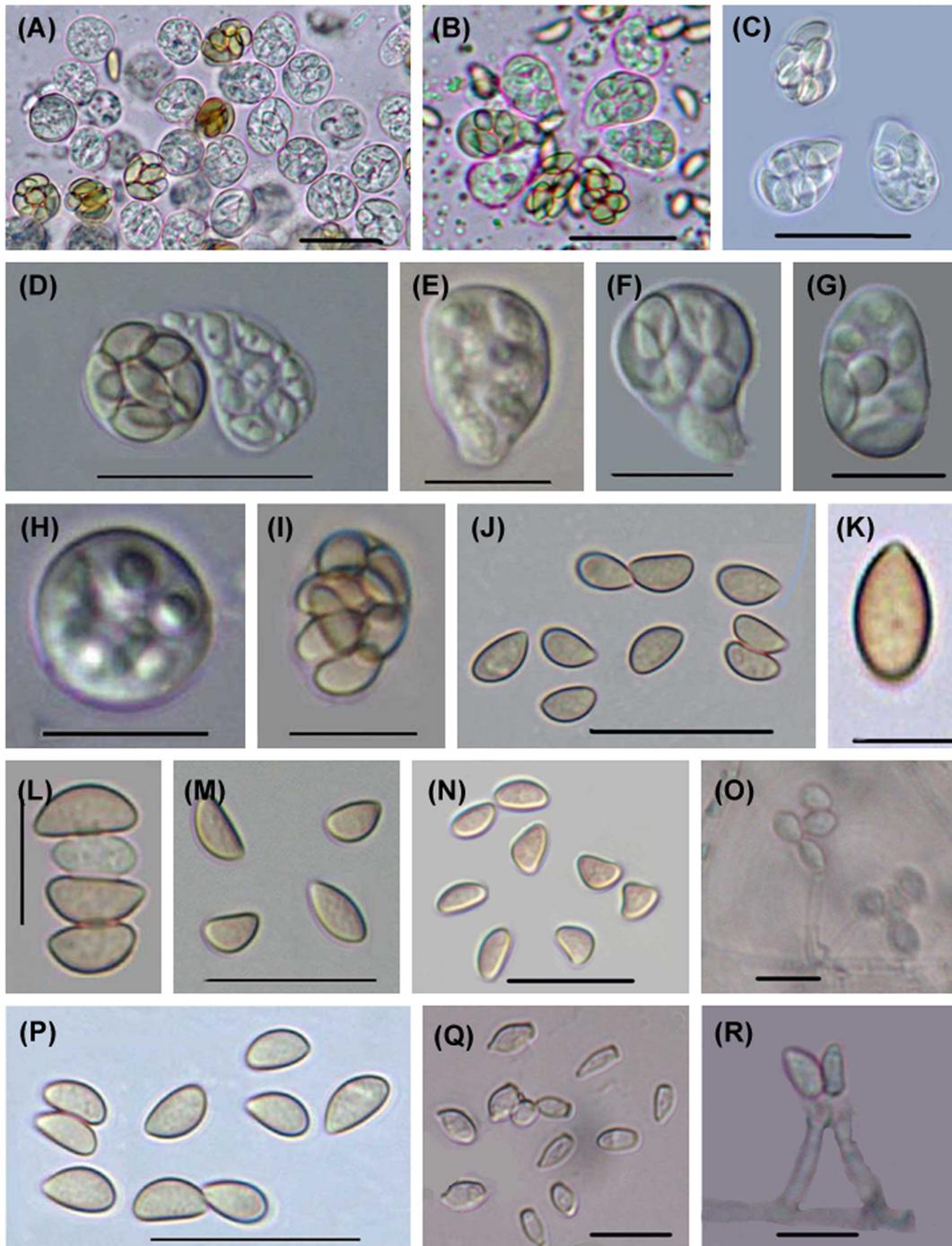


Figure 2: *Microascus cinereus*. (A–I) Asci. (J–N, P) Ascospores. (O, Q, R) Anamorphic *Scopulariopsis cinerea* of *Microascus cinereus*. Scale bars: (A–D, K, M, P–Q) = 20 μm , (E–J, L, N–O, R) = 10 μm .

2.5 Notes on marine fungal species

2.5.1 *Asteromyces cruciatus*

Asteromyces cruciatus was introduced by Moreau and Moreau (1941) from sand dunes of the Atlantic Coast of

France. This species has a worldwide distribution and reported from a wide range of substrata (Jones and Ward 1973). Despite its profuse growth in culture and its wide occurrence in the marine milieu, its taxonomic position has remained unresolved. *Asteromyces cruciatus* was classified as *incertae sedis* in Index Fungorum and Species Fungorum,

while Mycobank classified it under the old family name Dematiaceae. In a new study, Torres-Garcia et al. (2022) placed *A. cruciatus* in the Pleosporaceae based on a phylogenetic analysis of five gene markers (ITS, LSU, gapdh, rbp2, and tef1-a). *Asteromyces* is in a well-supported distinct clade with two marine *Paradendryphiella* species as its sister taxa, and closely related to both *Paradendryphiella* and *Stemphylum*, but they are markedly different in morphology. Brown (1958), Hennebert (1962), Kohlmeyer and Kohlmeyer (1964–1969), and Jones (1968), all report the conidia of *A. cruciatus* as ovoid or pyriform, smooth, thin-walled, one-celled without germ slit or pore, $10\text{--}20 \times 4\text{--}9 \mu\text{m}$, with up to 13 μm conidia developing in basipetal succession, singly on cylindrical denticles $3\text{--}6 \times 0.5\text{--}1 \mu\text{m}$. The first formed conidium is apical and retains this position. On germination, conidia often become 1-septate and these have been illustrated by Kohlmeyer and Kohlmeyer (1964–1969), Hennebert (1962), and Nolan (1972), who also reports 2-septate conidia. Jones and Ward (1973) investigated the effect of light on the sporulation of *A. cruciatus*: continuous illumination and in total darkness when conidia were unicellular. However, when subjected to black light (fluorescent lamp with a continuous spectrum maximum at 360 nm, 18 in. above plates), 1–6-septate conidia were formed depending on the growth media. *Asteromyces cruciatus* is also of interest because it can tolerate concentrations of up to 2.0 M NaCl in liquid media (Jones and Jennings 1965), with tolerance increased to 2.5 M NaCl with the addition of 0.05 M CaCl_2 . *Asteromyces cruciatus* is beautifully illustrated in Kohlmeyer and Kohlmeyer (1964–1969).

2.5.2 *Biatriospora borsei*

Biatriospora, typified by *B. marina*, was described as a sexual genus from mangrove roots in Seychelles with fusiform, 1–4 septate, brown to dark brown ascospores with hyaline polar chambers which release mucilage (Hyde and Borse 1986). Sequences of *B. marina* from a collection made in Singapore placed this species basal to Lophiostomataceae, Sporormiaceae and a group of unclassified taxa in a phylogenetic analysis of 18S, 28S rDNA, RPB2 and TEF-1 α (Suetrong et al. 2009).

The genus *Nigrograna* was established to accommodate *N. mackinnonii*, a species originally described in *Pyrenochaeta* (de Gruyter et al. 2013). Hyde et al. (2013) established a new family Biatriosporaceae to accommodate *Biatriospora*. In a phylogenetic analysis using the same genes, Ahmed et al. (2014) found that *N. mackinnonii* grouped with *B. marina*, and thus referred the former species to *Biatriospora*. Later, four more species of *Biatriospora*

were described from woody plants as endophytes: *B. antibiotica*, *B. carollii*, *B. yasuniana* and *B. peruviansis* (Kolařík et al. 2017), unaware that a new family Nigrogranaceae was established to accommodate *Nigrograna* with *N. mackinnonii* as the type, and the new combination of *Melanomma fuscidulum* in *Nigrograna* and the description of the new species *N. mycophila*, *N. norvegica* and *N. obliqua* (Jaklitsch and Voglmayr 2016). Jaklitsch and Voglmayr (2016) voiced doubts on the identification of the *Biatriospora marina* isolate and the validity of the Biatriosporaceae. Consequently, Kolařík (2018) accepted the genus *Nigrograna* and the family Nigrogranaceae, and transferred *B. antibiotica*, *B. carollii*, *B. yasuniana* and *B. peruviansis* to *Nigrograna*. After these revisions, *Biatriospora* became a monotypic genus but *B. borsei* was described as a new species in Hongsanan et al. (2020a). *Biatriospora borsei* clustered with *B. marina* (with a good support) within a group of *Nigrograna* spp. based on 18S, 28S, ITS rDNA, RPB2 and TEF-1 α , although *B. borsei* is a hyphomycete with no known sexual stage. As discussed here, fresh isolates of *B. marina* should be collected to clarify the taxonomic position of this species, *B. borsei*, the genus *Nigrograna* and the families Biatriosporaceae and Nigrogranaceae.

2.5.3 *Coniochaeta krabiensis*

Coniochaeta krabiensis formed a monophyletic group with *C. tetraspora* and another new species (*C. arenariae*) in the same study (Dayarathne et al. 2020a). Morphologically, *C. krabiensis* fits within the generic description of *Coniochaeta* with its two-layered peridium, cylindrical asci with an apical apparatus and dark brown, ellipsoidal ascospores with a germ slit which are arranged uniseriately in the asci (García et al. 2006). *Coniochaeta krabiensis* differs from *C. tetraspora* in having longer, narrower, 8-spored asci and smaller ascospores (Cain 1961).

2.5.4 *Cryptosphaeria avicenniae* and *C. halophila*

Cryptosphaeria avicenniae and *C. halophila* were described as new species from the marine environment based on phylogenetic analyses of ITS rDNA and from India, based on ITS and β -tubulin genes for *C. avicenniae* and of 18S and 28S rDNA for *C. halophila* (Dayarathne et al. 2020b). However, the different trees shown in the study suggested that *Cryptosphaeria* was not a monophyletic genus. *Cryptosphaeria avicenniae* is morphologically similar to *Cryptosphaeria bathurstensis* in terms of both the sexual and asexual stages but differs in the morphology of the asci and ascospore (Dayarathne et al. 2020b; Hyde

and Rappaz 1993). *Cryptosphaeria halophila* is an asexual fungus which is morphologically similar to *C. avicenniae*. The phylogenetic position of *C. halophila* was unstable in different analyses based on 18S and 28S rDNA genes (Dayarathne et al. 2020b).

2.5.5 *Halosphaeriopsis alopallonella* (Meyers et R.T. Moore) Devadatha et E.B.G. Jones, comb. nov.

Basionym: *Humicola alopallonella* Meyers et R.T. Moore, Am. J. Bot. 47: 346 (1960).

Synonymy: *Trichocladium alopallonellum* (Meyers et R.T. Moore) Kohlm. et Volkm.-Kohlm., Mycotaxon 53: 352 (1995).

Mycobank number: MB332021.

Type species: CBS 207.60; IFO 7833; MUCL 8014; UPSC 2185.

Saprobic on wood. Sexual morph: Undetermined. Asexual morph: Hyphomycetous. Hyphae hyaline to light brown, septate, branched. Conidiophores micronematous, mononematous, resemble non-specialised short lateral vegetative hyphae or conidiophore indistinct, conidia developing directly on hyphae. Conidia 14–24 $\mu\text{m} \times 7$ –11 μm , solitary, thick-walled, smooth, straight, 2–4-septate, strongly constricted at the septa, apical cell large subglobose, ellipsoidal, ovoidal to obpyriform, fuscous, reddish-brown to dark brown, basal cell smaller, obconical, light brown (Description based on Pang et al. 2011).

Material examined: USA, *Tilia americana*, wood, in seawater; Culture isolated by S.P. Meyers, No. F-123, Sept. 1960 (Holotype); USA Florida, Marine Laboratory, Univ. Miami.

Distribution: Aden, Australia, Bahamas, Bermuda, Cameron, Canada, France, Germany, India, Italy, Ivory Coast, Japan, Liberia, Norway, UK (England Scotland, Wales), USA (Alaska, Hawaii, Washington).

Molecular data: ITS GenBank MH857957 and LSU (MH869509) of CBS 207.60.

Notes: Taxonomically, the seven marine *Trichocladium* species were difficult to resolve until the advent of molecular phylogeny (Jones et al. 2009). Cultures of *T. achrasporum* were shown to be the asexual morph of *Halosphaeriopsis mediosetigera* (Shearer and Crane 1977). Based on sequence data *Trichocladium constrictum* has been designated the type species of a new genus *Cucurbitinus* as *Cucurbitinus constrictus* (Liu et al. 2020). *Trichocladium medullare* has been transferred to the new genus *Kohlmeyeriopsis* as *K. medullaris* (Klaubauf et al. 2014). Jones et al. (2019) listed four marine *Trichocladium* species *T. alopallonellum*, *T. griseum*, *T. lignicola*, and *T. melhae*. Here we refer *T. alopallonellum* to *Halosphaeriopsis* based on sequence data of the type collection (Meyers and Moore 1960). The taxonomic status of the remaining marine *Trichocladium* species remains unresolved as does that of many other terrestrial and

freshwater *Trichocladium* species (Index Fungorum, viewed April 2023).

In Figure 3, *T. alopallonella* groups in a sister clade with *H. mediosetigera* with high statistical support (100 %) in the Halosphaeriaceae, while other *Trichocladium* species form a sister clade to *Humicola* species. The phylogenetic tree was based on a combined analysis of the 28S and 18S rRNA sequence data. Morphologically, *Trichocladium* and *Humicola* species are difficult to separate resulting in confusing taxonomy, which is not surprising as they are phylogenetically closely related. Goh and Hyde (1999), in their review of the genus *Trichocladium*, illustrated the great diversity of conidial morphology of its species, with *T. alopallonella* often confused with *Humicola* as illustrated in the above synonymy.

2.5.6 *Hypoxylon aurantium* and *H. mangrovei*

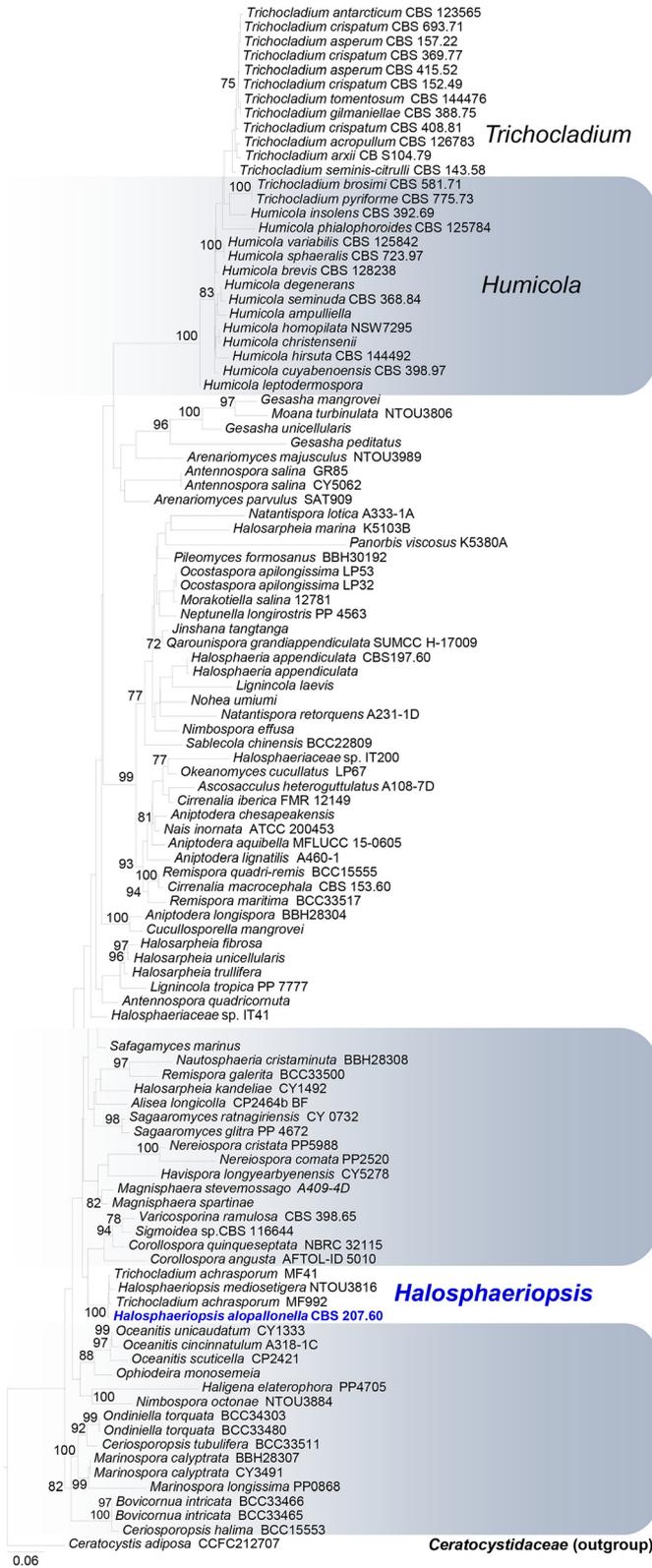
Dayarathne et al. (2020a) introduced these two species based on morphological observations and nucleotide differences of the ITS and tub2 gene loci. *Hypoxylon aurantium* is a distinctive *Hypoxylon* species in possessing a bright orange ascostromatal surface which is somewhat similar to *H. fendleri* (Vasilyeva et al. 2007). *Hypoxylon aurantium* and *H. fendleri* formed a sister lineage with high statistical support (97 % ML, 0.97 PP) and the base pair difference of ITS and tub2 gene loci accounts 52 out of 604 (84 %) and 163 bp out of 1028 bp (15 %), respectively. *Hypoxylon mangrovei* strains formed a well-separated (100 % ML, 1.00 PP) lineage in a sister clade to *H. lenormandii*, with which it shares some morphological features. They differ in the size of stromata (2–3.5 \times 1.5–2.8 \times 0.4–1 mm vs. 13–85 \times 6–27 \times 0.5–1 mm) and base pair difference: ITS, 27 bp out of 470 bp (5.7 %) and tub2 73 out of 594 (12.3 %) and RPB2 data.

2.5.7 *Hypoxylon teeravasati*

Hypoxylon teeravasati was introduced by Devadatha et al. (in Phookamsak et al. 2019) on decaying wood of *Avicennia marina*, and decaying branches and twigs of *Suaeda monoica* from Tamil Nadu, India. *Hypoxylon teeravasati* groups with *H. jaklitschii* and *H. lenormandii* (terrestrial species) as a basal taxon, in a single monophyletic clade with high support. *Hypoxylon teeravasati* can be easily distinguished from *H. lenormandii*, *H. jaklitschii*, and *H. croceum* in having a burnt sienna surface, with KOH extractable pigments eye brown and larger perithecia (Phookamsak et al. 2019).

2.5.8 *Halorosellinia xylocarpi*

Halorosellinia is a phylogenetically well circumscribed genus with four of its five species forming a strongly supported clade



Chaetomiaceae

Halosphaeriaceae

Halosphaeriaceae

Figure 3: Randomized axelerated maximum likelihood (RAxML) phylogenetic tree based on a combined analysis of the 28S and 18S rRNA sequence data. Bootstrap support values for ML (>70 %) are given above each branch. The newly transferred isolate is shown in blue. The tree is rooted to *Ceratocystis adiposa* CCFC212707.

in a phylogenetic analysis of 28S, ITS rDNA, tub2 and RPB2 genes (Dayarathne et al. 2020a). *Halorosellinia xylocarpi* is distinguishable from the other *Halorosellina* spp. by the unique opaque green colouration of the ascospores.

2.5.9 *Monosporascus cannonballus* (Figure 4)

Pollack and Uecker (1974) introduced this species from the roots of *Cucumis melo* (Cucurbitaceae) in Arizona. It causes root rot and vine decline (MRVD) of muskmelon in Greece (Markakis et al. 2018), and is reported as ubiquitous as a root endophyte (Robinson et al. 2020). The genomes of *Monosporascus* species were assembled by Robinson et al. (2020). The species was recorded for the first time from the marine environment by Jin and Huang (2009) from incubated drift and intertidal woods collected from the coasts of Yellow Sea and Bohai Sea (China). It groups in the Diatriypaceae (Xylariales, Xylariomycetidae, Sordariomycetes) (Maharachchikumbura et al. 2015).

2.5.10 *Neocamarosporium aestuarinum*

Gonçalves et al. (2019) described three new *Neocamarosporium* species from marine habitats, *N. aestuarinum* from seawater and *N. halimiones* and *N. endophyticum* from *Halimione*

portulacoides based on a phylogenetic analysis of ITS rDNA sequences. *Neocamarosporium aestuarinum* grouped with *N. jorjanensis* with good support. Morphologically, both species are similar with slight differences in conidial dimension (Papizadeh et al. 2018), and 23 nucleotide positions (substitution or insertion/deletion) in ITS rDNA. It is important to calculate, however, the genetic differences within and between species of *Neocamarosporium* in order to use differences in nucleotide positions in differentiating species in the genus. Currently nine marine *Neocamarosporium* species are included in the marine fungi checklist, with new saltmarsh species *N. aquaticum*, *N. chenopodii*, *N. maritimae*, *N. phragmitis* and *N. salsolae* (Calabon et al. 2021; Dayarathne et al. 2020a; Prematunga et al. 2023; Wanasinghe et al. 2017).

2.5.11 *Neocosmospora rhizophorae*

Dayarathne et al. (2020a) described this species from *Rhizophora* sp. collected in Thailand. Morphologically, this species is similar to *Kallichroma tethys*. Although Dayarathne et al. (2020a) distinguished *Neocosmospora rhizophorae* from *K. tethys* in having papillate ascomata, lacking a clypeoid ascomata, and an ascospore sheath, no ascospore sheath was actually reported for either *K. tethys* or *K. glabra* (Kohlmeyer and Volkmann-Kohlmeyer 1993).

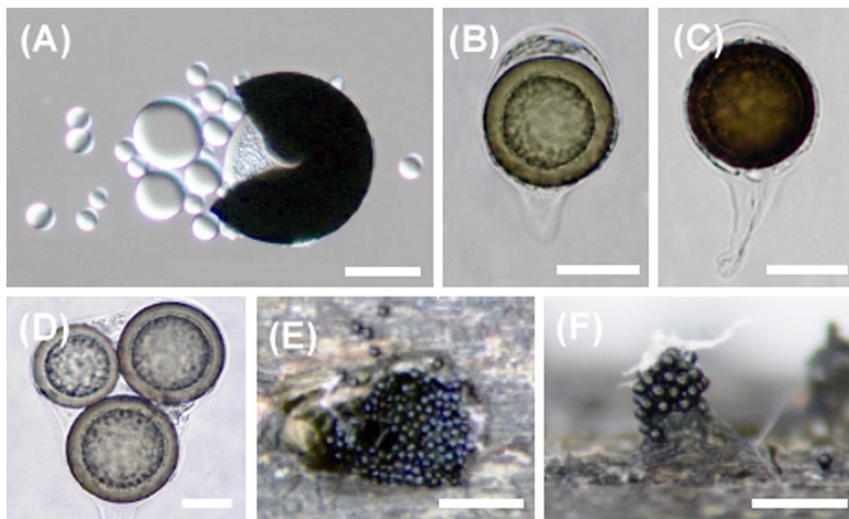


Figure 4: *Monosporascus cannonballus*. (A) Oil globules realised from squashed ascospore. (B) Ascus with single globose ascospore. (C) Thick-walled ascospore. (D) Ascus with three globose ascospores. (E, F) Released ascospores around the projecting neck of the ascoma. Scale bars: (A–D) = 20 μm , (E–F) = 300 μm .

Also, a nucleotide BLAST search of 18S, 28S and ITS rDNA sequences available for *N. rhizophorae* resulted in predominantly *Fusarium* spp. The validity of this new species is doubtful.

2.5.12 *Okeanomyces marinus*

Okeanomyces marinus is an asexual fungus collected in Thailand (in Hyde et al. 2020a). This is the second species in the genus along with the type species *O. cucullatus*. The asexual stage of *O. cucullatus* is *Periconia prolifica* (Pang et al. 2004). *Okeanomyces marinus* is morphologically similar to *P. prolifica* and *P. abyssa* but differs from *P. prolifica* in lacking hyaline erect conidiophores and from *P. abyssa* in having smaller conidia (in Hyde et al. 2020a). In the same study, *O. marinus* formed a monophyletic group with isolates of *O. cucullatus* and *P. prolifica* based on a combined analysis of 18S and 28S rDNA.

2.5.13 *Parathyridariella dematiacea*

Poli et al. (2020b) introduced a monotypic genus *Parathyridariella* with *Parathyridariella dematiacea* as the type species isolated from the seagrass *Posidonia oceanica* in Italy. Multi-locus phylogenetic analysis shows that *Parathyridariella dematiacea* strains form a distinct clade within Thyridariaceae. *Parathyridariella* only developed solitary and chained chlamydospores in the mycelium above the wood surface of *Pinus pinaster* and *Quercus ruber* (cork).

2.5.14 *Periconia salina*

Six *Periconia* species were listed as marine in our last treatise of marine fungi: *P. byssoides*, *P. cookei*, *P. digitata*, *P. echinocloae*, *P. minutissima*, and *P. salina* (Jones et al. 2019). *Periconia salina* was introduced by Dayarathne et al. (2020a) on buried bark in sand dunes in Wales (UK).

2.5.15 *Peroneutypa indica* and *P. polysporae*

Both *P. indica* and *P. polysporae* formed a strongly supported group with other *Peroneutypa* spp. in a phylogenetic analysis of ITS rDNA and tub2 gene (Dayarathne et al. 2020a). *Peroneutypa indica* grouped with *P. kochiana* but, morphologically, *P. indica* has longer asci with a J-apical ring and a marine occurrence. *Peroneutypa polysporae* grouped with *P. mangrovei* but it is unique in the genus in having polysporous asci.

2.5.16 *Phaeoseptum carolshearerianum*

Phaeoseptum (type species *P. aquaticum*) was originally described from submerged wood in a freshwater swamp, and is characterized by black ascomata under a pseudoclypeus, narrowly cellular pseudoparaphyses, cylindrical-clavate asci with a short pedicel and brown ascospores, with 10–13(–15)-transversely septate and one vertical septum in each cell (Zhang et al. 2013). Using a combined LSU, SSU, TEF-1 α , ITS, and RPB2 analysis, two isolates of *Phaeoseptum carolshearerianum* formed a sister clade with other *Phaeoseptum* species (*P. aquaticum*, *P. mali*, *P. manglicola*, *P. terricola*) (Dayarathne et al. 2020a). Morphologically, *P. carolshearerianum* fits in the generic description of *Phaeoseptum* in having dark pigmented, immersed ascomata, cylindrical to clavate, pedicellate asci and muriform brown ascospores. However, *P. carolshearerianum* lacks a clypeus and has asymmetric oblong to broadly fusiform ascospores. Currently, there are seven species in *Phaeoseptum* from terrestrial, freshwater, and marine habitats.

2.5.17 *Qarounispora grandiapendiculata*

Nourel-Din et al. (2022) introduced the monotypic genus *Qarounispora* to accommodate *Q. grandiapendiculata* that was identified from decaying submerged wood that was collected from Qaroun Lake, El-Faiyum governorate, Egypt. *Qarounispora grandiapendiculata* is characterized by having membranous ascomata that are yellow to orange in colour with one-layered peridium, semi-persistent asci and one-septate, thick-walled, distoseptate, hyaline to yellow-orange, broadly ellipsoidal ascospores with one polar appendage that is amorphous in structure, large in size and irregular in shape. Multigene analyses based on LSU, SSU and ITS rDNA placed *Q. grandiapendiculata* in the Halosphaeriaceae in a branch distinct from morphologically related fungal taxa with one polar appendage to the ascospores: *Moana*, *Okeanomyces*, *Ophiodeira*, and *Tirisporea*. *Qarounispora* is phylogenetically related to *Nimbospora*, but *Nimbospora* has two types of appendages: an enlarged sheath surrounding the ascospores and fibrillar equatorial appendages (Koch 1982; Kohlmeyer and Volkmann-Kohlmeyer 1991).

2.5.18 *Raghukumaria keshaphalae*

Jones et al. (2020) introduced a monotypic genus *Raghukumaria* with *Raghukumaria keshaphalae* as the type species isolated from decayed wood of *Aegiceras corniculatum* in India. Multi-locus phylogenetic analysis showed that *Raghukumaria* forms a distinct clade within the Trematosphaeriaceae and shares a close phylogenetic affinity to

Halomassarina species. *Raghukumaria* differs from the latter in ascomatal (e.g., immersed, without a clypeus and periphyses, covered by hyphae-like setae) and ascospore morphology (e.g., broadly fusiform, with narrowly rounded ends, rough-walled or slightly verruculose, lacking globules, appendages or gelatinous sheaths) (Jones et al. 2020).

2.5.19 *Remispora submersa*

This new species was described based on the close phylogenetic relationship with *Remispora quadri-remis* and *R. stellata* in a phylogenetic tree of 28S and ITS rDNA (Gonçalves et al. 2021). This is an asexual fungus producing white mycelia and abundant cylindrical conidia. The conidiogenesis was unclear although it was described as “conidiophores reduced to conidiogenous cells”. This type of asexual morphology is unusual in the Halosphaeriaceae, as they generally have brown, septate conidia. A wider range of taxa should have been included in the phylogenetic analysis, especially the type species of *Remispora*, *R. maritima*. Holotype material was requested, especially slides of the conidiophores and conidia, but these were not available. A culture of *R. submersa* was provided, but failed to sporulate, despite growth on three different media and wood picks (Figure 5). The culture was re-sequenced, grouping in the *Sarocladium* clade and the species *S. kiliense* with high statistical support (Figure 6), a species with hyaline

conidia as in those reported for *R. submersa*. Further studies are required to resolve this anomaly.

2.5.20 *Rhytidhysteron bruguierae* (Figure 7)

Rhytidhysteron bruguierae occurring on decaying *Bruguiera* wood, is phylogenetically related to the species *R. mangrovei* and *R. thailandicum* based on 18S, 28S rDNA and TEF-1 α genes (Dayarathne et al. 2020a). Morphologically, *R. bruguierae* differs from the two species in having a red epithecium and thicker exciple (Kumar et al. 2019; Thambugala et al. 2016). Base pair differences of TEF-1 α gene between *R. bruguierae* and *R. mangrovei*/*R. thailandicum* were over 3% and were regarded as sufficient to warrant description of a new taxon (Jeewon and Hyde 2016). The type species of *Rhytidhysteron* is *R. brasiliense* which has no available sequences in GenBank (Spegazzini 1881). It is essential to obtain a culture of the type species to validate the taxonomic position of *R. bruguierae* and other species.

2.5.21 *Safagamyces marinus*

Bakhit and Abdel-Wahab (2022) introduced the monotypic genus *Safagamyces* for the marine asexual species *S. marinus* that was recorded from decaying stem of *Phragmites australis* inside Safaga mangrove, Red Sea, Egypt. The taxon is characterized by straight or slightly curved, branched, smooth, 2–6 septate conidia and the sympodial conidial proliferation. Conidial cells increase in size and pigmentation from hyaline at the base to dark brown at the apex.

Phylogenetic analysis of a combined SSU and LSU rDNA sequences dataset placed *S. marinus* in the Halosphaeriaceae as a distinct basal branch to a node that contains the following marine genera: *Antennospora*, *Cirrenalia*, *Cucullosporella*, *Cucurbitinus*, *Halosarpheia*, *Morakotiella*, *Pileomyces*, *Pseudolignicola* and *Remispora* (Bakhit and Abdel-Wahab 2022). *Safagamyces marinus* is phylogenetically distant from the other two asexual genera: *Cirrenalia* and *Cucurbitinus* by having straight or slightly curved, branched conidia that are brown in colour with sympodial conidial proliferation. Conidia in *Cirrenalia macrocephala* are helicoid, reddish fuscous with determinate conidiogenesis (Meyers and Moore 1960; Zhao et al. 2007). *Cucurbitinus* species have straight or slightly curved conidia with constricted septa with determinate

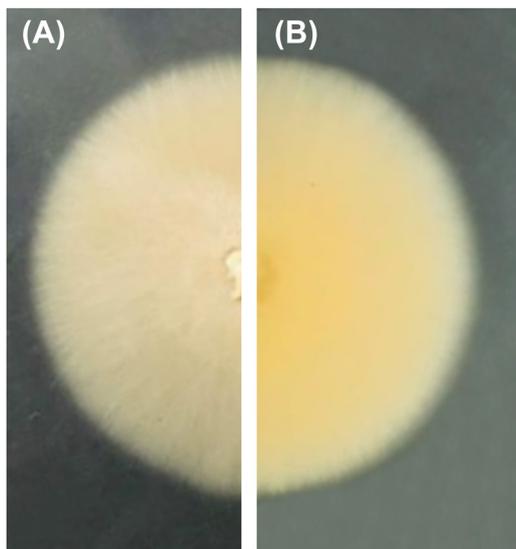


Figure 5: Colony of *Remispora submersa* (MUM 20.48) in malt extract agar (MEA) for 7 days at 25 °C: (A) obverse, (B) reverse.

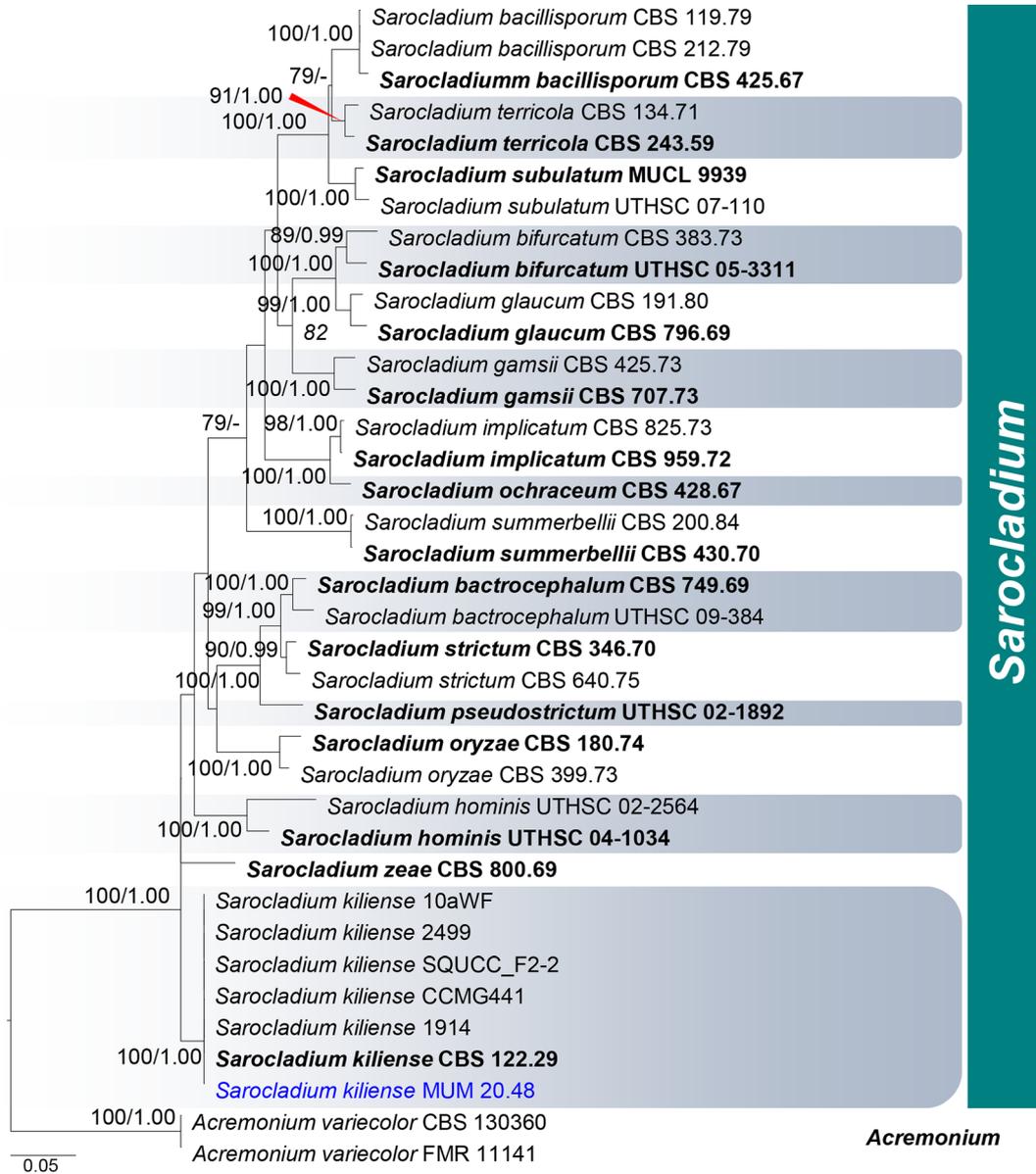


Figure 6: Phylogram generated from maximum likelihood (ML) analysis based on combined LSU, ITS, and *act1* sequence data representing Sarocladiaceae (Hypocreales). Thirty-seven strains are included in the combined analyses which comprised 1753 characters (504 characters for LSU, 478 characters for ITS, 771 characters for *act1*) after alignment. *Acremonium varicolor* strains CBS 130360 and FMR 11141 in Bionectriaceae (Hypocreales) were used as the outgroup taxa. The best scoring RAxML tree with a final likelihood value of -8526.836 is presented. The matrix had 435 distinct alignment patterns, 356 parsimony-informative, 73 singleton sites, and 1332 constant sites. Estimated base frequencies were as follows: $A = 0.216$, $C = 0.298$, $G = 0.265$, $T = 0.221$; substitution rates: $AC = 2.09479$, $AG = 3.08268$, $AT = 2.09479$, $CG = 1.00000$, $CT = 10.05849$, $GT = 1.000000$; gamma distribution shape parameter $\alpha = 0.574$. Bootstrap support values for ML equal to or greater than 75 % are given above the nodes (left side). Bayesian posterior probabilities (BYPP) equal to or greater than 0.95 are given above the nodes (right side). Ex-type strains are in bold and newly generated sequences are in blue.

conidiogenesis. Both species of *Cucurbitinus* have larger conidial dimensions than *S. marinus* (Hernández-Restrepo et al. 2017; Kohlmeyer and Volkmann-Kohlmeyer 1991; Liu et al. 2020; Schmidt 1985).

2.5.22 *Savoryella sarushimana* (Figure 8)

Abdel-Wahab (2011) reported 27 marine taxa from driftwood collected at Sarushima Island, Japan, among which

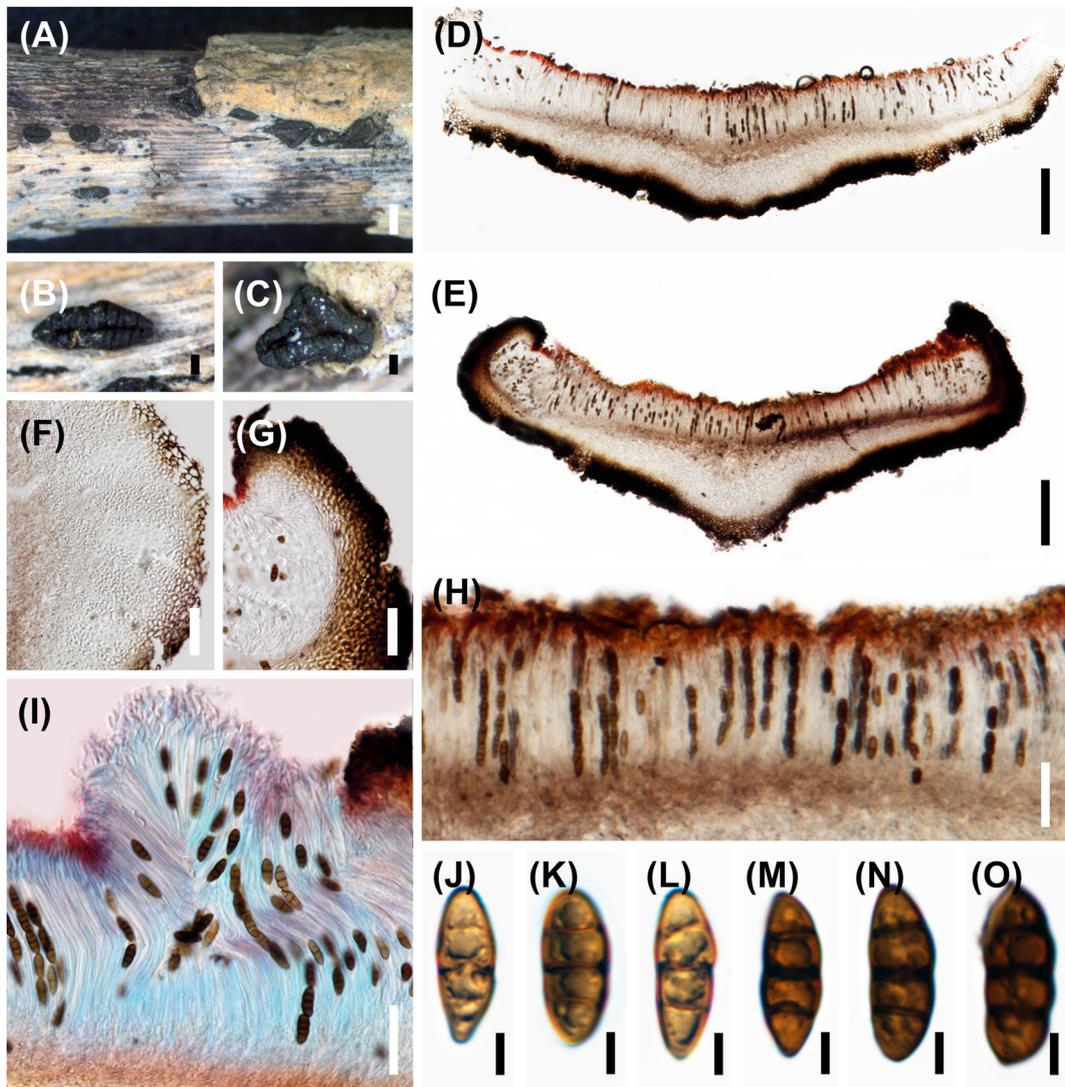


Figure 7: *Rhytidhysteron bruguierae*. (A–C) Appearance of hysterothecia on host. (D, E) Vertical section through hysterothecium. (F, G) Cells of peridium. (H, I) Pseudoparaphyses, asci, and ascospores. (I) Stained with lactophenol cotton blue. (J–O) Ascospores. Scale bars: (A) = 1 mm, (B–E) = 200 μ m, (F–I) = 50 μ m, (J–O) = 5 μ m.

seven were suspected to be possibly new to science. *Savoryella sarushimana* is an asexual fungus forming a monophyletic group with *Savoryella nypae* in a combined analysis of 18S, 28S, ITS rDNA, RPB2, and TEF-1 α (Zhang et al. 2019a). The conidia of *S. sarushimana* are characteristic in having 3–5-septa, not or slightly constricted at the septa, thick septa with dark-coloured bands, reddish brown to black mature conidia, with a rough surface and sometimes with long tapering projections forming hairy tufts. *Savoryella sraushimana* can be distinguished

from *S. nypae* by its much larger conidia and wall ornamentations.

2.6 Additional marine fungal taxa

Species not included in Jones et al. (2019) on the classification of marine fungi are listed in Supplementary Table 1. Higher taxonomic ranks are included for each species.

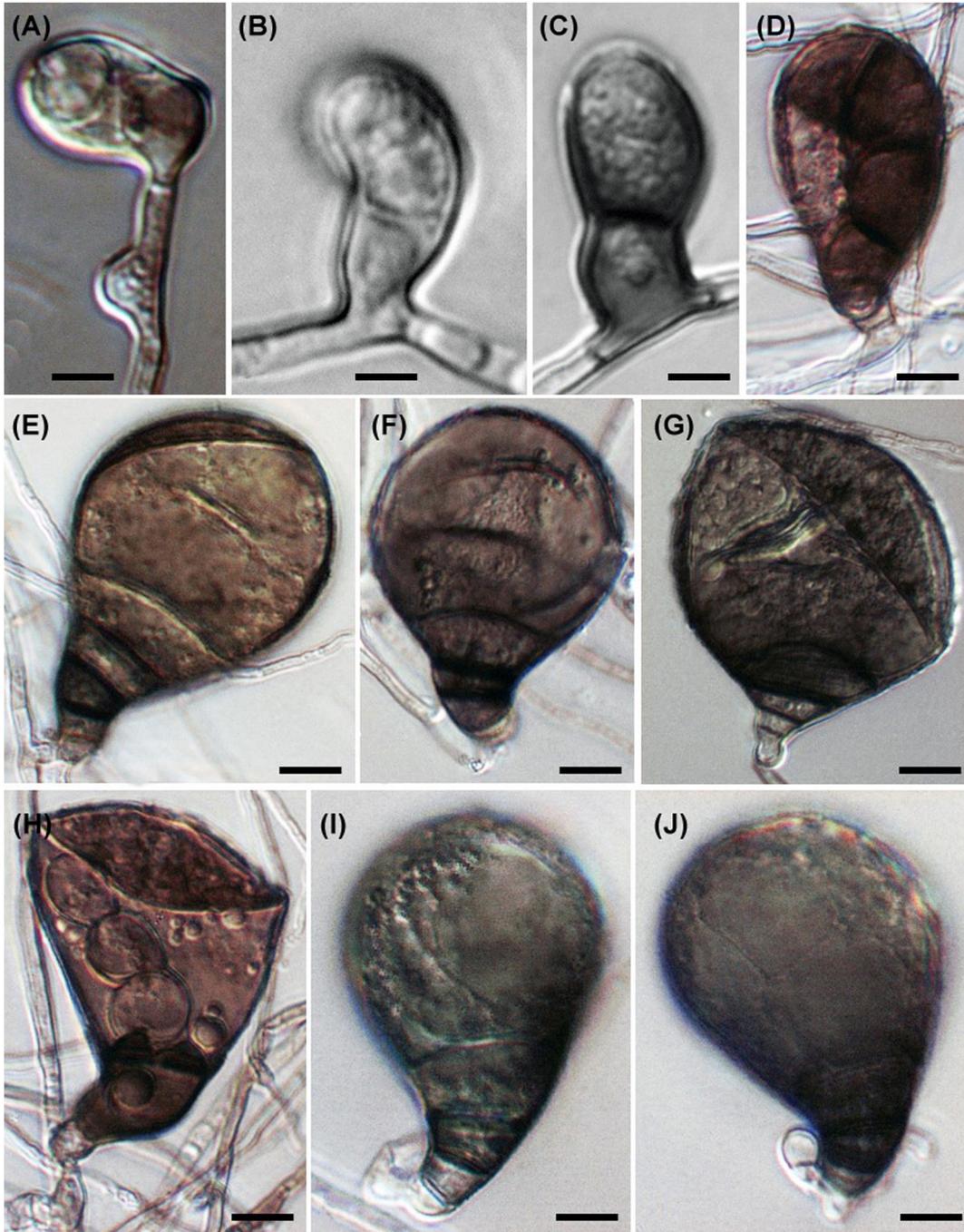


Figure 8: *Savoryella sarushimana*. (A–C) Holoblastic conidiogenous cells. (D–J) Variously shaped conidia. Note the proliferating conidia in (D, H). Scale bar = 10 µm.

3 Conclusions

Since Jones et al. (2019), a total of 641 marine species have been discovered from various substrata, and recent updates in the classification of marine fungi. Most of these additions are novel taxa or new observations of extant species thriving in various marine substrata. The classification has been continuously updated with new data from molecular studies

incorporating robust multi-locus phylogenetic analyses to large-scale whole genome sequencing techniques.

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Conflict of interest statement: The authors declare that they have no conflicts of interest regarding this article.

Data availability: The datasets analysed during the current study are available from the corresponding author on reasonable request. All sequences generated here are available from GenBank with accession numbers: OR162608 (ITS).

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